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EVOLUTION OF THE LIZARD FAMILY PHRYNOSOMATIDAE AS INFERRED FROM DIVERSE TYPES OF DATA

TOD W. REEDER[1] AND JOHN J. WIENS[2]

Department of Zoology and Texas Memorial Museum, The University of Texas at Austin, Austin, TX 78712, USA

ABSTRACT: The phylogenetic relationships within the iguanian lizard family Phrynosomatidae are inferred from diverse types of data (i.e., mitochondrial rDNA, osteology, coloration, scalation, karyology, and behavior). All 10 currently recognized genera (*Callisaurus, Cophosaurus, Holbrookia, Petrosaurus, Phrynosoma, Sator, Sceloporus, Uma, Urosaurus,* and *Uta*) are included in the phylogenetic analyses. The phylogenies inferred from the separate analyses of the DNA sequence data (779 bp; 162 informative characters; 40 species) and non-DNA data (155 informative characters; 59 species) share 26% (10) of their respective clades. Four of the congruent clades (i.e., sand lizards + *Phrynosoma, Petrosaurus, Urosaurus, Uta*) are strongly supported (≥70% bootstrap) in both of the separate analyses while five others are strongly supported in only one, but not both, of the separate analyses. All conflicting hypotheses leading to the taxonomic incongruence (e.g., *Sceloporus* group interrelationships) are weakly supported (<70% bootstrap) in one or both of the separate analyses. Combining the DNA and non-DNA data for phylogenetic analysis results in a single shortest tree. Overall, the phylogeny from the combined analysis shares more clades in common with the hypotheses inferred from the separate DNA analysis (74%) than with the separate analysis of the non-DNA data (53%). The intergeneric relationships inferred from the combined analysis are more similar to recently published hypotheses based on morphological data, except the *Sceloporus* group is paraphyletic. Although phrynosomatid intergeneric relationships are well resolved by the combined analysis of the DNA and non-DNA data, the relationships among most genera are nevertheless weakly supported by the separate and combined analyses. This weak support is most likely the result of rapid speciation. The monophyly of the speciose genus *Sceloporus* (exclusive of *Sator*) is supported by the separate non-DNA and combined analyses. The inclusion of numerous incomplete taxa (19 species lacking DNA data) in the combined analysis did not decrease resolution among the complete taxa (40 species with DNA and non-DNA data), but the addition of the incomplete taxa did affect the relationships among the complete taxa. Overall, the DNA data are more homoplastic than the non-DNA data, but the degree of character incongruence exhibited within the different partitions and/or sources of the DNA and non-DNA data sets varies greatly.

Key words: Phrynosomatidae; Phylogeny; Congruence; Incomplete taxa; *Sceloporus*; *Sator*; *Urosaurus*; *Petrosaurus*; *Uta*; *Phrynosoma*; *Uma*; *Callisaurus*; *Cophosaurus*; *Holbrookia*

THE IGUANIAN LIZARD family Phrynosomatidae consists of approximately 120 recognized species distributed among 10 genera (Table 1). The phrynosomatids have traditionally been known as the sceloporine iguanids (Etheridge, 1964; Savage, 1958), but were elevated to familial status by Frost and Etheridge (1989) to avoid paraphyly of the Iguanidae (sensu lato). Phrynosomatid monophyly is well supported (Frost and Etheridge, 1989; Wiens, 1993*a*), being corroborated by eight synapomorphies (Table 2). Phrynosomatids occur from southern Canada to western Panama. They are a dominant component of the herpetofauna of the southwestern U.S. and Mexico, the region where they reach their greatest diversity. Phrynosomatids generally are small (<0.1 m total length), insectivorous, active, diurnal lizards that are terrestrial, saxicolous, arenicolous, and/or arboreal. These conspicuous and abundant lizards have been intensively studied in many areas of research, including morphology (e.g., de Queiroz, 1982, 1989; Etheridge, 1962, 1964; Etheridge and de Queiroz, 1988; Frost and Etheridge, 1989; Montanucci, 1987; Presch, 1969; Wiens, 1993*a*,*b*), karyology (e.g., Gorman et al., 1967, 1969; Pennock et al., 1969; Sites et al., 1992), behavior (Car-

[1] PRESENT ADDRESS: Department of Biology, San Diego State University, San Diego, CA 92182-4614, USA.

[2] PRESENT ADDRESS: Section of Amphibians and Reptiles, Carnegie Museum of Natural History, Pittsburgh, PA 15213-4080, USA.

TABLE 1.—Genera of phrynosomatid lizards, species diversity, and number of species sampled for DNA and non-DNA data.

Genus	Number of species in genus	Number sampled for DNA*	Number sampled for non-DNA
Callisaurus	1	1	1
Cophosaurus	1	1	1
Holbrookia	3	1	1
Petrosaurus	2	2	2
Phrynosoma	13	4	4
Sator	2	1	2
Sceloporus†	77	23	36
Uma	5	1	1
Urosaurus	9	4	9
Uta	6	2	2

* Species sampled for the DNA sequence data were also sampled for the non-DNA data.

† The estimated number of species for *Sceloporus* is taken from Sites et al. (1992). However, more evolutionary species (Frost and Hillis, 1990) certainly exist.

TABLE 2.—Synapomorphies corroborating the monophyly of the Phrynosomatidae. Synapomorphies 1–6 are from Frost and Etheridge (1989) and 7 and 8 are from Wiens (1993*a*).

1. Pterygoid teeth lost
2. Clavicular flange reduced
3. Posterior process of interclavicle invested by sternum anteriorly
4. Sink-trap nasal apparatus
5. Enlarged posterior lobe of hemipenis
6. *M. retractor lateralis* posterior
7. Peroneal innervation of the dorsal shank muscle
8. Diploid chromosome number 34

penter, 1962, 1963, 1967, 1978; Clarke, 1965; Ferguson, 1971; Lynn, 1965; Purdue and Carpenter, 1972*a,b*), and population biology (recent reviews in Dunham et al., 1988*a,b*; Sites et al., 1992).

The phylogenetic systematics of the Phrynosomatidae has recently been an active area of research. The relationships and monophyly of the phrynosomatid genera were addressed by Etheridge and de Queiroz (1988), Frost and Etheridge (1989), and Wiens (1993*a*), using primarily morphological data, while mitochondrial DNA sequence data were recently used by Reeder (1995). Morphological and allozyme data were used by de Queiroz (1989, 1992) to infer the relationships among the sand lizard genera (*Callisaurus, Cophosaurus, Holbrookia,* and *Uma*). Relationships within *Phrynosoma* (Montanucci, 1987) and *Urosaurus* (Wiens, 1993*b*) have also been addressed.

Despite these recent studies, the phylogenetic relationships of most phrynosomatid species have not been adequately examined (e.g., *Sceloporus*), and many parts of the phylogeny that have been studied remain highly unstable (Reeder, 1995; Wiens, 1993*a,b*). For example, Wiens (1993*a*) resolved the phylogenetic relationships among phrynosomatid genera (except the relationships within the sand lizard clade), but the placement of *Petrosaurus* as the sister taxon of the *Sceloporus* group (*Sator, Sceloporus, Urosaurus,* and *Uta*) was weakly supported. It required only an increase of one step in tree length to place *Petrosaurus* as the sister taxon of all other phrynosomatids, as hypothesized by Etheridge and de Queiroz (1988). In addition, while Wiens (1993*a*) corroborated *Sceloporus* monophyly exclusive of *Sator* (contra Etheridge and de Queiroz, 1988, and Frost and Etheridge, 1989), support for this clade was weak. The monophyly of both the *Sceloporus* group and *Sceloporus* was not supported in the recent analysis based on DNA sequence data (Reeder, 1995).

Goals of Study

The primary purpose of this study is to combine all the currently available data to infer the phylogenetic relationships within the Phrynosomatidae. The morphological data from Wiens (1993*a,b*) will be augmented with the recently collected mitochondrial DNA sequence data from Reeder (1995). Also, since the publications of Wiens (1993*a,b*), new morphological data have been collected by Wiens. Additional characters will also be derived from other sources of data in the literature (i.e., karyology, behavior, life history, protein electrophoresis). The combined analysis will allow us to test the different intergeneric relationships proposed in recent years (i.e., de Queiroz, 1992; Etheridge and de Queiroz, 1988; Frost and Etheridge, 1989; Reeder, 1995; Wiens, 1993*a*), as well as the recently hypothesized intrageneric re-

lationships within *Urosaurus* (Wiens, 1993*b*). Finally, ~45% of the species of *Sceloporus* (representing all 16 species groups) will be included in the phylogenetic analysis, providing the most rigorous test of *Sceloporus* monophyly to date.

In addition to estimating phrynosomatid phylogeny, we will address several other questions regarding the analysis of these diverse data sets: (1) Are the trees from the separately analyzed DNA and non-DNA data congruent with each other and with the tree based on the combined data (i.e., Chippindale and Wiens, 1994), and is the tree from the combined data more congruent with either of these sets of trees than the other? (2) Are there strongly supported clades that differ between the separately analyzed data sets (i.e., de Queiroz, 1993), or is most of the incongruence between these trees the result of weakly supported groupings in either of the data sets? (3) Are some types of evidence particularly homoplastic, or do all the types of data contribute similarly to the levels of noise in the combined tree? (4) What are the consequences of including or excluding those species lacking DNA data in the combined analysis of the data sets (i.e., Wiens and Reeder, 1995)? We are particularly interested in whether or not there are insights gained from combining the separate data sets and including the incomplete taxa that could not be obtained without the simultaneous (versus separate) analysis of the different types of taxa and characters (i.e., Donoghue et al., 1989). Our results suggest that there are, and these results should be useful for other studies that integrate diverse data sets for phylogenetic analysis.

METHODS

DNA Sequence Data

Mitochondrial ribosomal DNA sequence data were collected from 40 phrynosomatid species. Details regarding DNA isolation, amplification, and sequencing were described in Reeder (1995). The DNA sequences were aligned using the pairwise sequence alignment program of MacVector (IBI). All sequences were aligned against the outgroup species *Tropidurus plica*. Two sets of alignments were performed, differing in the penalties assessed for the insertion of gaps (gap cost = 5 and 10). Regions of sequence alignment that were sensitive to gap costs were excluded from phylogenetic analysis. The DNA sequence alignment is given in Reeder (1995), and all DNA sequences are deposited in GenBank (accession numbers L40436–58, 41416–89). These sequences consist of 253 aligned nucleotide positions from the 12S ribosomal RNA (rRNA) gene (73 phylogenetically informative characters) and 429 aligned positions from the 16S rRNA gene (89 informative characters), yielding a total of 162 informative positions.

Non-DNA Data

A total of 59 phrynosomatid species (encompassing all 40 species for which DNA data are available) were coded for all or some of 155 phylogenetically informative characters from the following sources: scalation (n = 60 characters), osteology (n = 55), coloration (n = 15), behavior (n = 9), myology (n = 9), karyology (n = 4), protein electrophoresis (n = 2), and life history (n = 1). Because many of the characters are not generally thought of as anatomical (= morphological), we will refer to this as the non-DNA data set.

The myological, behavioral, karyotypic, protein electrophoretic, and life history characters were obtained from the literature as follows: myology (Blackburn, 1978), behavior (Carpenter, 1962, 1963, 1978; Clarke, 1965; Ferguson, 1971; Lynn, 1965), karyology (Gorman et al., 1967, 1969; Pennock et al., 1969; Sites et al., 1992), protein electrophoresis (de Queiroz, 1992; Wiens, 1993*b*), and life history (Guillette et al., 1980). Many of the squamation and coloration characters were taken from Smith (1939). External and osteological data were obtained from museum specimens by Wiens. Descriptions of the characters in the non-DNA data set appear in Appendix I, and a list of specimens examined is provided in Appendix II.

For the data collected for this study, characters were chosen and character states

(traits or conditions) were defined so that the observed variation could be described objectively and unambiguously. Characters either appeared to be discrete or were not truly discrete but were defined in a qualitative manner. Stevens (1991) has pointed out that many so-called qualitative characters used in phylogenetic analyses are quantitative characters reified through the language of description. This criticism applies to many of the characters used in this study, but the important issue is whether such characters contain phylogenetic information. Thiele (1993) showed that continuous characters can contain significant phylogenetic structure, and tests of phylogenetic signal on the morphological data used in this study confirm their nonrandom covariance (Wiens, 1995). Characters that could not be described unambiguously, such as those involving continuous variation in shape and size, were avoided.

Many of the external and osteological characters exhibited considerable intraspecific variation. Wiens (1995) showed that "discrete" intraspecifically variable characters do provide significant phylogenetic information, although levels of noise (homoplasy) tend to increase with increasing intraspecific variability. Wiens (1995) also found that a frequency approach appears to be the best method for treating polymorphic data: upon comparing eight parsimony methods for up to five optimality criteria using seven real data sets, he found that the frequency approach possessed the unique ability to extract significant phylogenetic information from the polymorphic characters in all the data sets examined. Furthermore, results from computer simulation studies (Wiens and Servedio, 1997) show the frequency method to be the most accurate parsimony method under a wide variety of conditions (e.g., branch lengths, sample sizes, and different numbers of characters and taxa). In this study, discrete or qualitatively coded characters were not excluded because of intraspecific variability, and they were coded using a frequency approach.

All characters with only two conditions (e.g., scale present or absent, binary in the usual sense of the term) were coded using the frequency-bins approach described by Wiens (1995). Each species was assigned a letter from "a" to "y" based on the observed frequency of the putative derived trait (Table 3; see Wiens, 1995), and traits were ordered from trait absence to fixation (a → y). In cases in which a derived trait was not obvious *a priori*, one of the traits was arbitrarily chosen; this choice has no impact on the results.

TABLE 3.—Character state designations (a to y) for frequencies of the derived trait used for the frequency-bins method.

Character state	Frequency range
a	0–3
b	4–7
c	8–11
d	12–15
e	16–19
f	20–23
g	24–27
h	28–31
i	32–35
j	36–39
k	40–43
l	44–47
m	48–51
n	52–55
o	56–59
p	60–63
q	64–67
r	68–71
s	72–75
t	76–79
u	80–83
v	84–87
w	88–91
x	92–95
y	96–100

Characters with multiple conditions (three or more) could not be coded using the frequency-bins approach. To analyze frequency data with multiple conditions, Wiens (1995) used a method utilizing differences in frequencies between species (expressed as Manhattan distances) to weight changes between taxa in a step matrix. However, the use of step matrices was impractical for the present study because of the large number of taxa. Instead, these characters were simply coded by using the majority method. Species were coded based on the condition found in the majority of

the specimens, and in cases where two traits were found at equal frequency, the species was coded as polymorphic (e.g., [0,1]). Wiens (1995) found that the majority approach generally gives results similar to the frequency approach, although less information is used. Character state transformations in the majority method were considered equivalent to a frequency change of 100%. These characters were weighted by 24 in order to maintain their equivalency to the frequency-coded characters (e.g., 24 steps from a to y). Overall tree lengths were then reported after dividing by 24, to make lengths comparable to those reported in other studies.

Individuals that were bilaterally variable or asymmetric were included in calculations of frequencies. However, when only one side of the specimen could be scored, it was assumed that the individual was homogeneous or symmetrical for that character in calculations of frequencies. Some species could not be scored for a given character because of absence of the relevant feature (e.g., color of the belly patch in a species lacking belly patches). In this situation, species were coded as unknown ("?"). Similarly, in species in which only certain specimens could be scored for a feature (e.g., color of the belly patch in a species that is polymorphic for the presence of belly patches), the estimate of the frequency of the trait in that species was based only on the potentially informative specimens. For example, a species could be considered invariant for color of the belly patch if the species was polymorphic for presence of the belly patch.

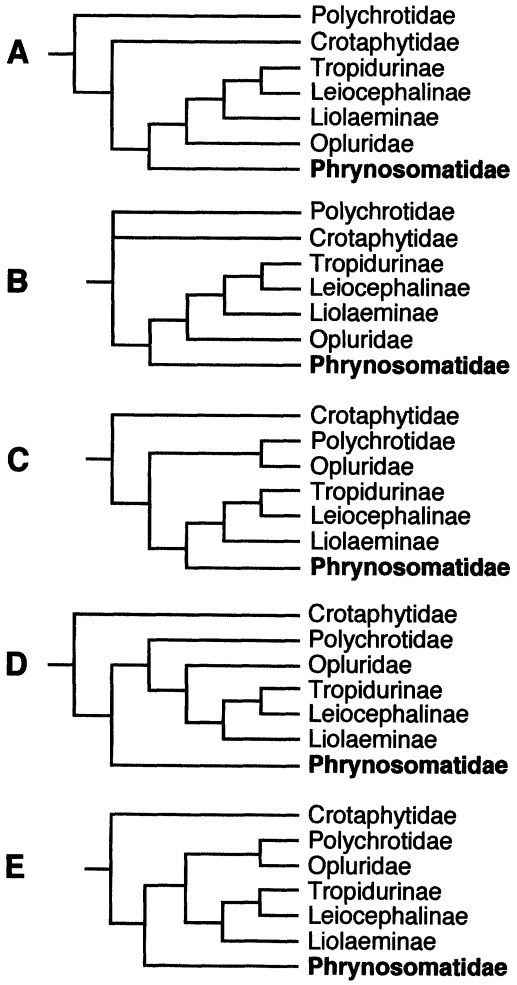

FIG. 1.—Five different iguanian outgroup relationships to the Phrynosomatidae (Frost and Etheridge, 1989). The Leiocephalinae, Liolaeminae, and Tropidurinae are subfamilies of the Tropiduridae. All five hypotheses were used to construct a hypothetical ancestor for the Phrynosomatidae.

Phylogenetic Analyses

Character polarity was determined by using the outgroup method. The Crotaphytidae, Opluridae, Polychrotidae, and Tropiduridae are iguanian families that have been postulated to be closely related to phrynosomatids (Frost and Etheridge, 1989). Estimates of the ancestral character state for outgroup families were based on whatever species were available and/or scored for that family for that character. Frost and Etheridge (1989) discovered five equally parsimonious topologies relating these families to the Phrynosomatidae (Fig. 1). The algorithm of Maddison et al. (1984) was used to reconstruct a hypothetical ancestor using each of the five topologies. Final character polarity decisions were considered unequivocal only if the inferred state was the same and unambiguous for all five familial level topologies (Wiens, 1993*a*). Because of the paucity of outgroup information for the behavioral data, behavioral characters were left unpolarized in the phylogenetic analyses. The

reconstructed hypothetical ancestor was used to root the ingroup tree(s).

The number of taxa scored for morphological characters (n = 59) exceeded the number available for molecular analysis (n = 40). Should those taxa scored for only one of the data sets be included or excluded from the analysis of combined data sets? Wiens and Reeder (1995) addressed this question through a series of subsampling experiments with data from viruses (with a known phylogeny) and phrynosomatid lizards (a preliminary version of the combined data matrix used in this study). They found that adding these incomplete taxa generally caused a small decrease in the similarity of the combined tree to the true phylogeny (for the viruses) or the tree based on only the complete data (for the lizards), but allowed a phylogenetic hypothesis (that was mostly correct) to be postulated for the incomplete taxa as opposed to having no hypothesis at all. To further evaluate the effects of including versus excluding these taxa, we analyzed the combined data both with and without these taxa to determine: (1) if including the incomplete taxa decreases the overall resolution of the combined tree, (2) if including the incomplete taxa affects relationships among the complete taxa, and (3) if the incomplete, non-DNA-only taxa can be parsimoniously mapped onto a tree for the complete taxa *a posteriori*, based on their positions in the tree based on non-DNA data only.

Phylogenetic analyses were performed with PAUP 3.0s (Phylogenetic Analysis Using Parsimony) (Swofford, 1990). Because of the large number of taxa involved, the Heuristic Search routine was used. To increase the total amount of tree space searched and to discover different islands of equally parsimonious trees (Maddison, 1991), each search used 50 different starting trees (random taxon addition option of PAUP). For each replication, up to 25 trees were held at each step of taxon addition and the tree bisection–reconnection (TBR) option for branch swapping was used. When multiple equally parsimonious trees resulted from a search, the trees were summarized with a strict consensus tree (Sokal and Rohlf, 1981), thus depicting only those relationships held in common among all shortest trees.

A character state change was considered to support a clade unambiguously if it was placed along the branch by both ACCTRAN (Farris, 1970) and DELTRAN (Swofford and Maddison, 1987) optimizations. Whereas ambiguously placed synapomorphies do provide support and are important in phylogeny reconstruction, only unambiguously placed synapomorphies were listed when describing character support for tree branches. Some clades were supported by small changes in frequencies of morphological traits. Because small interspecific differences in frequencies are easily misinterpreted because of sampling error, less confidence is placed in these minor changes. Therefore, both the number of synapomorphies and amount of character change (= branch length) supporting the branches are reported.

Separate and combined phylogenetic analyses were performed on the DNA and non-DNA data. The data were divided in this way because the mtDNA data are genetically linked and may be estimating a gene tree rather than a species tree (Pamilo and Nei, 1988). The various types of non-DNA data were combined into a single data set to avoid spurious incongruence between the trees from the separate analyses because of subsampling among characters (de Queiroz, 1993). The taxonomic congruence approach (Mickevich, 1978) was employed in order to investigate the congruence between the hypotheses of relationships inferred from the separate analyses. Before constructing a strict consensus tree to depict those relationships held in common between the separate analyses of the DNA sequence data and non-DNA data, the 19 species not represented in the DNA analysis were pruned from the non-DNA trees. The combined phylogenetic analysis was chosen as the best estimate of phylogeny for phrynosomatid lizards (Kluge, 1989), because it incorporates the maximum number of characters and accuracy generally increases with increasing number of characters (Wiens and Chippindale, 1994). All characters (DNA and

non-DNA) were uniformly weighted in the separate and combined analyses. Reeder (1995) demonstrated that transitions were essentially as informative as transversions in the phrynosomatid mitochondrial rDNA, so differential weighting between these two classes of base substitutions was not performed in the combined analysis. In the combined analysis, DNA characters were weighted by 24 so that a change in a DNA character had weight equivalent to a change in frequency of a morphological character from 0 to 100%.

Examination of Homoplasy and Confidence

The consistency index (Kluge and Farris, 1969) and retention index (Farris, 1989, 1990) were used to examine the overall levels of character incongruence exhibited within and between data sets, as well as among different classes and/or sources of characters. Consistency indices reported were calculated after the exclusion of uninformative characters. Uninformative characters do not affect the retention index. Besides the ensemble consistency and retention indices (CI and RI), which describe the fit of all the data to the phylogeny, mean character consistency and retention indices (ci and ri) were used to illustrate and compare the levels of homoplasy exhibited by different sources and/or classes of characters in the combined phylogenetic analysis. All mean ci values were calculated after the exclusion of uninformative character states, following Sanderson and Donoghue (1989). Because the presence of missing data can decrease the possibility of detecting character incongruence (Campbell and Frost, 1993), the mean ci and ri of the DNA data (lacking for 19 species) are probably not directly comparable to those of the non-DNA data. Comparable indices for the non-DNA data were obtained by pruning the 19 incomplete species from the combined phylogeny before calculating non-DNA mean ci and ri for these data.

Support for individual branches was determined by bootstrapping (Felsenstein, 1985). The bootstrap analyses were based on 200 replications, and each replication consisted of two random taxon addition tree searches (holding $\leq$25 trees during each step of taxon addition) with TBR branch swapping. Based on the results of Hillis and Bull (1993), we considered clades with bootstrap proportions of $\geq$70% to be strongly supported. Whereas clades receiving lower bootstrap proportions were considered weakly supported and have a higher probability of being incorrect, such clades should not necessarily be interpreted as inaccurate.

RESULTS

DNA Data

Phylogenetic analysis of the 162 phylogenetically informative DNA characters resulted in 40 shortest trees (length [L] = 749.00) with a CI of 0.35 and RI of 0.57 (Reeder, 1995). The strict consensus of the 40 shortest trees is shown in Figure 2. Additional details regarding the separate analysis of the DNA data can be found in Reeder (1995).

Non-DNA Data

Phylogenetic analysis of the 155 phylogenetically informative non-DNA characters (Appendix III) resulted in two shortest trees (L = 419.83) with a CI of 0.38 and RI of 0.72. The intergeneric relationships are completely resolved in the strict consensus of the two shortest trees (Fig. 3) and are identical to those previously reported by de Queiroz (1992) for sand lizards and Wiens (1993*a*) for the other genera. The numbers of unambiguous synapomorphies and the branch lengths supporting the branches of the phylogeny are given in Table 4.

The sand lizard + *Phrynosoma* clade (Branch 2) represents one of the more strongly supported hypotheses, with 12 synapomorphies. Sand lizard monophyly is supported by seven synapomorphies, with sand lizard intergeneric relationships being identical to those proposed by Etheridge and de Queiroz (1988) and de Queiroz (1992). Thirty-two synapomorphies corroborate *Phrynosoma* monophyly.

Three synapomorphies support a basal clade (Branch 9) containing the remaining

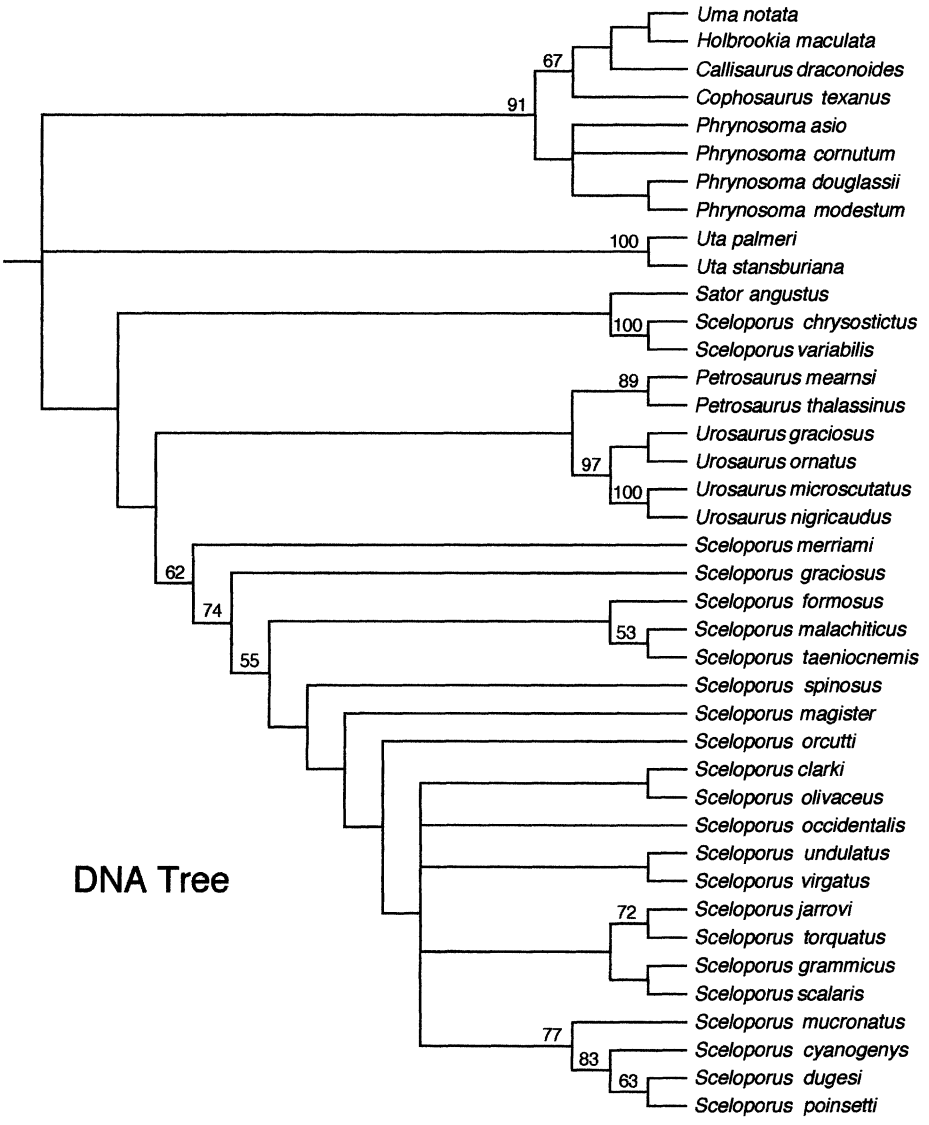

FIG. 2.—Strict consensus of 40 equally parsimonious shortest phylogenies (L = 749.00, CI = 0.35, RI = 0.57) inferred from the separate analysis of the DNA data. The numbers above the branches are bootstrap values from 200 bootstrap replicates. Branches without bootstrap values were supported in <50% of the replicates.

phrynosomatid genera (*Petrosaurus, Sator, Sceloporus, Urosaurus,* and *Uta*). However, these synapomorphies represent very little actual character change (L = 1.50), with this clade being supported in <50% of the bootstrap replicates. The phylogenetic placement of *Petrosaurus* as the sister taxon of the *Sceloporus* group (Branch 11), as hypothesized by Wiens (1993*a*), is supported by four synapomorphies. However, even with the addition of new data, the *Petrosaurus* + *Sceloporus* group relationship is still weakly supported, being found in <50% of the bootstrap replicates. Within the *Sceloporus* group, the only intergeneric relationship that is strongly supported is a clade (Branch 13; seven synapomorphies) containing *Sator, Sceloporus,* and *Urosaurus,* recovered in 73% of the bootstrap replicates. Within this

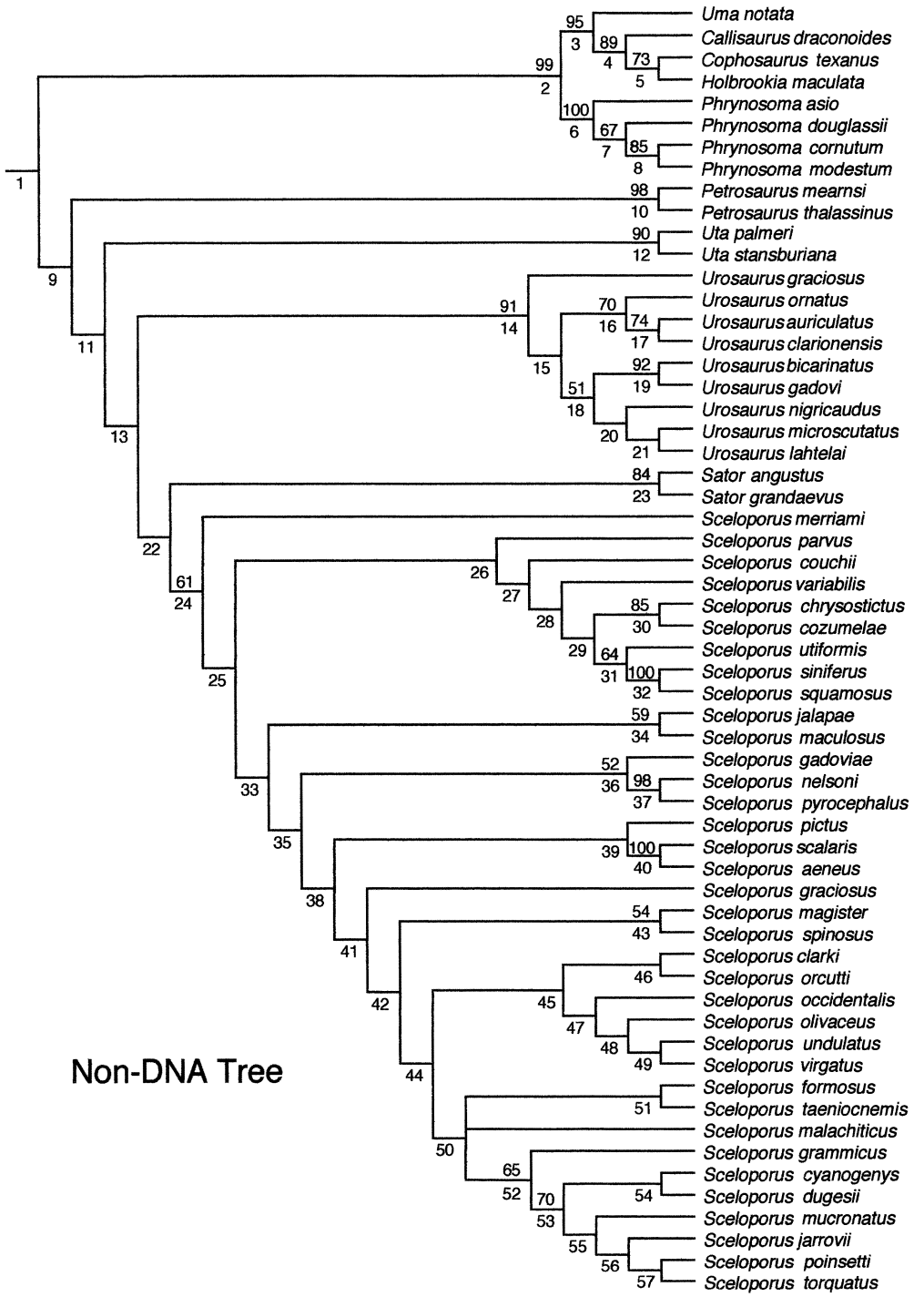

FIG. 3.—Strict consensus of two equally parsimonious shortest phylogenies (L = 419.83, CI = 0.38, RI = 0.72) inferred from the separate analysis of the non-DNA data. The numbers below the branches denote the different clades of the strict consensus tree. The numbers above the branches are bootstrap values from 200 bootstrap replicates. Branches without bootstrap values were supported in <50% of the replicates.

TABLE 4.—The number of unambiguously placed synapomorphies distributed along the branches of the phylogeny inferred from the non-DNA analysis.

Branch	Number of unambiguous character states	Branch length*
1 (Phrynosomatidae)	3	3.00
2	12	10.17
3 (sand lizards)	7	6.71
4	7	5.42
5 (earless lizards)	8	4.13
6 (*Phrynosoma*)	32	28.60
7	7	3.75
8	8	4.58
9	3	1.50
10 (*Petrosaurus*)	8	5.71
11	4	2.83
12 (*Uta*)	5	3.17
13	7	6.08
14 (*Urosaurus*)	4	2.00
15	4	1.63
16	3	2.04
17	3	2.13
18	3	1.50
19	6	3.96
20	3	1.83
21	4	0.38
22	3	2.21
23 (*Sator*)	3	1.92
24 (*Sceloporus*)	6	4.71
25	2	1.63
26	8	4.42
27	5	2.00
28	7	4.96
29	2	2.00
30	4	2.17
31	10	5.46
32	14	9.29
33	3	1.42
34	3	2.38
35	4	1.54
36	3	2.67
37	9	4.79
38	3	2.17
39	5	1.46
40	12	6.13
41	2	1.67
42	5	2.83
43	4	2.25
44	4	0.54
45	2	0.33
46	5	3.58
47	3	1.17
48	2	1.33
49	3	0.75
50	1	1.00
51	3	1.25
52	5	2.25
53	3	1.79
54	3	1.46
55	1	0.33
56	2	0.46
57	6	2.42

* Minimum branch length for the unambiguous non-DNA characters.

more exclusive clade, the monophyly of *Sator* and of *Urosaurus* is well supported (84 and 91%, respectively), while support for monophyly of *Sceloporus* is weaker (61%). Although a relationship of *Urosaurus* (*Sator* + *Sceloporus*) is inferred from this analysis, as hypothesized by Wiens (1993*a*), this intergeneric relationship was discovered in <50% of the bootstrap replicates.

Taxonomic Congruence between DNA and Non-DNA Data

In all, 26% (10/38) of the clades from the separate DNA and non-DNA analyses are shared. Three additional clades are unambiguously supported by one data set but ambiguously supported by the other. For example, a clade containing *Petrosaurus, Sator, Sceloporus, Urosaurus,* and *Uta* is supported in all trees from the separate analysis of the non-DNA data. This specific clade is also present in some, but not all, trees inferred from the separate analysis of the DNA data. The consensus tree (Fig. 4; = taxonomic congruence tree) constructed from the 40 trees inferred from the DNA data and the two pruned trees inferred from the non-DNA data supports the monophyly of the following genera for which multiple species were sampled: *Phrynosoma, Petrosaurus, Urosaurus,* and *Uta.* Whereas monophyly of *Sceloporus* is not confirmed in the separate analysis of the DNA data, a clade containing 20 of the 23 species is shared between the separate analyses of the DNA and non-DNA data. The only unambiguous phrynosomatid intergeneric relationships supported in the taxonomic congruence tree are sand lizard monophyly and the sand lizard + *Phrynosoma* clade. The intergeneric relationships within the sand lizard clade and between the remaining phrynosomatid genera (*Petrosaurus* and the *Sceloporus* group) are in weak conflict (bootstrap values <70%) and/or ambiguous between the separate analyses.

Combined Analysis

The combined DNA and non-DNA data included 317 phylogenetically informative characters. Analysis of the combined data

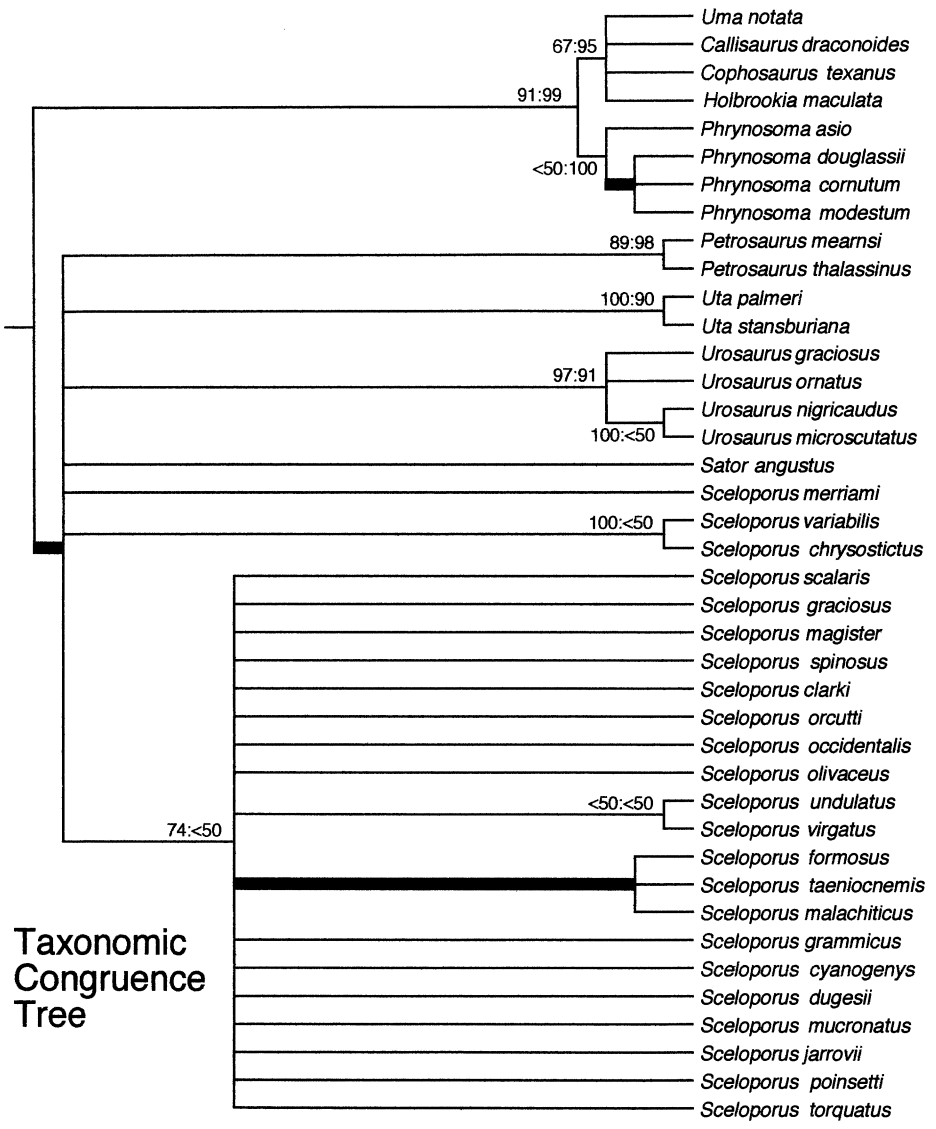

FIG. 4.—A consensus tree summarizing the level of taxonomic congruence exhibited between the relationships inferred from the separate analyses of the DNA and non-DNA data sets. This is a strict consensus of the 40 trees from the DNA analysis and the two trees from the non-DNA analysis. The three thick branches were not supported in all trees from each separate analysis, but were shared in some trees between both analyses. The numbers along the branches represent the bootstrap values of the clades in the respective separate analyses (DNA:non-DNA).

resulted in a single shortest tree (Fig. 5; L = 1235.00) with a CI of 0.35 and RI of 0.63.

The numbers of unambiguous synapomorphies and the branch lengths supporting the branches of the phylogeny are given in Table 5. Thirty-four of the 56 internodes are supported by unambiguously placed DNA and non-DNA synapomorphies. One clade is supported by only DNA synapomorphies. Twenty-two clades are supported by only non-DNA synapomorphies, but 21 of these clades seemingly lack unambiguous DNA synapomorphies because of the absence of DNA data for several species. Character states supporting the tree are given in Appendix IV.

Eleven synapomorphies (8 DNA:3 non-

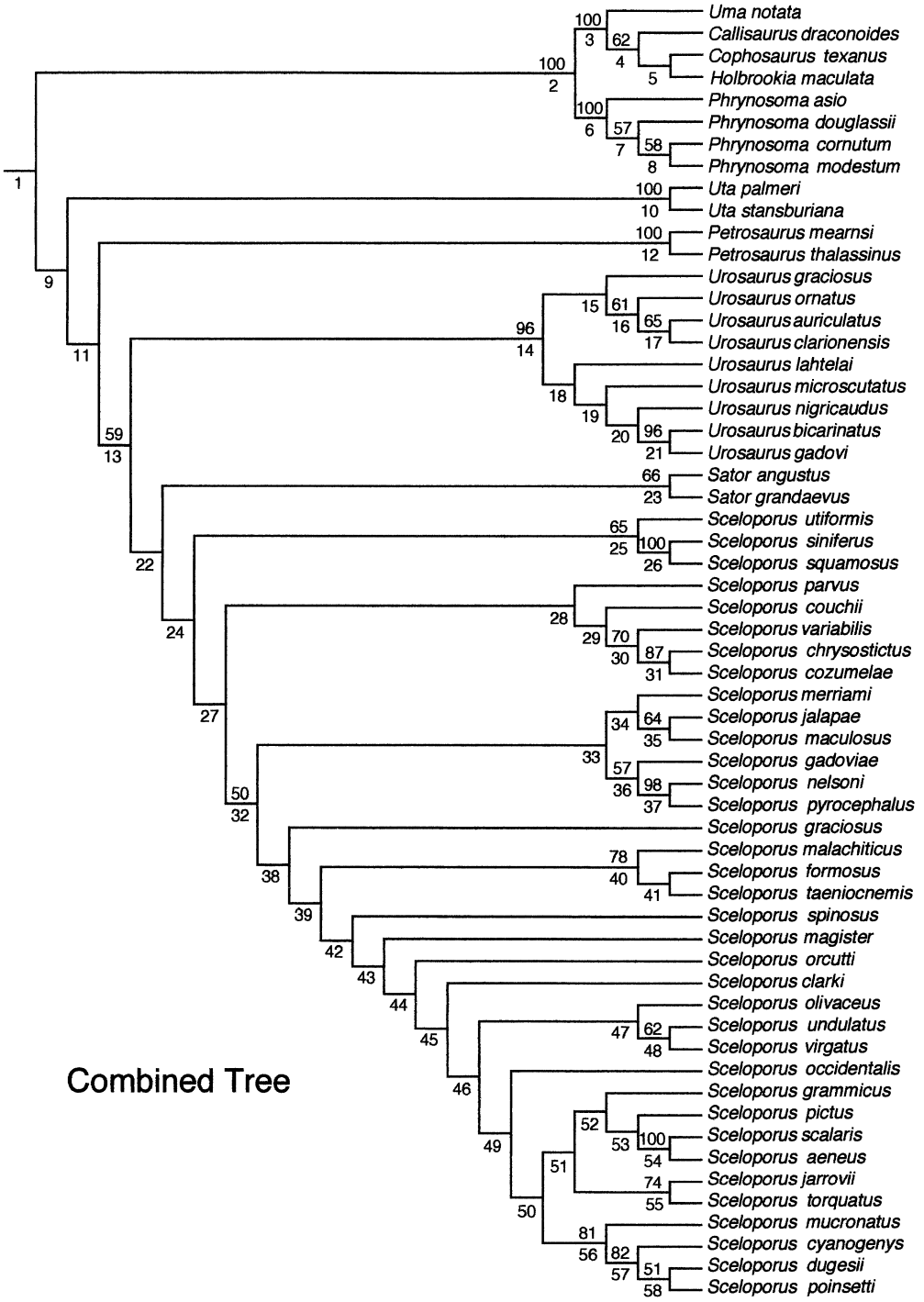

FIG. 5.—Single shortest phylogeny (L = 1235.00, CI = 0.35, RI = 0.63) inferred from the combined analysis (simultaneous analysis of the DNA and non-DNA data). The numbers below the branches denote the different clades of the phylogeny. The numbers above the branches are bootstrap values from 200 bootstrap replicates. Branches without bootstrap values were supported in <50% of the replicates.

TABLE 5.—The number of unambiguously placed synapomorphies distributed along the branches of the phylogeny inferred from the combined analysis.

Branch	Number of unambiguous character states*	Branch lengths†
1 (Phrynosomatidae)	8:3	3.00
2	8:12	10.01
3 (sand lizards)	7:7	6.71
4	1:7	5.42
5 (earless lizards)	3:8	4.13
6 (*Phrynosoma*)	6:32	28.60
7	6:7	3.75
8	2:8	4.58
9 (*Sceloporus* group)	5:4	1.63
10 (*Uta*)	16:4	2.49
11	3:0	0.00
12 (*Petrosaurus*)	8:8	7.25
13	4:4	3.67
14 (*Urosaurus*)	10:6	3.67
15	4:3	1.51
16	0:4	2.05
17	0:3	2.13
18	0:3	2.54
19	0:1	1.00
20	0:3	0.21
21	0:9	6.95
22	3:2	2.00
23 (*Sator*)	0:4	2.45
24 (*Sceloporus*)	0:2	2.00
25	0:9	4.55
26	0:18	12.55
27	0:4	2.55
28	0:7	4.16
29	0:5	1.42
30	0:7	5.42
31	0:7	4.99
32	9:4	1.84
33	0:2	1.17
34	0:3	0.83
35	0:2	2.00
36	0:4	3.67
37	0:9	4.37
38	7:6	2.54
39	4:4	3.50
40	2:3	1.33
41	2:1	1.00
42	2:4	1.00
43	2:2	1.38
44	2:5	1.46
45	5:3	1.46
46	2:3	2.50
47	1:2	1.33
48	3:5	0.96
49	0:3	0.49
50	2:5	4.67
51	2:1	0.42
52	3:3	1.16
53	0:8	3.81
54	0:15	9.17
55	5:3	0.46
56	4:2	0.62
57	3:1	0.21
58	2:2	0.88

TABLE 5.—Continued.

* Number of DNA characters:number of non-DNA characters.

† Minimum branch lengths for the unambiguous non-DNA characters.

DNA; this convention followed throughout, only non-DNA characters listed) provide support for the monophyly of the Phrynosomatidae (Branch 1): 39.y (primary coracoid foramen formed mostly in bone), 131.y (dorsal shank muscle innervation from peroneal nerve), and 141.1 (20 microchromosomes). This is in addition to the six synapomorphies discovered by Frost and Etheridge (1989) (Table 2). Branch 2 (*Phrynosoma* + sand lizards) is supported by 20 synapomorphies (8:12): 4.y (lacrimal absent), 7.y (postfrontal absent), 15.y (posterolateral processes of basisphenoid elongate), 17.y (scleral ossicle 6 reduced or absent), 41.y (median process of interclavicle reduced), 57.k or v (polymorphic presence of reduced rostral scale), 61.f or h (polymorphic presence of unpaired median postrostral), 84.2 (first sublabial posterior to second infralabial), 85.y (mental scale reduced), 108.m (polymorphic presence of ≥3 interpostanals), 111.v or y (polymorphic or fixed presence of discontinuous femoral pore rows), and 136.y (direct insertion of *m. transversus abdominis*). *Phrynosoma* monophyly is corroborated by 38 synapomorphies (6:32): 8.y (supraorbital bar present), 10.y (squamosal–parietal horns present), 11.y (jugal expanded posteriorly), 14.q (polymorphic reduction of epipterygoid), 18.y (scleral ossicle 8 reduced), 20.y (cusps of posterior dentary teeth absent), 21.y (ceratobranchial I dorsoventrally flattened), 23.y (retroarticular process vertically flattened), 25.y (coronoid contacts anterior inferior alveolar foramen), 32.y (number of caudal vertebrae reduced), 35.y (caudal autotomy septa absent), 42.2 (sternal fontanelle shape enlarged), 43.y (sternum pentagonal shaped), 45.y (xiphisternal rib connections re-

duced), 46.y (suprascapula rectangular), 50.y (pubic symphysis flat), 51.y (hypoischiac foramen absent), 54.y (phalangeal formula of hand reduced), 55.y (phalangeal formula of foot reduced), 56.y (cephalic scales rugose), 57.y (rostral scale narrow), 65.a (frontal scale undifferentiated), 75.y (superciliaries not or barely overlapping), 81.y (subocular fragmented), 83.u (polymorphic presence of dentate labial margin), 87.y (enlarged, keeled chinshields present), 92.2 (dorsal scales heterogeneous), 96.y (row of enlarged dorsolateral scales present), 97.y (enlarged flank scales present), 99.y (upper row of lateral abdominal fringe scales present), 108.q or y (increase in frequency of increased number of interpostanals), and 113.y (transverse rows of caudal scales absent).

Fourteen synapomorphies (7:7) support sand lizard monophyly (Branch 3): mandible countersunk (27.u or y), first pair of cervical ribs on fifth vertebra (28.2), scapular fenestra present (37.a), labials elongate, keeled, and overlapping (82.y), tibial scales smooth (102.y), polymorphic presence of dark ventrolateral spots or stripes (121.v), and black transverse stripes on ventral surface of tail (123.y). The placement of *Uma* as the sister taxon of a clade containing *Callisaurus, Cophosaurus,* and *Holbrookia* (Branch 4) is supported by eight synapomorphies (1:7): 16.y (stapedial footplate expanded), 65.g (increase in frequency of differentiated frontal scale), 70.y (large interparietal), 122.y (two dark ventrolateral spots or stripes), 138.y (*m. intermandibularis anterior superficialis* lost), 139.y (*m. constrictor colli* reduced), and 156.0 (tail raised during display). The *Cophosaurus* + *Holbrookia* clade (Branch 5) is supported by 11 synapomorphies (3:8): 2.f (polymorphic presence of large nutritive foramina in maxilla), 9.y (large parietal foramen), 61.w (polymorphic presence of unpaired median postrostral), 65.l (polymorphic presence of differentiated frontal scale), 89.y (covered tympanum), 108.y (≥3 interpostanals), 111.p (decrease in frequency of discontinuous femoral pore rows), and 146.1 (allozyme allele Aat^c).

The remaining phrynosomatid genera (*Petrosaurus, Sator, Sceloporus, Urosaurus,* and *Uta*) are included in a clade (Branch 9) supported by nine synapomorphies (5:4): 9.y (large parietal foramen), 65.y (differentiated frontal scale), 70.y (large interparietal), and 117.d (polymorphic presence of white spots on nape). Three DNA synapomorphies support a more exclusive clade containing *Petrosaurus, Sator, Sceloporus,* and *Urosaurus* (Branch 11), whereas unambiguous non-DNA support for this clade is lacking. Eight synapomorphies unite *Urosaurus, Sator,* and *Sceloporus* (Branch 13), leaving *Petrosaurus* as the sister taxon of this less inclusive clade (4:4): heart-shaped sternal fontanelle (42.1), sternum–xiphisternum fused (47.y), recurved clavicular flange (48.y), and dorsal shank muscle innervation from interosseous nerve (131.0). The *Sator* + *Sceloporus* clade (Branch 22) is supported by five synapomorphies (3:2): 103.y (strongly imbricate gulars) and 105.2 (gular fold completely absent).

Uta monophyly (Branch 10) is corroborated by 20 synapomorphies (16:4): polymorphic presence of five non-autotomous caudal vertebrae (36.i), first supralabial contacting second infralabial (84.1), increase in frequency of white spots on nape (117.l), and polymorphic presence of ventrolateral spots or stripes (121.u). The *Petrosaurus* clade (Branch 12) is supported by 16 synapomorphies (8:8): 30.y (thoracic vertebrae depressed), 44.2 (four sternal ribs), 49.q (polymorphic presence of elongate epipubic cartilage), 53.y (metatarsal III longer than IV), 74.y (increase in superciliaries), 76.y (first canthal contacts lorilabial), 108.y (increase in interpostanals), and 116.3 (wide black collar). Sixteen synapomorphies support the monophyly of *Urosaurus* (Branch 14; 10:6): 6.p (polymorphic presence of frontal–postorbital contact), 62.y (loss of supranasals), 69.f or j (increase in the frequency of frontal–interparietal contact), 76.a (loss of first canthal–lorilabial contact), 93.y (narrow band of enlarged dorsals), and 152.1 (four-legged push-up display).

Sator monophyly (Branch 23) is supported by four synapomorphies (0:4): reduction in size of parietal foramen (9.a),

polymorphic presence of fused frontal scale (66.u), first canthal contacts lorilabial (76.y), and increase in frequency of white spots on nape (117.e). Two synapomorphies support the monophyly of *Sceloporus* (Branch 24; 0:2): 71.a (increase in posterior circumorbital rows) and 91.y (pointed, overlapping dorsals). Neither *Sator* or *Sceloporus* is unambiguously supported by any DNA synapomorphies. DNA sequence data are available for only a single species of *Sator* and none of the basal species of *Sceloporus*, making the unambiguous placement of DNA characters impossible.

Bootstrap values are shown in Figure 5. While the combined phylogenetic analysis corroborates the monophyly of all phrynosomatid genera (for which multiple species were sampled), only the monophyly of *Petrosaurus*, *Phrynosoma*, *Urosaurus*, and *Uta* is very strongly supported (all four ≥96%). The monophyly of *Sator* was more weakly supported (66%). *Sceloporus* is weakly supported, with monophyly being confirmed in <50% of the bootstrap replicates. The most strongly supported intergeneric relationships are sand lizard monophyly (100%) and the sand lizard + *Phrynosoma* clade (100%). Within the sand lizards, the placement of *Uma* as the sister taxon of *Callisaurus*, *Cophosaurus*, and *Holbrookia* is relatively better supported (62%) than the *Cophosaurus* + *Holbrookia* clade (<50%). The intergeneric relationships among *Petrosaurus*, *Sator*, *Sceloporus*, *Urosaurus*, and *Uta* (as well as the relationship between these genera and the sand lizard + *Phrynosoma* clade) are weakly supported in the combined phylogenetic analysis, with only the *Sator-Sceloporus-Urosaurus* clade being recovered in >50% of the bootstrap replicates (59%).

Relative Homoplasy Exhibited by the Different Types of Data

The mean character ci and ri of the different types of data are presented in Table 6. Overall, the non-DNA data (ci = 0.64, ri = 0.66) are less homoplastic than the DNA sequence data (ci = 0.46, ri = 0.49). Within the non-DNA data, the allozyme characters (ci = 1.00, ri = 1.00) are perfectly congruent with the hypotheses inferred from the combined phylogenetic analysis. However, the two allozyme characters are coded only for a small subset of taxa (character 146 for sand lizards and character 147 within *Urosaurus*). More homoplasy probably would have been discovered if additional taxa had been surveyed. The myological characters (ci = 0.94, ri = 0.99) are also highly congruent, whereas characters based on coloration (ci = 0.44, ri = 0.62) are the least congruent. Within the DNA sequence data, informative nucleotide positions exhibiting only two bases (= character states) are less homoplastic (ci = 0.54, ri = 0.52) than positions exhibiting three or four states (ci = 0.31, ri = 0.47 and ci = 0.33, ri = 0.37, respectively).

DISCUSSION

Phrynosomatid Relationships

Phylogenetic relationships.—All phrynosomatid genera for which multiple species are sampled (*Petrosaurus*, *Phrynosoma*, *Sator*, *Sceloporus*, *Urosaurus*, and *Uta*) are supported as monophyletic in the combined phylogenetic analysis. *Petrosaurus*, *Phrynosoma*, *Urosaurus*, and *Uta* are some of the most strongly supported clades. Although the combined analysis corroborates the monophyly of *Sceloporus*, this clade is relatively weakly supported by only two non-DNA synapomorphies (total length = 2.0 steps). Because of the lack of DNA sequence data for members of the basal *utiformis* + *siniferus* species group clade (Branch 25), identification of unambiguous DNA synapomorphies for *Sceloporus* is not possible. Monophyly of *Sceloporus* is moderately well supported by six synapomorphies in the separate analysis of the non-DNA data. However, in spite of the congruence between the non-DNA and combined analyses, only one of the six original synapomorphies (i.e., non-DNA character 71) confirms *Sceloporus* monophyly in the combined analysis. One of the rejected synapomorphies (non-DNA character 127) is ambiguously placed, supporting *Sceloporus* monophyly only under ACCTRAN optimization. The other four (non-DNA

TABLE 6.—Mean consistency (ci) and retention (ri) indices for different classes and/or sources of characters from the combined phylogenetic analysis.*

Source/class of characters	*n*	ci	ri
DNA			
All informative characters	152	0.46	0.49
12S rDNA	66	0.45	0.46
16S rDNA	86	0.46	0.52
Two states†	63	0.54	0.52
Transitions†	55	0.52	0.50
C ↔ T	32	0.51	0.49
G ↔ A	23	0.55	0.50
Transversions†	11	0.63	0.64
A ↔ T	8	0.55	0.56
A ↔ C	3	0.83	0.83
Three states†	53	0.31	0.47
Four states†	15	0.33	0.37
Informative gaps only‡	5	0.57	0.58
Non-DNA			
All informative characters	155 (143)	0.58 (0.64)	0.71 (0.66)
Osteology	55 (52)	0.64 (0.70)	0.77 (0.78)
Squamation	60 (56)	0.46 (0.56)	0.64 (0.60)
Coloration	15 (12)	0.44 (0.36)	0.62 (0.51)
Behavior	9 (9)	0.74 (0.77)	0.69 (0.69)
Myology	9 (9)	0.94 (0.94)	0.99 (0.99)
Karyology	4 (3)	0.68 (0.68)	0.64 (0.85)
Allozymes	2 (1)	1.00 (1.00)	1.00 (1.00)
Life history	1 (1)	0.20 (0.25)	0.64 (0.70)

* The index values in parentheses for the non-DNA data are when the 19 species lacking DNA data are removed. The indices in parentheses are therefore more comparable to those for the DNA data.

† The indices reported for these classes of base substitutions (= character transformations) are for those nucleotide positions exhibiting only nucleotides (no indels).

‡ Includes those positions where only the indel is the informative character transformation. Positions possessing indels and more than one type of nucleotide character state were not included in this comparison.

characters 5, 37, 59, and 112) now corroborate less general hypotheses within *Sceloporus*. The primary reason for the new distribution of these less general synapomorphies is the rearrangement of the basal clades of *Sceloporus* in the combined analysis, largely influenced by the addition of the DNA data.

The sand lizard clade is strongly supported (14 synapomorphies; 100% bootstrap proportion) and represents the sister taxon of *Phrynosoma*. This sand lizard + *Phrynosoma* clade is equally well corroborated by 13 synapomorphies (100% bootstrap proportion). Since Presch (1969) first hypothesized a sand lizard + *Phrynosoma* clade, this clade has been repeatedly corroborated by morphological and molecular data in all subsequent phylogenetic studies (Etheridge and de Queiroz, 1988; Frost and Etheridge, 1989; Reeder, 1995; Wiens, 1993*a*).

The sand lizard intergeneric relationships implied by the combined analysis, as well as by the separate non-DNA analysis, are identical to those proposed by de Queiroz (1989, 1992). Despite the apparent incongruence between the separate DNA (Reeder, 1995) and non-DNA (this study) analyses, the intergeneric relationships hypothesized by the combined analysis are unambiguously supported by both DNA and non-DNA synapomorphies. The earless lizard clade is confirmed in <50% of the bootstrap replicates.

The sister taxon of the sand lizard + *Phrynosoma* clade is a clade containing all remaining phrynosomatid genera. A clade containing *Petrosaurus, Sator, Sceloporus, Urosaurus,* and *Uta* was first suggested by Frost and Etheridge (1989), being found in two of their three equally parsimonious hypotheses of phrynosomatid relationships. Wiens (1993*a*) provided unambig-

uous morphological support for this clade, but molecular support for this clade was ambiguous (Reeder, 1995; this study). The intergeneric relationships within this clade are congruent with those of Frost and Etheridge (1989:fig. 12, "Topology 1") and essentially the same as those most recently proposed by Wiens (1993*a*), except that *Uta* and *Petrosaurus* have switched positions. In our combined analysis, *Uta* is now the sister taxon of *Petrosaurus* + the remaining members of the *Sceloporus* group (sensu Etheridge and de Queiroz, 1988).

Etheridge and de Queiroz (1988) implicitly defined the *Sceloporus* group as the most recent common ancestor of *Sator, Sceloporus, Urosaurus, Uta,* and all of its descendants. The inclusion of *Petrosaurus* in the *Sceloporus* group is supported by three DNA synapomorphies (Branch 11) but no unambiguously placed non-DNA synapomorphies. The placement of *Uta* as the sister taxon of the remaining members of the *Sceloporus* group is the most parsimonious hypothesis discovered in the combined analysis. However, the placement of *Petrosaurus* as the sister taxon of the *Sceloporus* group (as supported by Wiens, 1993*a*) is nearly as parsimonious, requiring a tree length increase of only 0.17 step. It requires a greater increase in homoplasy (2.25 steps) to place *Petrosaurus* as the sister taxon of all remaining phrynosomatids (as hypothesized by Etheridge and de Queiroz, 1988). Thus, while the phylogenetic placement of *Petrosaurus* remains weakly supported, the DNA and non-DNA data (separate and combined) are congruent in supporting a close relationship between *Petrosaurus* and the remaining members of the *Sceloporus* group, corroborating the studies of Frost and Etheridge (1989) and Wiens (1993*a*).

The remaining relationships within the *Sceloporus* group, *Urosaurus* (*Sator* + *Sceloporus*), are identical to those hypothesized by Wiens (1993*a*). A close relationship among these genera was first hypothesized by Savage (1958); he called the group the urosaurines. This clade was later corroborated by Etheridge and de Queiroz (1988), Frost and Etheridge (1989; in two of their three topologies), and Wiens (1993*a*) but not by Reeder (1995). In the combined analysis, this clade is the best supported intergeneric relationship within the *Sceloporus* group, being confirmed by eight synapomorphies and a bootstrap proportion of 59%.

Wiens (1993*b*) provided eight unambiguous synapomorphies to support the monophyly of *Urosaurus*. Our combined analysis continues to support this clade, corroborating three (i.e., frontal–postorbital contact, loss of supranasals, and narrow band of enlarged dorsals) of the original synapomorphies suggested by Wiens (1993*b*) and discovering 13 new synapomorphies (10 DNA:3 non-DNA). Two of Wiens's original synapomorphies are either ambiguously placed and/or now support more exclusive clades within *Urosaurus*. The reduction to two postrostrals is now ambiguously placed either as a *Urosaurus* synapomorphy (under ACCTRAN) or as independently derived synapomorphies for the *ornatus* and *bicarinatus* species groups (under DELTRAN). The presence of dorsolaterals now corroborates the *graciosus* + *ornatus* species group clade and the *bicarinatus* species group.

By including all nine currently recognized species of *Urosaurus* in our phylogenetic analysis, we were provided the opportunity to confirm or disconfirm the intrageneric relationships recently proposed by Wiens (1993*b*). The monophyly of the *ornatus* and *bicarinatus* species groups (Branches 16 and 18, respectively) is supported, but one of the two *bicarinatus* group subgroups is not monophyletic. The *nigricaudus* subgroup (*lahtelai, microscutatus,* and *nigricaudus*) represents a graded series of species leading to a monophyletic *bicarinatus* subgroup (Branch 21). Wiens (1993*b*) hypothesized that *U. graciosus* was the sister taxon of all other *Urosaurus* species, but acknowledged that such a relationship was weakly supported by only two synapomorphies. Our analysis supports *U. graciosus* as the sister taxon of the *ornatus* species group, supported by four DNA and three non-DNA synapomorphies. In all, four of the seven clades hypothesized by Wiens (1993*b*) are corroborated in this analysis. However, be-

cause five of the nine species lack DNA sequence data, we will defer making any formal taxonomic revisions until additional DNA sequence data are obtained (Reeder and Wiens, work in progress).

Wiens (1993*a*) found evidence that *Sator* was the sister taxon of *Sceloporus* instead of being nested within *Sceloporus* as suggested by Wyles and Gorman (1978). In order to more rigorously test *Sceloporus* monophyly, in our phylogenetic analyses we did not assume any specific internal phylogenetic structure within *Sceloporus*, as did Wiens (1993*a*). Instead, *Sceloporus* species were individually coded as terminal taxa. Of particular importance was the inclusion of *Sceloporus utiformis*. Based on allozymic and immunological data, this species has been postulated to be the sister taxon of *Sator* (Wyles and Gorman, 1978), thus rendering *Sceloporus* paraphyletic. With the inclusion of approximately 45% of the currently recognized species of *Sceloporus* as individual terminal taxa, representing all 16 species groups (Smith, 1939; Thomas and Dixon, 1976), our combined analysis further corroborates the *Sceloporus* clade with two unambiguously placed non-DNA synapomorphies. Thus, although *Sceloporus* monophyly is still considered weakly supported, the genus has withstood a more rigorous test of its monophyly.

In our combined phylogenetic analysis, all 16 *Sceloporus* species groups (Smith, 1939; Thomas and Dixon, 1976) are represented. The results of this analysis suggest that taxonomic revisions within *Sceloporus* are warranted, but we defer making such changes at this time for two reasons. First, only ~45% (34 of 77) of the currently recognized *Sceloporus* species (Sites et al., 1992) were included. The monophyly of some species groups could not be tested because only single species were included, whereas some species groups represented by multiple species are still poorly sampled (e.g., only 3 of 12 species of the *formosus* species group). Second, many of the inferred relationships (e.g., basal internodes, *pyrocephalus* species group) within *Sceloporus* are weakly supported in the combined analysis. A revision of *Sceloporus*, based on a more extensive phylogenetic analysis (additional characters and species), is presented in Wiens and Reeder (1997).

TABLE 7.—Number of congruent and incongruent (= conflicting) clades between the separate analyses of the DNA and non-DNA data sets. Clades are considered strongly supported if they possess bootstrap values of ≥70%.

Category	*n*
Congruent clades; strongly supported in both separate analyses	4
Congruent clades; strongly supported in one but not both separate analyses	5
Congruent clades; weakly supported in both separate analyses	1
Strongly supported DNA clades; conflicting non-DNA clades weakly supported	5
Strongly supported non-DNA clades*; conflicting DNA clades weakly supported	4
Strongly supported DNA clades; conflicting non-DNA clades strongly supported	0
Strongly supported non-DNA clades; conflicting DNA clades strongly supported	0

* There are eight additional strongly supported clades in the non-DNA trees that are not comparable with the DNA tree because the species involved were not present in the DNA analysis.

Why are relationships among phrynosomatid genera so hard to establish?—A major goal of this study was to produce a well-corroborated hypothesis for the relationships among the genera of the Phrynosomatidae. Despite our combined analysis of hundreds of diverse, phylogenetically informative characters, hypothesized relationships among most phrynosomatid genera remain weakly supported (Fig. 5). Why is this the case? One possibility—that the weak support is caused by incongruence between the trees inferred by the mtDNA and non-DNA characters—is unlikely, given that there are no strongly supported conflicts between the trees inferred from these separate data sets (Table 7). Another possibility is that we included too few characters to find strong support for many clades (or too few characters that were evolving at a rate appropriate for the phylogenetic problem), but both DNA and non-DNA sets provided strong support for the monophyly of most genera and for certain intergeneric relationships (Figs. 2, 3, 5). The fact that both data sets give only

weak support for the same parts of the tree suggests an underlying cause that is related to an intrinsic property of the true phylogeny rather than the characters used to estimate it (Wiens and Reeder, 1997). Rapid speciation (such that there is too little time for a large number of synapomorphies to evolve along a branch or branches) has been implicated in causing a lack of resolution and/or strong support in certain portions of trees in several molecular phylogenetic analyses (Kraus and Miyamoto, 1991; Lanyon, 1988; review in Donoghue and Sanderson, 1992). Congruent areas of weak support in trees from both molecular and morphological data provide more compelling evidence for a hypothesis of rapid speciation (Wiens and Reeder, 1997), and we believe that rapid speciation is the most likely explanation for the weakly supported intergeneric relationships in this study. If so, then large amounts of sequence data from several slowly evolving genes may be necessary to provide strong support for these parts of the tree (Kraus and Miyamoto, 1991). Although molecular and morphological data may often provide support for different parts of a phylogeny (they exhibit complementarity; Donoghue and Sanderson, 1992; Hillis, 1987), the dependence of character support on the amount of time between speciation events may cause the opposite phenomenon to be more common.

Congruence between and within Diverse Types of Data

Congruence between phylogenetic hypotheses.—Only 26% (10/38; Fig. 4) of the clades are shared between the phylogenies of the separate DNA and non-DNA analyses. Of these 10 shared clades, nine represent some of the most strongly supported hypotheses of the separate analyses (bootstrap values $\geq$70%; Fig. 4; Table 7). The single remaining shared clade (*Sceloporus undulatus* + *S. virgatus*) is not strongly supported (bootstrap values $<$70%) in either separate analysis. However, the congruence between the two separate analyses increases our confidence in the reality of this clade (Miyamoto and Fitch, 1995).

Chippindale and Wiens (1994) found that in over half of their examples (drawn from the literature), combined analyses resulted in phylogenies that are incongruent (= unique) with those from the separate analyses. In our study, the combined phylogenetic analysis resulted in a unique phylogeny incongruent with the hypotheses inferred from the separate analyses of the DNA and non-DNA data sets. Thus, in the combined analysis we discovered relationships that would not have been found had the DNA and non-DNA data only been analyzed separately (Barrett et al., 1991). This observation emphasizes the importance of performing combined as well as separate analyses of diverse data.

While the phylogeny from the combined analysis is not strictly congruent with either the DNA or non-DNA hypotheses, most of the individual clades of the combined phylogeny are supported in the DNA and/or non-DNA phylogenies. Thirty of 57 clades (53%; ingroup node not included) of the combined phylogeny are supported by the separate analysis of the non-DNA data, whereas 74% (28/38; species lacking DNA were pruned) of these clades are congruent with those supported by the separate analysis of the DNA data. Only two clades (Branches 46 and 49) in the combined phylogeny are absent from both of the separate analyses. Finally, while a clade containing *Petrosaurus, Sator, Sceloporus,* and *Urosaurus* was supported in both the DNA and the combined analyses (not supported in the non-DNA analysis), the specific hierarchical relationship inferred from the combined analysis—*Petrosaurus* (*Urosaurus* (*Sator* + *Sceloporus*))—was not observed in the DNA analysis.

Overall, the phylogeny inferred from the combined analysis is more similar to the results from the DNA analysis than the non-DNA analysis (74 vs. 53%). It appears that the DNA data are possibly having a greater influence on the final outcome of the combined phylogenetic analysis. However, this influence is not evenly distributed across the phylogeny. For example,

seven of eight (88%) of the clades involving intergeneric relationships are shared with the non-DNA analysis, whereas only three (38%) of these clades are shared with the DNA analysis. The similarity between the combined and DNA phylogenies is largely due to the high degree of congruence of relationships within *Sceloporus* between these two analyses. Over half of the phrynosomatid clades of our phylogeny are within *Sceloporus*, of which 81% are congruent between the combined and DNA analyses (only 37% shared between the combined and non-DNA analyses). The fact that different data sets have greater influence and/or are better at resolving different areas of a phylogeny in a combined analysis is not a weakness of the combined approach of phylogenetic analysis but instead is a strength. Combining diverse types of data for phylogenetic analysis potentially increases the chance of including characters that will effectively resolve relationships throughout a phylogeny (Hillis, 1987; Donoghue and Sanderson, 1992).

Bull et al. (1993) and de Queiroz (1993) have advocated that separate data sets should not be combined for phylogenetic analysis if the competing relationships are strongly supported in each of the separate analyses, suggesting that such results imply separate histories of the different data partitions. Arguments against the prior agreement approach of Bull et al. (1993) and de Queiroz (1993) have been presented by Chippindale and Wiens (1994) and Wiens and Chippindale (1994). While we advocate the combined approach for phylogenetic analysis, we are nonetheless interested in knowing if the separate data sets are providing strongly conflicting hypotheses of relationships. The majority (74%) of the clades from our separate analyses are incongruent with each other, but support for the conflicting clades is weak (bootstrap values <70%) in both analyses or strongly supported by only one of the two data sets (Table 7). For example, the intergeneric relationships within the *Sceloporus* group are completely incongruent (no shared clades), but neither analysis provided strong support for their conflicting hypotheses. The relationships among the sand lizards are strongly supported by the non-DNA data and incongruent with the relationships inferred from the DNA data, but the relationships supported by the DNA data are weakly supported (bootstrap values <70%). Thus, even though many of the relationships inferred from the separate analyses are incongruent, they do not conflict strongly.

Congruence within and between character partitions.—The different sources of data differentially contribute to the overall level of character incongruence (= homoplasy) in the combined analysis (Table 6). The levels of homoplasy exhibited by different partitions of the DNA data, when analyzed separately, have been discussed in Reeder (1995). The 12S and 16S rDNA sequences exhibit similar levels of character incongruence (ci = 0.45 vs. 0.46, ri = 0.46 vs. 0.52, respectively), with the ri suggesting that the 12S data are slightly more homoplastic. Within the DNA data set, nucleotide positions exhibiting only two states are generally less homoplastic than positions exhibiting three or four states. Also, among the binary positions, transversions appear to be less homoplastic than transitions (ci = 0.63 vs. 0.52, ri = 0.64 vs. 0.50). However, the greater level of character congruence within the transversion partition is largely influenced by A $\leftrightarrow$ C transversions (ci and ri = 0.83). The A $\leftrightarrow$ T transversion partition is essentially as homoplastic as the transitions, which is not what one would expect from the supposedly "conservative" transversions. Finally, except for transversions (but see above), the partition of informative gaps only was the least homoplastic of the different DNA data partitions. The degree of character congruence exhibited by indels (= insertions and/or deletions), relative to other DNA characters, is noteworthy because indels are often coded as missing data (e.g., Allard and Honeycutt, 1992). The results of our study suggest that indels are not necessarily more homoplastic or misleading than other DNA characters, as often assumed, and are consistent with the re-

sults of other recent studies supporting the informativeness of indels (Wheeler, 1993). These conclusions regarding the levels of homoplasy exhibited by the DNA data in the combined analysis are similar to those reached in the separate analysis of these data by Reeder (1995).

Within the non-DNA data set, the extent of homoplasy varied substantially (ci = 0.20–1.00; ri = 0.64–1.00) between the different types of data (Table 6). The allozyme and myological data were the least homoplastic types of non-DNA data within the context of the combined analysis. However, because of the small sample sizes (number of characters and number of species coded), the levels of homoplasy in these two types of data should be interpreted cautiously. Missing data effectively reduces the number of taxa (= removing opportunities to observe homoplasy), with a negative relationship between number of taxa and observed levels of homoplasy being documented by Archie (1989) and Sanderson and Donoghue (1989). Of the non-DNA data, the osteology, squamation, and coloration sources consisted of a large number of characters that were coded for most or all species. Of these three sources, the osteological characters were the least homoplastic (ci = 0.64; ri = 0.77), whereas the coloration characters exhibited the greatest amount of character incongruence (ci = 0.44; ri = 0.62).

In general, with few exceptions, virtually all of the ri's of the different data partitions fall within a very narrow range, indicating that the different partitions contribute similarly to the overall level of incongruence. However, as a whole, the non-DNA data are less homoplastic than the DNA data, even though the combined tree is largely influenced by the DNA data. This may be deemed problematic and may decrease confidence in the resulting tree, but such a conclusion should be made cautiously (Donoghue and Sanderson, 1992). Donoghue and Sanderson (1992) acknowledge that homoplastic characters may be "misleading," but the degree to which such characters confound an analysis depends on how they interact with other characters.

Inclusion of Incomplete Taxa

In our study, 19 of the 59 phrynosomatid species (13 *Sceloporus*, 6 *Urosaurus*) included in the combined phylogenetic analysis lacked DNA sequence data. However, in spite of the fact that one-third of the taxa were missing ≥51% of the total data, analysis of the combined data set resulted in the discovery of a single shortest tree. The inclusion of many incomplete taxa did not obscure the inferred relationships between the complete taxa by generating a multitude of equally parsimonious trees, but their inclusion did have an effect on the relationships among some species with complete data. A single shortest tree was discovered when the combined data set was reanalyzed with the 19 incomplete taxa excluded (= complete-only phylogeny; Fig. 6). When the 19 incomplete species are pruned from the phylogeny obtained from the original combined analysis of all 59 species (= combined phylogeny), the pruned phylogeny is nearly identical to the complete-only phylogeny. The alternative phylogenetic relationships among the complete taxa are restricted to a deeply nested clade of *Sceloporus* (Fig. 6). In the combined phylogeny, the *S. olivaceus* (*S. undulatus* + *S. virgatus*) clade is the sister taxon of the remaining *Sceloporus* species of the aforementioned affected clade, whereas in the complete-only phylogeny *S. occidentalis* is the sister taxon of these remaining *Sceloporus* species (Fig. 6). Also, in the complete-only phylogeny, the *torquatus* species group is monophyletic (contra the combined phylogeny). These analyses illustrate that the phylogenetic placement of the complete taxa can be affected by the inclusion of incomplete taxa, but generally the hypothesized phrynosomatid relationships are largely insensitive to the inclusion of the incomplete taxa.

Wiens and Reeder (1995) discussed several options for dealing with incomplete taxa when combining data sets with unequal taxonomic coverage, besides simple inclusion or exclusion. For example, the incomplete species can be mapped onto the complete-only combined phylogeny *a*

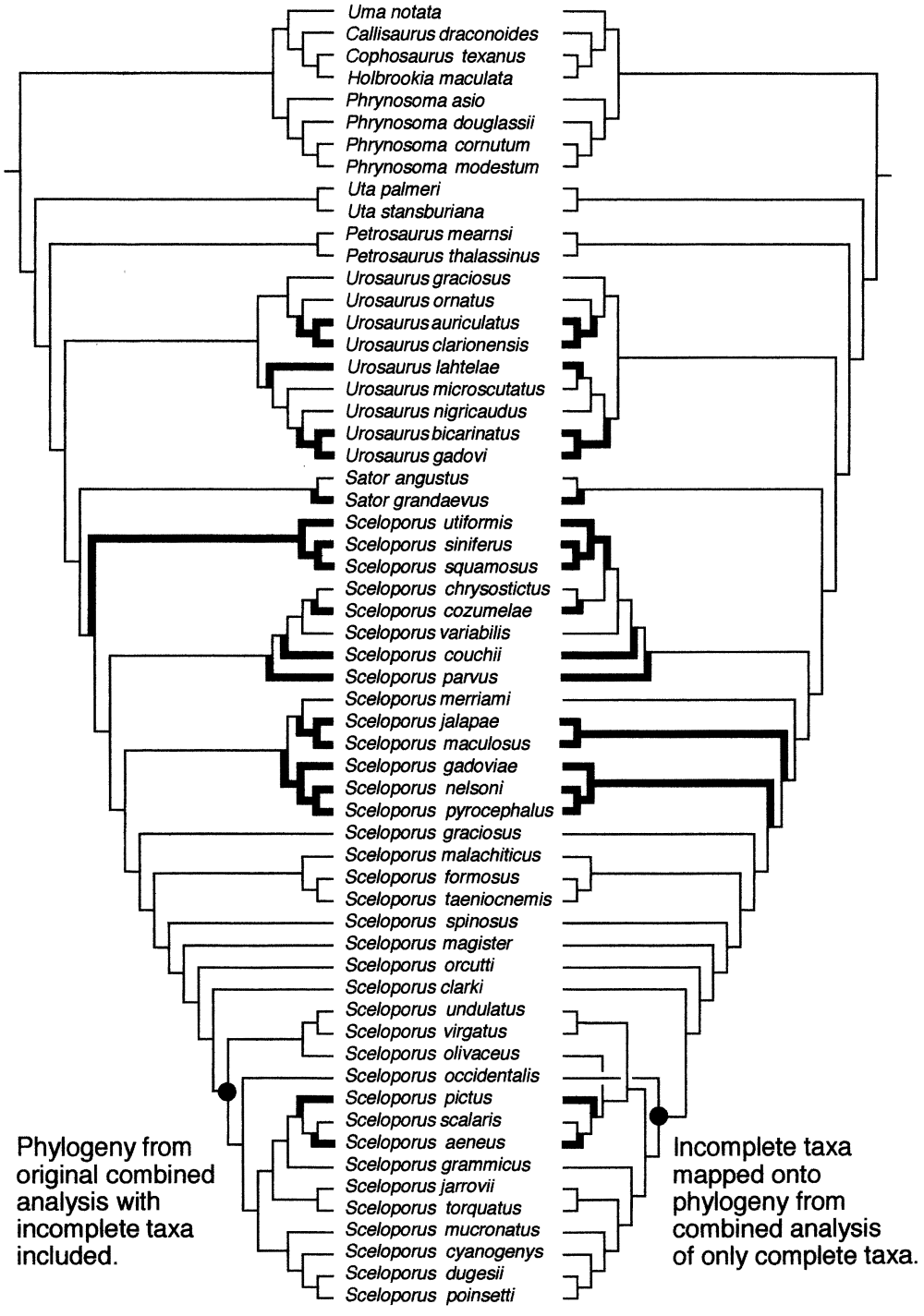

FIG. 6.—Combined phylogeny vs. the complete-taxa-only phylogeny. Thick branches lead to incomplete taxa (species lacking DNA data). The combined phylogeny (left) was inferred with the incomplete taxa included in the analysis. The complete-taxa-only phylogeny (right) was inferred from a combined analysis including only the complete taxa (possessing DNA and non-DNA data) and the incomplete taxa were mapped onto this phylogeny *a posteriori*.

posteriori by connecting the incomplete species to their sister taxa based on the non-DNA phylogeny. In our study, for example, the incomplete *Sceloporus cozumelae* can be connected to *S. chrysostictus*, and the non-DNA-only species *Urosaurus auriculatus* + *U. clarionensis* can be connected to *U. ornatus* in the complete-only phylogeny, as predicted in the non-DNA phylogeny (Figs. 3, 6).

One problem with this mapping procedure is that a certain level of congruence between the non-DNA and complete-only phylogenies is required (Wiens and Reeder, 1995). For example, the interpretation of the phylogenetic relationship of the clade containing *Sceloporus utiformis*, the *siniferus* species group, and members of the "*variabilis*" species group to remaining species of *Sceloporus* is troublesome (Fig. 6). Whereas the non-DNA phylogeny predicts that the *S. utiformis* + *siniferus* species group clade is closely related to *S. chrysostictus*, it also predicts that the clade containing *S. utiformis*, the *siniferus* species group, and the "*variabilis*" species group is the sister taxon of all *Sceloporus*, exclusive of *S. merriami*. However, this predicted relationship is not evident in the complete-only phylogeny with the incomplete species mapped onto it (Fig. 6). The *S. utiformis* + *siniferus* species group clade is still associated with the "*variabilis*" species group, as in the non-DNA phylogeny, but now this more inclusive clade is placed as the sister taxon of all remaining *Sceloporus* (including *S. merriami*).

A more disturbing problem with this mapping procedure is that the phylogenetic placement of many incomplete species in the combined analysis of all 59 species is not where they would be predicted based on their placement in the non-DNA phylogeny. For example, in the non-DNA phylogeny (Fig. 3), the *Urosaurus bicarinatus* + *U. gadovi* clade is the sister taxon of the clade containing *U. lahtelai* and the complete species *U. microscutatus* and *U. nigricaudus* (Fig. 6). However, in the combined 59-species phylogeny, *U. nigricaudus*, *U. microscutatus*, and *U. lahtelai* do not form a clade, but rather they form a paraphyletic series of three lineages leading up to the *U. bicarinatus* + *U. gadovi* clade (Figs. 5, 6). The interaction between the DNA and non-DNA data in the combined analysis appears to change the relationships among the complete taxa (relative to their relationships in the non-DNA phylogeny), which in turn affects the placement of the incomplete taxa (Wiens and Reeder, 1995). The result is alternative placements of incomplete taxa in the combined analysis that are more parsimonious than their predicted placements based on the non-DNA phylogeny. Because this *a posteriori* mapping procedure can lead to less parsimonious placements for the incomplete taxa than if they are included in the combined analysis *a priori*, we strongly discourage its use.

Conclusions

Diverse types of data (i.e., mitochondrial rDNA, osteology, coloration, scalation, karyology, behavior) were used to infer the phylogenetic relationships within the Phrynosomatidae. Simultaneous analysis of these data strongly supports the monophyly of *Petrosaurus*, *Phrynosoma*, *Urosaurus*, and *Uta*. The monophyly of *Sator* and *Sceloporus* is only weakly supported. Whereas *Sceloporus* monophyly is weakly supported, a large number of species were included in the combined analysis (representing all species groups) and no *a priori* assumptions were made regarding phylogenetic structure within the genus. Thus, this analysis provides the most rigorous test of *Sceloporus* monophyly to date. Most intergeneric relationships proposed by de Queiroz (1992) and Wiens (1993*a*) are corroborated, with a sand lizard + *Phrynosoma* clade being strongly supported. In this study, *Sceloporus* group (sensu stricto) relationships differ from those postulated by Wiens (1993*a*), with *Petrosaurus* and *Uta* switching phylogenetic positions.

This study has resulted in additional progress in the phylogenetic systematics of phrynosomatids, but more work is certainly warranted. For example, the intergeneric relationships of the *Sceloporus* group (sensu stricto) inferred from the combined phylogenetic analysis are still weakly sup-

ported, and the separately analyzed DNA and non-DNA data provide conflicting support for alternative interrelationships within this clade. The weakly supported relationships, in the separate and combined analyses, are most likely due to rapid speciation. The acquisition of new data for inferring *Sceloporus* group phylogeny is encouraged. Data that are independent of the sources of data examined thus far, such as nuclear gene sequences, would be most useful.

Besides phrynosomatid phylogeny, we also addressed other questions regarding the combining of diverse data in phylogenetic analysis. In this study, separate analysis of the data sets results in trees that are largely incongruent, sharing less than one-third of their respective clades. However, all incongruence between the trees is the result of weakly supported groupings in one and/or both of the data sets. When the data sets are combined, a unique and fully resolved tree is discovered. All but two of the clades of the combined tree are supported in the DNA and/or non-DNA trees, with the combined tree being most similar to the DNA hypothesis. Overall, in the combined analysis the DNA data are more homoplastic than the non-DNA data. However, many of the partitions of the DNA and non-DNA data exhibit similar levels of homoplasy. We demonstrated that the inclusion of incomplete taxa in the combined analysis can have an affect on the phylogenetic placement of the complete taxa, but most of the hypothesized phrynosomatid relationships among the complete taxa are largely insensitive to the inclusion of incomplete taxa. In conclusion, simultaneous analysis (including taxa and characters) of diverse data sets has revealed relationships that were hidden by the separate analyses and has allowed us to address questions of fundamental interest in systematic biology.

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APPENDIX I

Non-DNA Characters Used in the Phylogenetic Analysis

Different conditions are denoted by "0" to "4." Except for unpolarized characters, "0" indicates the plesiomorphic condition. The different frequencies of the conditions listed here were used to make the data matrix of character states (a–y, or 0–4) shown in Appendix III. The first author to use the character for phylogenetic analysis is cited. Many of the squamation and coloration characters were taken from Smith's (1939) revision. Terminology for osteological features follows Oelrich (1956) and Etheridge (1964), and terminology for scale characters follows Smith (1946). Characters used in this study that were not described in previous studies are illustrated and/or described in more detail in a monograph on *Sceloporus* (Wiens and Reeder, 1997).

Osteology

1. Angle of ascent of premaxilla: (0) gradual (40–75°); (1) steep (85–90°) (Montanucci, 1987).
2. Nutritive foramina in maxilla: (0) small or absent; (1) large (diameter exceeds that of largest tooth).
3. Nasal–maxilla relationship: (0) separate; (1) in contact (Montanucci, 1987).
4. Lacrimal: (0) present; (1) absent (Etheridge and de Queiroz, 1988).
5. Anterolateral processes of frontal: (0) exposed; (1) covered by nasals (Etheridge and de Queiroz, 1988).
6. Frontal–postorbital contact: (0) prevented by postfrontal; (1) present (Wiens, 1993*a*).
7. Postfrontal: (0) present; (1) absent (Etheridge and de Queiroz, 1988).
8. Supraorbital bar: (0) absent; (1) present (Montanucci, 1987).
9. Parietal foramen: (0) small, at frontoparietal boundary; (1) large, mostly in parietal (Wiens, 1993*a*).
10. Squamosal–parietal horns: (0) absent; (1) present (Etheridge and de Queiroz, 1988).
11. Jugal: (0) not expanded posteriorly; (1) expanded posteriorly (Montanucci, 1987).
12. Jugal surface: (0) smooth; (1) rugose, with tuberosities (Montanucci, 1987).
13. Ectopterygoid: (0) not expanded; (1) expanded (Montanucci, 1987).
14. Epipterygoid: (0) normal length, attached to parietal dorsally; (1) reduced, attached to prootic dorsally (Etheridge and de Queiroz, 1988).
15. Posterolateral processes of basisphenoid: (0) not extending onto spheno-occipital tubercle; (1) elongate, extending onto spheno-occipital tubercle.
16. Stapedial footplate: (0) not expanded; (1) expanded (modified from Etheridge and de Queiroz, 1988).
17. Scleral ossicle 6: (0) approximately same size as other ossicles; (1) reduced or absent. Data and character from de Queiroz (1982).
18. Scleral ossicle 8: (0) present; (1) absent. Data and character from de Queiroz (1982).
19. Cusps of posterior dentary teeth: (0) normal; (1) expanded.
20. Cusps of posterior dentary teeth: (0) present; (1) absent.
21. Ceratobranchial I: (0) not dorsoventrally flattened; (1) dorsoventrally flattened (Etheridge and de Queiroz, 1988).
22. Ceratobranchial II: (0) not reduced; (1) reduced, much shorter than ceratohyal or ceratobranchial I (Etheridge and de Queiroz, 1988).
23. Retroarticular process of mandible: (0) normal; (1) vertically flattened (Etheridge and de Queiroz, 1988).
24. Meckel's groove: (0) open; (1) fused for some or all of its length (Etheridge and de Queiroz, 1988).
25. Coronoid: (0) not extending to anterior inferior alveolar foramen of the splenial; (1) contacts anterior inferior alveolar foramen.
26. Lateral surface of surangular: (0) smooth; (1) with protuberances and horns (modified from Montanucci, 1987).
27. Mandible: (0) not countersunk; (1) countersunk (Etheridge and de Queiroz, 1988).
28. First pair of cervical ribs on vertebra: (0) four; (1) three; (2) five (Etheridge and de Queiroz, 1988).
29. Terminal cartilages of ribs of vertebrae 5 and 6: (0) hooked, expanded; (1) simple.
30. Thoracic vertebrae: (0) not depressed; (1) depressed (Etheridge and de Queiroz, 1988).
31. Ribs on last presacral vertebra: (0) present; (1) absent (Wiens, 1993*b*).
32. Caudal vertebrae: (0) 25–55; (1) 11–23 (Etheridge and de Queiroz, 1988).
33. Posterior flange on second sacral diapophyses: (0) present; (1) absent.
34. Tail shape in males: (0) cylindrical or depressed; (1) laterally compressed.
35. Caudal autotomy septa: (0) present; (1) absent (Etheridge and de Queiroz, 1988).
36. Number of non-autotomous caudal vertebrae: (0) six to eight; (1) five.
37. Scapular fenestra: (0) present; (1) absent (Etheridge and de Queiroz, 1988).
38. Secondary coracoid fenestra: (0) absent; (1) present.
39. Primary coracoid fenestra: (0) formed nearly 50% in cartilage anteriorly; (1) formed mostly in bone.
40. Supracoracoid foramen: (0) present; (1) absent (Montanucci, 1987).
41. Interclavicle, median process: (0) normal length; (1) reduced, not extending close to sternal fontanelle (Etheridge and de Queiroz, 1988).
42. Sternal fontanelle shape: (0) roughly ovoid; (1) "heart-shaped," narrow posteriorly, wide anteriorly; (2) enlarged, narrow anteriorly, wide posteriorly (Wiens, 1993*a*).

43. Sternum shape: (0) narrow posteriorly (diamond shape); (1) wide anteriorly (pentagonal shape) (Etheridge and de Queiroz, 1988).
44. Sternal ribs: (0) three; (1) two; (2) four (Etheridge and de Queiroz, 1988).
45. Xiphisternal rib connections: (0) two or more; (1) one or none (Etheridge and de Queiroz, 1988).
46. Suprascapula: (0) wide distally (fan-shaped); (1) narrow distally (rectangular) (Etheridge and de Queiroz, 1988).
47. Sternum–xiphisternum relationship: (0) articulating; (1) fused (Wiens, 1993*a*).
48. Clavicular hooks: (0) posterior flange on clavicle absent or not recurved; (1) clavicular flange recurved, hooklike (Etheridge and de Queiroz, 1988).
49. Epipubic cartilage: (0) normal; (1) elongate, extending past level of pubic symphysis (Wiens, 1993*a*).
50. Pubic symphysis: (0) not flat; (1) flat.
51. Hypoischiac foramen: (0) present; (1) absent.
52. Proischiac and epipubic cartilages: (0) separate; (1) fused.
53. Metatarsal lengths: (0) IV > III; (1) III > IV (Wiens, 1993*a*).
54. Phalangeal formula of hand: (0) normal (2-3-4-5-3); (1) reduced (2-3-4-4-2) (Etheridge and de Queiroz, 1988).
55. Phalangeal formula of foot: (0) normal (2-3-4-5-3); (1) reduced (2-3-4-5-2) (Etheridge and de Queiroz, 1988).

Squamation

56. Cephalic scales: (0) smooth; (1) rugose.
57. Rostral scale: (0) wider than internarial distance; (1) equal to or narrower than internarial distance (Wiens, 1993*a*).
58. Rostral–nasal contact: (0) absent (prevented by postrostrals); (1) present (postrostrals separated or absent).
59. Number of postrostrals: (0) six; (1) four; (2) two (Wiens, 1993*a*).
60. Median postrostrals: (0) in contact; (1) separated, rostral contacts internasal (Wiens, 1993*b*).
61. Unpaired median postrostral: (0) absent; (1) present.
62. Supranasals: (0) present; (1) absent (Wiens, 1993*a*).
63. Frontonasals: (0) small or undifferentiated; (1) enlarged (Wiens, 1993*a*). The condition of the frontonasals was assessed based on the size of the posterior row of frontonasal scales, the row of scales in contact with the prefrontals.
64. Median and lateral frontonasals: (0) in contact; (1) separated.
65. Frontal scale: (0) undifferentiated; (1) present (Wiens, 1993*a*).
66. Frontal scale: (0) divided into anterior and posterior scales; (1) fused, single scale (Wiens, 1993*a*).
67. Frontal scale: (0) not divided bilaterally; (1) anterior and/or posterior scales divided along anteroposterior axis.
68. Frontal scale: (0) present as one, two, or three scales; (1) divided into four asymmetric scales, divided along both anteroposterior and mediolateral axes.
69. Frontal–interparietal contact: (0) absent; (1) present.
70. Interparietal: (0) small or absent; (1) greater than or equal to interorbital space (Etheridge and de Queiroz, 1988).
71. Posterior circumorbital rows: (0) two; (1) one (Wiens, 1993*a*).
72. Supraocular–parietal contact: (0) absent (prevented by circumorbitals); (1) present.
73. Supraoculars: (0) normal (≥2 rows of scales between superciliaries and median supraoculars); (1) enlarged (≤1 row of scales between superciliaries and median supraoculars.
74. Superciliaries: (0) four to six; (1) seven to nine (Wiens, 1993*a*).
75. Superciliaries: (0) broadly overlapping; (1) not or barely overlapping (Etheridge and de Queiroz, 1988).
76. First canthal–lorilabial contact: (0) absent; (1) present.
77. Canthal–subnasal fusion: (0) absent; (1) present.
78. Canthals: (0) two; (1) one.
79. Number of lorilabials contacting both subocular and labials: (0) one or more; (1) none (lorilabials in two vertical rows).
80. Maximum height of lorilabial series: (0) two scales high; (1) single row high.
81. Subocular: (0) single; (1) fragmented (Etheridge and de Queiroz, 1988).
82. Labials: (0) not distinctly overlapping; (1) elongate, keeled, and overlapping (Etheridge and de Queiroz, 1988).
83. Labial margin: (0) not dentate; (1) partly to entirely dentate (Montanucci, 1987).
84. Sublabials: (0) first (anteriormost) contacts first infralabial; (1) first sublabial contacts second infralabial; (2) first sublabial posterior to second infralabial (Wiens, 1993*a*).
85. Mental scale: (0) larger than labials; (1) reduced, roughly same size as labials (Wiens, 1993*a*).
86. Mental–sublabial contact: (0) absent; (1) present.
87. Enlarged, keeled chinshields: (0) absent; (1) present (Montanucci, 1987).
88. Second infralabial contacts: (0) one or two sublabials; (1) three sublabials (Wiens, 1993*b*).
89. Tympanum: (0) exposed; (1) covered (Etheridge and de Queiroz, 1988).
90. Preauricular fringe: (0) not reduced dorsally; (1) reduced to few small scales at ventral part of opening (Wiens, 1993*b*).
91. Dorsals: (0) rounded, nonoverlapping; (1) pointed, overlapping (Wiens, 1993*a*).
92. Dorsals: (0) smooth; (1) keeled; (2) heterogeneous: smooth, keeled, and enlarged scales (Etheridge and de Queiroz, 1988).
93. Dorsals: (0) enlarged dorsals in wide band posteriorly (extending laterally to insertion of forelimb); (1) in narrow band restricted to dorsal midline (Wiens, 1993*a*).
94. Median keeled dorsals: (0) keeled dorsals more-

or-less homogeneous in size; (1) keeled dorsals reduced in size medially, one or more rows of larger scales laterally (Wiens, 1993*b*).
95. Posterior lateral dorsals: (0) grade evenly in size into laterals; (1) lateralmost row of dorsals large, strongly keeled, forming angle between dorsum and flanks.
96. Row of enlarged dorsolateral scales: (0) absent; (1) present (Wiens, 1993*b*).
97. Enlarged flank scales: (0) absent; (1) present (Wiens, 1993*b*).
98. Posterior laterals: (0) granular; (1) imbricate.
99. Upper row of lateral abdominal fringe scales: (0) absent; (1) present (Montanucci, 1987).
100. Lower row of lateral abdominal fringe scales: (0) absent; (1) present (Montanucci, 1987).
101. Posterior thigh scales: (0) granular; (1) imbricate.
102. Tibial scales: (0) keeled; (1) all smooth (Wiens, 1993*b*).
103. Gulars: (0) granular or not strongly imbricate; (1) strongly imbricate (Wiens, 1993*a*).
104. Enlarged gulars: (0) absent; (1) present (modified from Montanucci, 1987).
105. Gular fold: (0) present, complete; (1) interrupted medially, remnant laterally; (2) completely absent (Etheridge and de Queiroz, 1988).
106. Ventrals: (0) smooth; (1) keeled (Montanucci, 1987).
107. Postanals: (0) enlarged in males; (1) absent or about same size as surrounding scales.
108. Interpostanals: (0) two; (1) three or more (Wiens, 1993*b*).
109. Preanal scales in females: (0) all smooth; (1) some or all keeled.
110. Femoral pore number: (0) >6 per row; (1) ≤6 per row.
111. Femoral pore rows: (0) continuous, median pores all in contact; (1) discontinuous, some median pores separated by smaller scales (Wiens, 1993*a*).
112. Interfemoral scales: (0) >4; (1) ≤4 (Wiens, 1993*a*).
113. Caudal scales: (0) in distinct transverse rows; (1) heterogeneous, not arranged in transverse rows (Etheridge and de Queiroz, 1988).
114. Male preanal scales: (0) lacking distinct glands; (1) with distinct glands.
115. Deep postfemoral dermal pocket: (0) absent; (1) present.

Coloration

116. Dark collar: (0) absent; (1) dark wedge anterior to insertion of forelimbs; (2) dark spot dorsal to forelimb; (3) wide, black collar, complete dorsally.
117. Distinct white spots on nape: (0) absent; (1) present.
118. "Scalaris" pattern on head: (0) no distinct pattern on head; (1) characteristic color pattern consisting of dark inverted "V" anterior to pineal eye and dark transverse bar over each eye.
119. Black interparietal spot: (0) absent; (1) present (Frost and Etheridge, 1989).
120. Continuous, dark middorsal stripe on tail: (0) absent; (1) present.
121. Dark ventrolateral spots or stripes: (0) absent; (1) present (Wiens, 1993*a*).
122. Dark ventrolateral spots or stripes: (0) single; (1) two spots or stripes.
123. Black transverse stripes on ventral surface of tail: (0) absent; (1) present (Etheridge and de Queiroz, 1988).
124. Male belly patches: (0) absent; (1) present (Etheridge and de Queiroz, 1988).
125. Male belly patches: (0) dark transverse bars; (1) no dark transverse bars.
126. Male belly patches: (0) separate; (1) fused medially.
127. Male belly patches: (0) no distinct dark margins; (1) dark margin on each belly patch.
128. Female belly patches: (0) absent; (1) present.
129. Male gular coloration: (0) absent; (1) reticulate pattern; (2) paired lateral blotches; (3) single blotch or wash.
130. Male dorsal coloration: (0) not bright blue or green; (1) bright blue or green (Wiens, 1993*b*).

Myology

131. Dorsal shank muscle innervation: (0) from interosseous nerve; (1) from peroneal nerve (Etheridge and de Queiroz, 1988). Data from Etheridge and de Queiroz (1988) and Jullien and Renous-Lècuru (1972).
132. Retractor lateralis anterior: (0) anterior fibers not reflected outwards or anteriorly; (1) anterior fibers reflected outwards or posteriorly (Etheridge and de Queiroz, 1988). Data from Arnold (1984).
133. External abdominal oblique: (0) two layers; (1) single layer. Data and character from Blackburn (1978).
134. External abdominal oblique (profundus II): (0) one slip: (1) absent. Data and character from Blackburn (1978).
135. Internal intercostals (between dorsal ribs): (0) present; (1) absent. Data and character from Blackburn (1978).
136. *M. transversus abdominis*: (0) inserts to xiphisternal ribs via fascia; (1) inserts directly to xiphisternal ribs. Data and character from Blackburn (1978).
137. *M. branchiohyoideus*: (0) not expanded; (1) expanded. Data and character from Blackburn (1978).
138. *M. intermandibularis anterior superficialis*: (0) present; (1) absent. Data and character from Blackburn (1978).
139. *M. constrictor colli*: (0) size moderate; (1) reduced in width and thickness. Data and character from Blackburn (1978).

Life History

140. Reproductive mode: (0) oviparous; (1) viviparous. Data from Guillette et al. (1980).

Karyology

141. Number of microchromosomes: (0) 24; (1) 20; (2) 18; (3) 16; (4) 10 (Etheridge and de Queiroz, 1988; Hall, unpubl., *in* Sites et al., 1992). Data from Sites et al. (1992).
142. Number of metacentric (or slightly submetacentric) macrochromosomes: (0) 10; (1) 8; (2) 2 (Hall, unpubl., *in* Sites et al., 1992). Data from Sites et al. (1992).
143. Sex chromosome system: (0) XX/XY, minute Y; (1) $X_1X_1X_2X_2/X_1X_2Y$, Y–autosomal fusion; (2) XY indistinct (Hall, unpubl., *in* Sites et al., 1992). Data from Sites et al. (1992).
144. Secondary constriction near centromere on large microchromosome: (0) absent; (1) present. Data and character from Sites et al. (1992).
145. Em9 mutation: (0) absent; (1) present (Hall, unpubl., *in* Sites et al., 1992). Data from Sites et al. (1992).

Allozymes

146. Aat: (0) allele *c*; (1) allele *e*. Data and character from de Queiroz (1992).
147. General protein locus: (0) slow allele; (1) fast allele. Data and character from Murphy (unpubl., *in* Wiens, 1993*b*).

Behavior

The behavioral characters are based on the extensive comparative database on the aggressive male–male display behaviors of phrynosomatid lizards. A detailed discussion and description of the standard behavioral repertoire is presented in Carpenter (1978). Behavioral data for individual phrynosomatid species were taken from the following published sources: *Callisaurus*, *Cophosaurus*, and *Holbrookia* (Clarke, 1965); *Uma* (Carpenter, 1963); *Phrynosoma* (Lynn, 1965); *Sceloporus* (Carpenter, 1978); *Petrosaurus* and *Urosaurus* (Carpenter, 1962); *Uta* (Carpenter, 1962; Ferguson, 1971). These behavioral studies were all conducted by Carpenter and/or his former students; this "standardization" greatly facilitated the extraction of phylogenetically informative characters from this important behavioral database.

148. Body presentation: (0) in a challenge display, the orientation of the body of the challenging lizard is presented laterally (i.e., perpendicular to the challenged lizard); (1) no lateral presentation.
149. Neck display: (0) dewlap presentation (= ventral expansion of the throat); (1) no dewlap presented or extended.
150. Body compression: (0) during display, the trunk region of the body is laterally compressed; (1) no lateral body compression. Lateral compression of the body increases both the presentation surface area and exposure of ventral color patches (if present).
151. Elevation of body: (0) during display, lizard elevates body off substrate by raising on all four legs; (1) raises on front legs only, supporting only anterior portion of body off substrate; (2) does not raise body off substrate during display.
152. Push-up display: (0) during display, lizard repeatedly performs two-legged push-ups (using front legs only); (1) performs four-legged push-ups (using all four legs); (2) no push-ups performed during display.
153. Confrontation during display: (0) face-off (i.e., challenging males lie parallel to each other); (1) no face-off.
154. Body expansion: (0) body is bloated or expanded during display; (1) no bloating.
155. Tail curling: (0) tail is curled during display; (1) no tail curling.
156. Raising tail: (0) tail raised off substrate during display; (1) tail not raised during display.
157. Body movement: (0) only head and neck moved during display (= head bobs only); (1) head, neck, and anterior portion of body moved during display.

APPENDIX II

Specimens Examined

Specimens were examined by John J. Wiens for morphological data. Institutional abbreviations follow Leviton et al. (1985). Other abbreviations: (D) = dry skeleton, (DS) = dry skull, (DA) = dry skull, alizarin–alcian stained postcranial skeleton, (AA) = alizarin–alcian stained skeleton, REE = Richard E. Etheridge, private collection, JJW = John J. Wiens field series.

Osteological Specimens

Phrynosomatidae.—Callisaurus draconoides: UMMZ 181661, 181662 (D); SDSNH 22314 (D). *Cophosaurus texanus:* UMMZ 149088, 149089 (D); KU 19562, 73394 (D); UMMZ 149090 (D); TNHC 32561 (DA). *Holbrookia maculata:* KU 13921 (D); UMMZ 149077, 149078, 149080 (D); TNHC 18387 (DA). *Phrynosoma asio:* AMNH 74838, 74839 (D); MVZ 137771 (D). *Phrynosoma cornutum:* AMNH 77117 (D); KU 19554 (D); TNHC 4085 (DA); UMMZ 190377 (D). *Phrynosoma douglassii:* KU 13945 (D); TNHC 1175 (DA); UMMZ 149118, 149120 (D). *Phrynosoma modestum:* AMNH 74597 (D); KU 473 (D); TNHC 32468 (DA). *Petrosaurus mearnsi:* CAS 90879, 16544 (DA); KU 61560 (AA), 176009 (DS). *Petrosaurus thalassinus:* CAS 3009 (DA), 3012 (DS). *Sator angustus:* LACM 134749, 134752 (DA). *Sceloporus chrysostictus:* KU 70453 (AA), 74948 (DA). *Sceloporus clarki:* KU 13956, 16439 (D). *Sceloporus cyanogenys:* KU 9124, 13971 (D); TNHC 22559 (DA). *Sceloporus dugesii:* REE 859 (D). *Sceloporus formosus:* KU 71764, 87477 (D). *Sceloporus graciosus:* KU 87521 (AA); SDSNH 57111, 63250, 64450 (D). *Sceloporus grammicus:* KU 182608, 182609 (DA), 182610 (AA); FMNH 98418, 98430 (D). *Sceloporus jarrovii:* KU 13962 (D); TNHC 15332 (DA). *Sceloporus magister:* FMNH 216159 (DS); SDSNH 57112 (D); TNHC 12734 (DA). *Sceloporus malachiticus:* FMNH 31039, 210649 (D); KU 68666, 68667 (D); TNHC 32152 (DA). *Sceloporus merriami:* FMNH 216153 (D); KU 61655 (DA), 128835, 128836 (AA). *Sceloporus mucronatus:* TNHC 32823 (DA). *Sceloporus occidentalis:* KU 68991 (AA), 1898 (D); SDSNH 65175, 65838 (D). *Sceloporus olivaceus:* FMNH 216160 (D); KU 16418 (D); TNHC 32435 (DA). *Sceloporus orcutti:* SDSNH 60416, 60417, 60419 (D); FMNH 216158 (D); TNHC 33501 (D). *Sceloporus poinsetti:* FMNH 216517 (D); KU 9123 (D); TNHC 49930 (DA). *Sceloporus scalaris:* FMNH 98436, 216155 (D); KU 102927 (AA), 102928 (DA); UMMZ 149264 (D). *Sceloporus spinosus:* FMNH 98439, 98440, 216156 (D); MCZ 136350 (D); REE 1183, 1711, 1712 (D); TNHC 30043 (DA). *Sceloporus torquatus:* FMNH 216165 (D); REE 881, 1713, 1761 (D); TNHC 30386 (DA); UMMZ 149266 (D). *Sceloporus undulatus:* JJW 24, 25 (AA); KU 2206, 2210, 20995 (D). *Sceloporus variabilis:* KU 67295 (AA), 187174 (DA); UMMZ 149275 (D). *Sceloporus virgatus:* KU 74454 (AA); SDSNH 63218, 63253, 64544 (D). *Uma notata:* SDSNH 38548, 38552, 64526, 65166 (D). *Urosaurus graciosus:* KU 72740 (DA); LACM 19040, 19066 (DA); SDSNH 63124 (D). *Urosaurus microscutatus:* LACM 128138, 128172 (DA); SDSNH 49912, 66278 (D). *Urosaurus nigricaudus:* KU 78732, 78754 (AA), 78746 (DA); SDSNH 65036 (D). *Urosaurus ornatus:* KU 77868 (DA); SDSNH 63219, 63240, 63245 (D). *Uta palmeri:* CAS 14123, 14124 (DA); KU 91525 (DA). *Uta stansburiana:* KU 194130, 194136 (AA), 7215, 73396 (D).

Crotaphytidae.—Crotaphytus collaris: KU 7202 (D), 21003 (D). *Crotaphytus reticulatus:* KU 147277, 147278 (D). *Gambelia silus:* KU 121755, 121762 (DS). *Gambelia wislizenii:* KU 121776 (DS), 121781 (DS); UMMZ 149100 (D), 190372 (D).

Opluridae.—Chalarodon madagascariensis: KU 187756 (DS); USNM-FS 59443, 59444 (D). *Oplurus fierinensis:* KU 187770 (DS). *Oplurus quadrimaculatus:* USNM-FS 58383, 58678 (D). *Oplurus saxicola:* USNM 59247, 59267 (D).

Polychrotidae.—Anolis frenatus: KU 77668 (D). *Diplolaemus darwini:* KU 160897 (D). *Polychrus marmoratus:* UMMZ 189461 (D).

Tropiduridae.—Leiocephalus carinatus: AMNH 57461 (D); FMNH 22754 (DS). *Leiocephalus loxogrammus:* KU 192293 (D). *Leiocephalus schreibersi:* KU 93358 (D). *Liolaemus chilensis:* FMNH 24023 (D). *Liolaemus elongatus:* KU 161108, 161109 (D). *Liolaemus multiformis:* KU 163537 (D). *Liolaemus simonsii:* AMNH 77625 (D). *Microlophus occipitalis:* KU 142721 (DA). *Microlophus stolzmanni:* MCZ 131769 (D). *Ophryoessoides scapularis:* FMNH 40612 (D). *Phymaturus palluma:* KU 160923, 161972 (D). *Stenocercus huancabambae:* MCZ 18784, 18785 (D). *Uranoscodon superciliaris:* KU 135269 (D).

Specimens Examined for External Characters

Phrynosomatidae.—Callisaurus draconoides: KU 13179, 72115, 72117, 72123, 72126; TNHC 16767, 16768, 18485, 27727, 46163, 33312, 33313. *Cophosaurus texanus:* TNHC 48586, 48588, 48590, 32398, 32399, 32401, 32555, 32559, 32562. *Holbrookia maculata:* TNHC 16940–45, 18390, 18399, 21910, 22488. *Petrosaurus mearnsi:* CAS 90878, 90882; KU 31346, 61561, 90881, 91504, 176008, 176009. *Petrosaurus thalassinus:* CAS 3010, 91100, 91102, 91103; KU 178967, 182075. *Phrynosoma asio:* KU 40388, 40389, 61484; LSUMZ 38460, 38463; TNHC 29768. *Phrynosoma cornutum:* TNHC 1180, 3155, 3365, 3359, 3595, 3616, 4036, 4082, 4143, 31126. *Phrynosoma douglassii:* LSUMZ 22947, 30498–551, TNHC 11654, 11655, 11842. *Phrynosoma modestum:* TNHC 12601, 24717, 30238, 32461, 32463, 32465, 32593, 33179, 48502, 48508. *Sator angustus:* KU 91476, 91477; LACM 134739, 134755, 135475, 135918. *Sceloporus chrysostictus:* KU 171514, 171516, 171518, 171519, 157365, 157367, 157369, 157371, 157372. *Sceloporus clarki:* KU 48578, 48582–84, 48586, 77812, 77821; TNHC 22283, 16779, 16780. *Sceloporus cyanogenys:* TNHC 22552, 22557, 23086, 29979, 30307, 30311, 30318, 30328, 33488, 33489. *Sceloporus dugesii:* AMNH 62313, 136770; KU 67555, 67558, 67559. *Sce-*

loporus formosus: KU 70533, 70534, 101133, 101134. *Sceloporus graciosus:* KU 87530–33, 87535, 87551, 105964, 105966, 105972, 105980. *Sceloporus grammicus:* AMNH 67436–38, 67455; KU 59631, 70515, 87375, 200966; TNHC 32240, 32241. *Sceloporus jarrovii:* AMNH 77238, 77240; KU 51799–802; MCZ 129415, 129416, 20066, 20067. *Sceloporus magister:* TNHC 12855, 12866, 12960, 12963, 12990, 14927, 14931, 14933, 48527. *Sceloporus malachiticus:* KU 62050, 62052, 62053, 62059, 67245, 67246, 67259, 67260, 67266, 184216. *Sceloporus merriami:* TNHC 32864, 32869, 32870, 32879, 32882, 32883, 32897, 49187, 49913, 49916. *Sceloporus mucronatus:* TNHC 32828–30; AMNH 98060, 102784, 106461, 106863, 114569, 117858. *Sceloporus occidentalis:* TNHC 19175–77, 32624–26, 33517; KU 192064, 192065. *Sceloporus olivaceus:* TNHC 32434, 42261, 47241, 46354, 46355, 50038, 50043, 50044, 50434, 50435. *Sceloporus orcutti:* AMNH 20645, 60510, 60531, 64333, 65425, 75597 TNHC 33502, 35645, 35646, 35648. *Sceloporus poinsetti:* TNHC 32430–33, 32585, 49226, 49228, 49231, 49232, 49803. *Sceloporus scalaris:* AMNH 15522, 15524, 15525, 18485; KU 63710, 63711, 47408, 47410. *Sceloporus spinosus:* TNHC 30005, 30046, 30053, 30085, 30125, 30173, 30201, 30343, 30344, 30396. *Sceloporus taeniocnemis:* AMNH 98055, 98056, 90872, 90873, 90876, 90877, 99139, 102790, 113394, 114825. *Sceloporus torquatus:* AMNH 88855, 109052, 129220, 129221, 118380, 118579; TNHC 30402, 30420, 30422, 30472. *Sceloporus undulatus:* AMNH 31930, 43275, 43278, 109238; TNHC 21766, 28076, 32436, 32438, 33474, 42279. *Sceloporus variabilis:* AMNH 107695, 107696, 10708, 10709; TNHC 28193, 29992, 30002, 32807, 32810, 32618, 32816, 32818. *Sceloporus virgatus:* KU 49531, 74453, 74455, 74456, 74458–60, 74462, 74463, 74468. *Uma notata:* KU 61507, 154465; TNHC 25526, 25527, 33314–16. *Urosaurus graciosus:* KU 72733, 72739, 72741, 72742; LACM 19038, 19042, 19076, 19083. *Urosaurus microscutatus:* KU 91505, 91507; LACM 128116, 128137, 128157, 128174; SDSNH 49912, 49923, 49924, 55384. *Urosaurus nigricaudus:* 78700–02, 78704–08, 78710, 91508. *Urosaurus ornatus:* TNHC 31101, 31132, 31135, 31136, 39035, 39041, 39050, 39074, 39077, 39085. *Uta palmeri:* CAS 14128, 14130, 14131, 14422; KU 91514, 91516, 91523, 91527, 91528. *Uta stansburiana:* TNHC 32908, 33325, 33329, 33334, 48662.

Crotaphytidae.—Crotaphytus collaris: KU 182266, 182272. *Crotaphytus reticulatus:* KU 121487, 121491. *Gambelia silus:* KU 121542, 121555. *Gambelia wislizenii:* KU 121688, 121689.

Opluridae.—Chalarodon madagascariensis: KU 187757, 187765. *Oplurus cuvieri:* KU 187767, 187768. *Oplurus fierinensis:* KU 187769, 187770, 187772. *Oplurus saxicola:* FMNH 72656, 72693.

Polychrotidae.—Chaemaelinorops barbouri: KU 245646. *Polychrus marmoratus:* KU 127224, 128122. *Pristidactylus scapulatus:* KU 160888. *Leiosaurus catamarcensis:* KU 160900.

Tropiduridae.—Leiocephalus carinatus: KU 242798, 242804. *Liolaemus archeforus:* KU 206472, 206476. *Liolaemus periglacialis:* KU 190412, 190413. *Phymaturus patagonicus:* KU 160925, 160926, 160931. *Plesiomicrolophus koepckeorum:* KU 163604, 212665. *Stenocercus apurimacus:* KU 134261.

APPENDIX III

Non-DNA Data Matrix

The non-DNA data matrix for phylogenetic analysis of the Phrynosomatidae is provided. Letter codes for character states correspond to the frequency of the putative derived conditions (a = 0–3%; b = 4–7%; c = 8–11%; d = 12–15%; e = 16–19%; f = 20–23%; g = 24–27%; h = 28–31%; i = 32–35%; j = 36–39%; k = 40–43%; l = 44–47%; m = 48–51%; n = 52–55%; o = 56–59%; p = 60–63%; q = 64–67%; r = 68–71%; s = 72–75%; t = 76–79%; u = 80–83%; v = 84–87%; w = 88–91%; x = 92–95%; y = 96–100%). All multistate characters (28, 42, 44, 59, 84, 105, 116, 129, 141–143, 151, 152) are unordered. Characters 7, 15, 19, 24, 25, 27–29, 35, 37, 38, 44, 51, 52, 57, 59, 63–65, 67, 74, 75, 79–81, 83, 86, 91–93, 102, 103, 105, 107, 108, 111, 117, 122, 125–127, 133–139, and 143–157 are not polarized. Abbreviations are as follow: HYPAN = hypothetical ancestor; CADRA = *Callisaurus draconoides*; COTEX = *Cophosaurus texanus*; HOMAC = *Holbrookia maculata*; PEMEA = *Petrosaurus mearnsi*; PETHA = *Petrosaurus thalassinus*; PHASI = *Phrynosoma asio*; PHCOR = *Phrynosoma cornutum*; PHDOU = *Phrynosoma douglassii*; PHMOD = *Phrynosoma modestum*; SAANG = *Sator angustus*; SAGRA = *Sator grandaevus*; SCAEN = *Sceloporus aeneus*; SCCHR = *Sceloporus chrysostictus*; SCCLA = *Sceloporus clarki*; SCCOU = *Sceloporus couchii*; SCCOZ = *Sceloporus cozumelae*; SCCYA = *Sceloporus cyanogenys*; SCDUG = *Sceloporus dugesii*; SCFOR = *Sceloporus formosus*; SCGAD = *Sceloporus gadoviae*; SCGRC = *Sceloporus graciosus*; SCGRM = *Sceloporus grammicus*; SCJAL = *Sceloporus jalapae*; SCJAR = *Sceloporus jarrovii*; SCMAC = *Sceloporus maculosus*; SCMAG = *Sceloporus magister*; SCMAL = *Sceloporus malachiticus*; SCMER = *Sceloporus merriami*; SCMUC = *Sceloporus mucronatus*; SCNEL = *Sceloporus nelsoni*; SCOCC = *Sceloporus occidentalis*; SCOLI = *Sceloporus olivaceus*; SCORC = *Sceloporus orcutti*; SCPAR = *Sceloporus parvus*; SCPIC = *Sceloporus pictus*; SCPOI = *Sceloporus poinsetti*; SCPYR = *Sceloporus pyrocephalus*; SCSCA = *Sceloporus scalaris*; SCSIN = *Sceloporus siniferus*; SCSPI = *Sceloporus spinosus*; SCSQU = *Sceloporus squamosus*; SCTAE = *Sceloporus taeniocnemis*; SCTOR = *Sceloporus torquatus*; SCUND = *Sceloporus undulatus*; SCUTI = *Sceloporus utiformis*; SCVAR = *Sceloporus variabilis*; SCVIR = *Sceloporus virgatus*; UMNOT = *Uma notata*; URGRA = *Urosaurus graciosus*; URMIC = *Urosaurus microscutatus*; URNIG = *Urosaurus nigricaudus*; URORN = *Urosaurus ornatus*; UTPAL = *Uta palmeri*; UTSTA = *Uta stansburiana*.

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          1         2         3         4         5         6         7         8
     1    0         0         0         0         0         0         0         0
HYPAN aaaaaaaaaaaaaaaaaaaaaaaa?a?0aaaaaaaa??aaa0a0aaaaaaa?aaaaaa1aaaa?aaaaaaaaaaaaaaa
           y       y  y    y  2y     y        2      y     y 2  y y y      yy   yy
CADRA aaayy?yaqaaaaayyya?yaaaaaau2aaaaaaaaaayay1a0aa?aaayyaaaaka??g?a?g????y??aaa??aa?
COTEX amayy?yayaaaaayyyaaaaaaaaay2aaaaaaaaaayay1a0aaaaagaaaaaka??y?a?y????y??aaa??aaa
HOMAC afayy?yayaaaaayyyaaaaaaaaay2gaaaaaaaaayay1a0famaaaiaaaaaka??w?a?l????y??afa??aaa
PEMEA aaaaaaaayaaaaaaa??aaaaaaaaa0myaaaaaayayaa0a2aaaaqaaayaaaaa0aaaa?yaaahyyaayayaaaa
PETHA aaaaaaaayaaaaaaaaaaaaaaaaa0ayaaaaaayayaa0a2aaaayaaayaaaaa0aaaa?yaiaayyaayayeaaa
PHASI aaayy?yyayyaaqyayy?yy?yayya0aaayaay?yayiy2y0yyaaayy?ayyyya??f?a?a????a????y?????
                                  1
PHCOR yayyy?yyayyyyyya???yyyyayya2yaqyyay?yayyy2y1yyaaayyyayyyya??d?a?a????a????y?????
PHDOU aaayy?yyayysgyyayy?yyyyayaa0yayyqay?yayay2y0yyaaayyyayyyya??w?a?a????a????y?????
PHMOD yayyy?yyayyyyyqyyy?yyyyayya0yyyyyay?yaymy2y1yyaaayyyayyyya??q?a?a????a????y?????
                                  2
SAANG aaaaaaaaaaaaaaa???aaaaaaaag0aaaaayaayayaa1a0aayyaaaaaaaaaaa0aakyayyaaayyeaaayaaaa
SAGRA aaaaaaaaaaaaaaaaaaaaaaaaaaa0aaaaaaaayayaa1a0aayyaaaaaaaaaa0aeeyayuaaeyyaaaayaaaa
SCAEN akaaggaayaaaaasa??aaaaaaaaa1aaaaaaaaaiyaa1a0aaayaayaaaayaa2aaayayaaayyadaaaaarya
SCCHR aaaaamaayaaaaaya??aaaaaaaaf1aaaaaaaaamyaa1a0aayyaaaaaaayaa2aaayuyayaayacwwayyacw
SCCLA ayaaamaayaaaaaya??aaaaaaaaa0?aaaaiaaaayaa1a0aa?yaaaaaa?aaa1acayayaaamyayyaaaacya
SCCOU aaaaquaayaaaaaaa??aaaaaaaaa0aaaaaaaayayaa1a0eayyaaaaaaaaaa1acaydyawacyafayayyaac
SCCOZ aaaamsaayaaaaaaa??aaaaaaaac0aaaamaaaamyaa1a0aayyaamaaaauaa2afjyuyaqacyahawayyaau
SCCYA aaaaiaaayaaaaaaa??aaaaaaaaa0aaaaaaaaaiyaa1a0aaayaaaaaaaaaa1aaayayacacyaaaaafaaya
SCDUG ayaaaaaayaaaaaaa??aa??aaaa?0?aaaaaa?aayaa1a0aaay????a??yaa2auaygyaaakyaaaaaaaaka
SCFOR ayaaaaaayaaaaaya??aaaaaaaaa0aaaaaaaaamyaa1a0aayyaaaaaaaaaa1aaayayaaayyaaaaaaaqa
                                  1
SCGAD ayaakgaayaaaaaaa??auaaayaaa0aaaaayayaayaa1a1aayyaaaaaaaaaa1aaayayaaalyaaaqaaaasa
SCGRC amaaqaaayaaaaaia??aaaaaaaaa0yaaaaaaaayaa1a0aamyaaiaaaaaaa1aaayayaaayyacaaakaawa
SCGRM apaaaaaayaaaaaa???aaaaaaaaa0aaaaaqaaaayaa1a0aayyaakaaaaaaa1aaayayaaapycaaaaccaya
SCJAL aaaayaaayaaaaa?a???y??aaaaa??????a?????????????????????aay???yycyacaiyaaaaasaaac
SCJAR amaaaaaayaaaaaaaaaaaaaaaaa0aaaaaaaaaayaa1a0aayyaamaaaaaaa1aaayayacacyaaacaaaaya
SCMAC ????????????????????????????????a?????????????????????aay2yayyayaaapyafaaawaaaa
SCMAG aiaaaaaayaaaayaaaaaaaaaaaa0aaaaaaaaaayaa1a0aaiyiaqaaaaaaa1aaayayacawyaysaaqaaya
SCMAL apaakaaayaaaaaua??aaaaaaaaa0maaaaaaakayaa1a0aaayaaaaaaaaaa1aaayayaaauyafagaaayja
```

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                1         2         3         4         5         6         7         8
        1       0         0         0         0         0         0         0         0
SCMER   amaayaaayaaaaaaa???yaaaaaaa0aaaaaaaaaayaa1a0aayyaagaaaaaaa1aaayayccacypaaaayhaaa
SCMUC   ayaaaaaayaaaaaaa??aaaaaaaaa0aaaaaaaaaayaa1a0aayyaaaaaaaaaa1aaayayafaayaaaaacaasa
SCNEL   aiaaaaaayaaaaaaa??aaaaaaaaa0aayaayayaayaa1a0aayyaamaaaaaah1gkkyayaaayyavaaayyaya
SCOCC   ayaaaaaayaaaaaqaaaaaaaaaaaa0aaaaaaaaaayaa1a0aayyaaaaaaaaaa1acaygyccgqyaaaaaaaaya
SCOLI   aaaaaaaayaaaaaya??aaaaaaaaa0aaaaaaaaaayaa1a0aayyaaiaaaaaaa1aaaycyaaapyaaccaaaara
SCORC   auaafaaayaaaaayaaaaaaaaaaaa0aaaaaaagfayaa1a0aayyaaaaaaaaaa1aaayayaaaryaycaawaaya
SCPAR   aaaayaaayaaaaaaa??aaaaaaaaa0aaaaaaaaa?yaa1a0aayyaaaaaaaaaa1cacyayahffyaiayajaaac
SCPIC   avaaadaayaaaaaaa??aaaaaaaaa0akaaaaamygyaa1a0aayyaagaaaaaaa1aaayayaaayyaaaaaaayua
SCPOI   aaaaaaaaqaaaaaya??aaaaaaaaa0aaaaaaaaiiyaa1a0aayyaaiaaaaaaa1arayayaoaayaaaaacaawa
SCPYR   akaafqaayaaaaaka??aaaaaaqaa0aaaaayaygfyaa1a0aayyaakaaaadaa1aaayayaaayyadkaayyama
SCSCA   amaaiiaauaaaaay???aaaaaaaaa1aaaakaaaamyaa1a0aagyaayaaaayaa2aaayeyaaayyaaaaddpya
SCSIN   aaayayaayaaaaaaa??yaaaayaaa0yaaaaaamymaaa1a0aayyaaaaaaakaa2acayayaytayaaccaaaaaw
SCSPI   amaaakaayaaaaaya??aaaaaaaaa0aaaaaaaaaayaa1a0aamyaaraaaaaaa1aaaydyaaawyacmaacaaya
SCSQU   aaayayaayaaaaaaa??yaaaayaaa0yaaaaaamyaaaa1a0aayyaamaaaayaa2aaaydyayydyaddaaaayay
                                  1
SCTAE   aaaayaaayaaaaay???aaaaaa?a?0?aaaaaaayayaa1a0aa?yaaa?a??aaa1aaayyyaaawyadaaaaaaua
SCTOR   aiaaaeaayaaaaama??aaaaaaaaa0aeaaeaaaeayaa1a0aaiyfauaaaaaaa1aoaydyacaryaacaaaaaya
SCUND   ayaaaaaayaaaaaya??aaaaaaaaa0aaaaaaafaayaa1a0aaqyaamaaaacaa1aaayfyaaapyaaaaaaaara
SCUTI   aaaaakaauaaaaaa???aaaaaaaaa0aaaaaaaiyayaa1a0yaayaaaaaayaa0adayayavkoyadayaaaaha
                                        2
SCVAR   aaaaamaaqaaaaama??aaaaaaaaa0aaaaaaaaaayaa1a0aamyaaaaaayaa1aaaywyayaayaeanaicaeg
SCVIR   ayaaayaayaaaaaya??aaaaaaaaa0aaaaaaaaaayaa1a0aaiyaayaaaaaaa1aaaymyacawyaaaaaaaaya
UMNOT   aaayy?yaqaaaaayayaaaaaaaay2aaaaaaaaaayay1a0aaaaaaaaaaava??h?a?d????r???aa??da?
URAUR   aaaaayaayaaaaaaa??aaaayayaa0aaaaaaayayaa1a0aayyaaaaaaaaa2aayyayaaamyyaaaaaaaj
URBIC   aaaaayaayaaaaaa??aaaaaaiad0aasaaaayayma1a1aayyaagaaaaaa2ucyyaysggayyaaaaaaac
URCLA   aaaagyaayaaaaaaaaaaaaayaaa0aamaaaayayaa1a0aayyaaaaaaaaa2fayyayaaaqyycaaaaaaaa
URGAD   aaaamyaayaaaaaaa??aaaaaaaaa0aaaaaaayayaa1a1aayyaaaaaaaaa2yayyfyyaakyyaaaaaaaar
URGRA   aaaaayaayaaaaaaaaaaaaaaaaa0aaaaaaayayaa1a0aayyaaiaaaaaa0aavyayaaajyyaaaaaaas
URLAH   aaaaypaayaaaaaaa??aaaaaaaaa0aagaaaayymyaa1a0aayyaaaaaaaaa2yayyayyaayyyaaaaaaam
URMIC   aaaaymaayaaaaaaaaaaaaaaaaa0iaaaaaayayaa1a0aayyaaaaaaaac2u?wyayyaafyyaaaaaaah
                                          1
URNIG   aaaayqaayaaaaa?a??aaaaaaaaa0aaaaaaayayaa1a1aayyaaaaaaaac2yayyhyyaafyyaaaaaaad
URORN   aaaaiyaayaaaaaaaaaaaasaaa0maiaaaaayayaa1a0aayyaagaaaaaac2iayyayaaaryycaaafaaaa
UTPAL   aaaayaaayaaaaaa??aaaaaaaaf0aaaaaaaiyayaa0a0aaaiaaaaaaaaaa0aaayayaaaayyaaaamaaac
UTSTA   aaaayaaayaaaaaaaaaaaaaaaaa0aaaaaayyayaa0a0iaayaaaaaaaaa0acayayaaaayyaaaaeaaaa


                        1         1         1         1         1         1         1
        8       9       0         1         2         3         4         5         5
        1       0       0         0         0         0         0         0         7
HYPAN   aaa0aaaaaaa0aaaaaaaaa?aa0aa?aaaaaaa0?aaaa?aa???a1aaa???????a00??????????????
        y y  y    y2y         y 2 y   y
CADRA   aya2yaa?aaa0???aaaaaayca0aajaavaaaa1caaavyyyyaaa3ayyaaayayya10???0?0000001001
COTEX   aya2yaa?y?a0???aaaaaayaa0aayaapaaaa0aaaaryyyyaaa1ayyaaayayya10???1?0000001001
HOMAC   aya2yaa?y?a0???aaaaaafaa0aayaaaaaaa0aaaayyaa???a0ayyaaayayya10???1?0000001101
PEMEA   aaa0aaaaaaa0???aaaaaaaaa0aayaaaaaaq3eaaaa?dyaaaa1ay????????a10??????001011111
PETHA   aaa0aaaaaaa0???aaaaaaaaa0aayaamaaaa3daaaa?aa???a3ayaaaaaaaaa10??????????????
PHASI   yau2yay?aa?2???yyayyaaay0yayyayayaa0aaaaa?aa???a0ay????????a10??????????????
PHCOR   yay2yay?aa?2???yyayyaaay0fy?iayayaa0aaaaa?aa???a0ay?yyyyyaaa10?????1112211110
PHDOU   yaw2yay?aa?2???yyayaaaaa0aaqaayiyaa0aaaaa?aa???a1ay?yyyyyaay10?????1112211110
PHMOD   yay2yay?y?a2???yyaaaaaaa0aayaayyyaa0aaaaa?aa???a0ay????????a10?????1112211110
SAANG   aaa0aaaaaaa1aaaaaaaaaaya2aaaaayaaaa1iaaaa?ayyaaa0aa????????a??????????????????
                                                  1
SAGRA   aaa0aaaaaaa1aaaaaaaaaaya1aiaaaaaaaaa1eaaaa?aa???a0aa????????a10??????????????
SCAEN   aaa0aaaaaay1?aaaayaaaaya2aaaaaayaaa1akaoa?ayaaaa1aa????????y50000??0001001111
SCCHR   aaa0aaauaay1aayaayayaaya1aaaaaaaaaa2aaaaa?aa???a0aa????????a10010??0001011111
SCCLA   aaa0acaaaay1?aaaayaayaya2aaeaaaaaaa1caaaa?ayauyy3?a?aaaaaaaa22001??0001001111
SCCOU   aaa0aaacaay1aaaaaaaaaaya1aaeaaaaaay1aaaaa?ayaaya1aa????????a10010??0001001111
SCCOZ   aaa0aaataay1aayaayaaaaya1aaaaaaaaay2paaaa?aa???a0aa????????a10010??0001011111
SCCYA   aaa0aaaaaar1?aaaayaayaya2aaaaaaaaaa3yaaaa?ayaaye3ya?aaaaaaay30100???????????
SCDUG   aaa0aaaaaaa1?aaaayaay?ya2aamaaaaaaa3yaaaa?ayaaya3aa????????y30100??0000001111
```

```
                                1         1         1         1         1         1         1
          8         9           0         1         2         3         4         5         5
          1         0           0         0         0         0         0         0         7
SCFOR     aaa0aaaaaay1?aaaayaayaya2aaaaaaaaaa1aaaaa?ayaaya3ya????????y50200??0000011111
SCGAD     aaa0aaaaaay1?aaaayaaaaya2aqmaaaqaay1aaaaa?ayayya1aa????????a10000???????????
SCGRC     aaa0acaaaay1?aaaayaaaaya2aaaaaaaaaa1aaaaa?ayaaym1aa????????a20200??0000001111
SCGRM     aaa0aaaaaay1?aaaayaa?aya2aahaaaaaaa1aaaaa?ayaaya3fa????????y??100??0001001111
SCJAL     aaa0aaaaaay1?aaaayaaaaya2aaaaaayaaa1aaaaa?ayaaua1aa????????a10000??0000111111
SCJAR     aaa0aaaaaap1?aaaayaayaya2aapaaaaaaa3waaaa?amaamm0aa?aaaaaaay30100??0001001111
SCMAC     aaa1aaaaaay1?aaaayaaaaya2aoiaaayaaylmaaaa?ayaayi1aa????????a20000???0001?1111
SCMAG     aaa0ayaaaay1?aaaayaayaya2aaaaaaaaya1aaaaa?ayapya3aa?aaaaaaaa41?00??0001001111
SCMAL     aaa0cfaaaay1?aaaayaayaya2aaaaaaaaoa1aaaaa?ayaaya3aa????????y50200???????????
SCMER     aaa1aaaaaaa1aaaaaaaaaa?a1aaeaaayaaa1aaaaa?fyaaya1aa????????a13000??0001101111
SCMUC     aaa0aaaaaay1?aaaayaayaya2aaiaaaaaaa3oaaaa?ayaqqm3aa????????y30100??0001001111
SCNEL     aaa0aaaaaay1?aaaayaayaya2ay?aaaaaaa1aayaa?ayayya1aa????????a10000??0000101111
SCOCC     aaa0aaaaaay1?aaaayaayaya2aagaaaaaaa0aaaaa?ayaayu3aa????????a50200??0001001111
SCOLI     aaa0acaaaay1?aaaayaayaya2aaaaaaaaya0faaaa?ayaaid2aa????????a50200??0?01001111
SCORC     aaa0aaaaaay0?aaaayaayaya2aaaaaaaaya1haaaa?ayamam3?a????????a10000??0001001111
                      1
SCPAR     aaa0aaacaay1aaaaaaaaaaya1aaaaaayafy?aaaaa?auaaaa1aa????????a10010??0001001111
SCPIC     aaa0aaaaaay1?aaaayaa?aya2aaaaaayaaa1aaaaa?ayaaua1aa????????a30102???0010?1111
SCPOI     aaa0acaaaay1?aaaayaayaya2aqyaaaaaaa3taaaa?ayaayv3aa????????y30100??0001000111
SCPYR     aaa0aaaaaay1?aaaayaayaya2ay?aaaaaaa1aayaa?ayyysy1aa????????a11000??0000101111
SCSCA     aaa0aaaaaay1?aaaayaaaaya2aaaaaayaaa1awaga?ayaaaa0aa????????a50000??0001001111
                                                                1
SCSIN     aaa0aaaaamy1aayaayaayaya2alayyaaaaa0aaaaa?aa???a0aa????????a10000??0001001111
                                          2
SCSPI     aaa0amaaaay1?aaaayaayaya2aaeaaaaaya1faaaa?ayaaua3aa????????a50200??0001001111
SCSQU     aaa0adaaaay1aayaayaayaya2apayyaaaaa0daaaa?aa???a0aa????????a?????????????????
SCTAE     aaa0acaaaay1?aaaayaay?ya2aafaaaaaaa1aaaaa?ayaayf3ya????????y50200???????????
SCTOR     aaa0ataaaay1?aaaayaayaya2aaaaaafaaa3uaaaa?ayaaya3aaa???????y30100??0001000111
SCUND     aaa0aaaaaay1?aaaayaayaya2aagaaagaaa1aaaaa?ayaaym2aa????????a50200??0001001111
SCUTI     aaa0aaaaayy1aayaaaaaaaya2afgyaaaaaa2daaaa?oa???a1aa????????a10000??0000111111
SCVAR     aaa0aaayaay1aayaayaaaaya1aaaaaaaaay2gaaaa?ayaayk1aa????????a10010??0001001111
SCVIR     aaa0caaaaay1?acaayaayaya2aaaaaajaaa0aaaaa?aa???a2aa????????a50200???????????
UMNOT     aya2yaa?aaa0???aaaaa?yaa0aamaayaaaa0aaaayaya???a1ayyaaayaaaa10???0?0000001111
URAUR     aaa0aaaaaaa1yy?waaaaayaa0aaaaaaaaaa1aaaaa?adayai0ya????????a10?????????????
URBIC     aaa0aaauaya1yy?yyaaaaaaa0aaraaaaaaa0aaaaa?ayayaa0aa????????a10?????????????
URCLA     aaa0aaafaaa1yy?yyaaaaaaa0aaaaaaaaaa1aaaaa?aa???a0ya????????a10?????????????
URGAD     aaa0aaawawa1ya?yyaaaaaaa0advaaaaaaa0aaaaa?ayayaa0aa????????a10?????????????
URGRA     aaa0aaaaaaa1ya?yaaaaaaaa0aaaaaaaaaa1aaaaa?ayaaaa0aa????????a10????00000101111
URLAH     aaa0aaaaaaa1ya?aaaaaaaaa0aaiaaaaaaa1daaaa?ayagaa0aa????????a10????0??????????
URMIC     aaa0aaaaaaa1ya?aaaaaaaaa0aaaaaaaaaa1laaaa?ayafaa3aa????????a10????1????1?????
URNIG     aaa0aaaaaaa1ya?aaaaaaaaa0aadaaaaaaa1aaaaa?ayahka0aa????????a10????1????1?????
URORN     aaa0aaaaaaa1yy?yfaaaaaca0aaaaaaaaaa1aaaaa?ayakaa3aa?aaaaaaaa10?????0000101111
UTPAL     aaa1aaaaaaa1aaaaaaaaaaaa0aaaaaaaaaa0raaauaaa???a3yy????????a100?????????????
UTSTA     aaa1aaaaaaa1aaaaaaaaaaaa0aaaaaaaaaa0laaayaaa???a3ayaaaaaaaaa100????0000001111
```

APPENDIX IV

Apomorphy List from the Combined Analysis

Apomorphies supporting the phylogeny from the combined analysis of the DNA and non-DNA data (Fig. 5) are listed. Character state transformations under ACCTRAN and DELTRAN optimizations are given. For non-DNA characters, the number in parentheses is the weight of that derived character state transformation along a given branch. Apomorphies in **bold** were unambiguously placed under both optimization routines. DNA character numbers (= nucleotide positions) correspond to the DNA sequence alignment given in Reeder (1995).

Branch 1 (Phrynosomatidae).—ACCTRAN: 5.y (1.00), 9.q (0.67), **39.y** (1.00), 59.0 (1.00), 70.r (0.71), 71.y (1.00), 76.k (0.42), **131.y** (1.00), **141.1** (1.00), **113.T**, **227.A**, **319.T**, 345.T, 403.T, **503.A**, **537.A**, **538.C**, **561.C**, **592.A**. DELTRAN: **39.y** (1.00), **131.y** (1.00), **141.1** (1.00), **113.T**, **227.A**, **319.T**, **503.A**, **537.A**, **538.C**, **561.C**, **592.A**.

Branch 2.—ACCTRAN: **4.y** (1.00), **7.y** (1.00), **15.y** (1.00), **17.y** (1.00), **41.y** (1.00), 42.1 (1.00), 51.i (0.33), **57.v** (0.88), **61.h** (0.29), **84.2** (1.00), **85.y** (1.00), **108.m** (0.50), **111.y** (1.00), 125.y (1.00), 132.y (1.00), **136.y** (1.00), **115.A**, **167.T**, 168.T, 180.T, **183.T**, 190.T, **256.A**, **314.A**, **359.T**, **497.G**, **505.C**, 531.A, 551.C. DELTRAN: **4.y** (1.00), 5.y (1.00), **7.y** (1.00), **15.y** (1.00), **17.y** (1.00), **41.y** (1.00), **57.k** (0.42), **61.f** (0.21), **84.2** (1.00), **85.y** (1.00), **108.m** (0.50), **111.v** (0.88), **136.y** (1.00), **115.A**, 124.A, **167.T**, **183.T**, **256.A**, **314.A**, **359.T**, 403.T, **497.G**, **505.C**.

Branch 3 (sand lizards).—ACCTRAN: **27.y** (1.00), **28.2** (1.00), **37.a** (1.00), **82.y** (1.00), **102.y** (1.00), **121.v** (0.88), **123.y** (1.00), **188.T**, **304.T**, 345.C, **400.T**, **407.T**, **495.–**, **608.T**, **610.T**. DELTRAN: 9.q (0.67), **27.u** (0.83), **28.2** (1.00), **37.a** (1.00), 42.1 (1.00), 61.g (0.04), 70.r (0.71), **82.y** (1.00), **102.y** (1.00), **121.v** (0.88), **123.y** (1.00), 132.y (1.00), **188.T**, **304.T**, **400.T**, **407.T**, **495.–**, 531.A, **608.T**, **610.T**.

Branch 4.—ACCTRAN: **16.y** (1.00), 57.k (0.46), **65.g** (0.13), **70.y** (0.29), 111.v (0.13), **122.y** (1.00), 124.y (1.00), **138.y** (1.00), **139.y** (1.00), 155.0 (1.00), **156.0** (1.00), 112.T, 121.T, 228.A, 327.T, **443.C**, 538.A. DELTRAN: **16.y** (1.00), 51.g (0.25), **65.g** (0.13), **70.y** (0.29), **122.y** (1.00), 125.y (1.00), **138.y** (1.00), **139.y** (1.00), **156.0** (1.00), **443.C**, 551.C.

Branch 5 (earless lizards).—ACCTRAN: **2.f** (0.21), **9.y** (0.33), **61.w** (0.63), **65.l** (0.21), **89.y** (1.00), **108.y** (0.50), **111.p** (0.25), **146.1** (1.00), **57.C**, 166.T, **167.A**, 180.A, **188.C**. DELTRAN: **2.f** (0.21), **9.y** (0.33), 27.y (0.17), **61.w** (0.67), **65.l** (0.21), **89.y** (1.00), **108.y** (0.50), **111.p** (0.25), **146.1** (1.00), **57.C**, **167.A**, **188.C**.

Branch 6 (*Phrynosoma*).—ACCTRAN: **8.y** (1.00), 9.a (0.67), **10.y** (1.00), **11.y** (1.00), **14.q** (0.67), **18.y** (1.00), **20.y** (1.00), **21.y** (1.00), 22.y (1.00), **23.y** (1.00), **25.y** (1.00), 26.y (1.00), **32.y** (1.00), **35.y** (1.00), 40.i (0.33), **42.2** (1.00), **43.y** (1.00), **45.y** (1.00), **46.y** (1.00), **50.y** (1.00), **51.y** (0.67), 52.y (1.00), **54.y** (1.00), **55.y** (1.00), **56.y** (1.00), **57.y** (0.13), **65.a** (0.13), 70.a (71), **75.y** (1.00), **81.y** (1.00), **83.u** (0.83), **87.y** (1.00), **92.2** (1.00), **96.y** (1.00), **97.y** (1.00), **99.y** (1.00), **108.y** (0.50), **113.y** (1.00), 129.0 (1.00), 133.y (1.00), 134.y (1.00), 135.y (1.00), 137.y (1.00), 148.1 (1.00), 149.1 (1.00), 150.1 (1.00), 152.2 (1.00), 153.1 (1.00), 157.0 (1.00), **12.C**, **99.C**, **166.C**, **168.C**, **180.C**, 190.C, 191.T, 508.C, **668.A**. DELTRAN: **8.y** (1.00), **10.y** (1.00), **11.y** (1.00), **14.q** (0.67), **18.y** (1.00), **20.y** (1.00), **21.y** (1.00), **23.y** (1.00), **25.y** (1.00), **32.y** (1.00), **35.y** (1.00), **42.2** (1.00), **43.y** (1.00), **45.y** (1.00), **46.y** (1.00), **50.y** (1.00), **51.y** (1.00), **54.y** (1.00), **55.y** (1.00), **56.y** (1.00), **57.y** (0.58), **65.a** (0.13), **75.y** (1.00), **81.y** (1.00), **83.u** (0.83), **87.y** (1.00), **92.2** (1.00), **96.y** (1.00), **97.y** (1.00), **99.y** (1.00), **108.q** (0.17), 111.y (0.13), **113.y** (1.00), **12.C**, **99.C**, **166.C**, **168.C**, **180.C**, **668.A**.

Branch 7.—ACCTRAN: **12.s** (0.75), **13.g** (0.25), **14.y** (0.33), **29.y** (1.00), **31.y** (1.00), **33.q** (0.67), 61.q (0.38), **83.w** (0.08), 112.i (0.33), **57.C**, **121.C**, **222.A**, **232.C**, 318.T, **319.A**, 399.T, **446.A**, 540.A, 666.A. DELTRAN: **12.s** (0.75), **13.g** (0.25), **14.y** (0.33), 22.y (1.00), **29.y** (1.00), **31.q** (0.67), **33.q** (0.67), 52.y (1.00), **83.w** (0.08), 133.y (1.00), 134.y (1.00), 135.y (1.00), 137.y (1.00), 148.1 (1.00), 149.1 (1.00), 150.1 (1.00), 152.2 (1.00), 153.1 (1.00), 157.0 (1.00), **57.C**, **121.C**, **222.A**, **232.C**, **319.A**, 345.T, **446.A**, 531.A.

Branch 8.—ACCTRAN: **1.y** (1.00), **3.y** (1.00), **12.y** (0.25), **13.y** (0.75), 28.2 (1.00), **33.y** (0.33), **40.m** (0.17), **44.1** (1.00), **83.y** (0.08), **166.T**, 191.C, 508.T, 558.G, **608.T**. DELTRAN: **1.y** (1.00), **3.y** (1.00), **12.y** (0.25), **13.y** (0.75), 26.y (1.00), **33.y** (0.33), **40.m** (0.50), **44.1** (1.00), **83.y** (0.08), 129.0 (1.00), **166.T**, **608.T**.

Branch 9 (*Sceloporus* group).—ACCTRAN: **9.y** (0.33), 48.i (0.33), 63.y (1.00), **65.y** (0.88), **70.y** (0.29), 92.1 (1.00), **117.d** (0.13), 129.3 (1.00), **61.–**, **222.A**, **228.C**, 360.A, 401.C, 402.T, 403.C, **443.C**, **446.A**, 499.T. DELTRAN: **9.y** (1.00), 59.0 (1.00), **65.y** (0.88), **70.y** (1.00), 71.y (1.00), 76.e (0.17), **117.d** (0.13), **61.–**, **222.A**, **228.C**, 345.T, 403.C, **443.C**, **446.A**.

Branch 10 (*Uta*).—ACCTRAN: **36.i** (0.33), **84.1** (1.00), **117.l** (0.33), **121.u** (0.83), 10.G, **99.C**, **121.C**, **187.C**, **193.–**, 232.T, **355.C**, **360.C**, **362.G**, **379.G**, **396.C**, **399.T**, **400.T**, **472.A**, **538.T**, **540.A**, **596.C**, **622.G**, 664.–. DELTRAN: 5.y (1.00), **36.i** (0.33), 48.i (0.33), 63.y (1.00), **84.1** (1.00), 92.1 (1.00), **117.l** (0.33), **121.u** (0.83), 129.3 (1.00), **99.C**, **121.C**, 124.A, **187.C**, **193.–**, **355.C**, **360.C**, **362.G**, **379.G**, **396.C**, **399.T**, **400.T**, 402.T, **472.A**, 499.T, **538.T**, **540.A**, **596.C**, **622.G**.

Branch 11.—ACCTRAN: 5.a (1.00), 69.f (0.21), 116.1 (1.00), 124.y (1.00), **57.A**, 112.G, 122.C, 123.T, 124.T, **188.C**, **305.T**, 313.A, 499.C. DELTRAN: **57.A**, **188.C**, **305.T**, 401.C.

Branch 12 (*Petrosaurus*).—ACCTRAN: **30.y** (1.00), **44.2** (1.00), 48.a (0.33), **49.q** (0.67), **53.y** (1.00), 63.a (1.00), **74.y** (1.00), **76.y** (0.58), 92.0 (1.00), **108.y** (1.00), **116.3** (1.00), 153.1 (1.00), **59.T**, **120.A**, **152.C**, **176.G**, **196.A**, 204.–, 400.G, **402.C**, **558.C**, **625.C**. DELTRAN: **30.y** (1.00), **44.2** (1.00), **49.q** (0.67), **53.y** (1.00), **74.y** (1.00), **76.y** (0.83), **108.y** (1.00),

116.3 (1.00), **59.T**, 112.G, **120.A**, 122.C, 123.T, **152.C**, **176.G**, **196.A**, 313.A, 360.A, **402.C**, **558.C**, **625.C**.

Branch 13.—ACCTRAN: **42.1** (1.00), **47.y** (1.00), **48.y** (0.67), 62.e (0.17), 129.0 (1.00), **131.a** (1.00), **62.A**, **112.A**, **228.T**, 357.G, **443.A**. DELTRAN: **42.1** (1.00), **47.y** (1.00), **48.y** (1.00), 63.y (1.00), 69.e (0.17), 92.1 (1.00), 116.1 (1.00), **131.a** (1.00), **62.A**, **112.A**, **228.T**, **443.A**.

Branch 14 (*Urosaurus*).—ACCTRAN: 5.g (0.25), **6.p** (0.63), 59.2 (1.00), 60.f (0.21), **62.y** (0.83), **69.j** (0.17), **76.a** (0.42), 80.h (0.29), **93.y** (1.00), 126.g (0.25), **152.1** (1.00), **53.C**, **114.T**, **117.A**, **156.T**, **165.A**, **226.A**, **256.A**, 313.G, **436.C**, **447.G**, **477.A**. DELTRAN: **6.p** (0.63), **62.v** (0.88), **69.f** (0.04), **76.a** (0.17), **93.y** (1.00), 124.y (1.00), 129.0 (1.00), **152.1** (1.00), **53.C**, **114.T**, **117.A**, 122.C, 123.T, **156.T**, **165.A**, **226.A**, **256.A**, 357.G, 402.T, **436.C**, **447.G**, **477.A**, 499.C.

Branch 15.—ACCTRAN: **6.y** (0.38), 51.g (0.25), **96.y** (1.00), **117.a** (0.13), 152.C, 191.T, **342.C**, **359.T**, **472.T**, **519.T**. DELTRAN: **6.y** (0.38), 69.j (0.17), **96.y** (1.00), **117.a** (0.13), **342.C**, **359.T**, **472.T**, **519.T**.

Branch 16.—ACCTRAN: **24.s** (0.75), 31.i (0.33), **69.q** (0.29), 72.c (0.08), 80.a (0.29), **94.y** (1.00), 97.f (0.21), **126.k** (0.17), 92.T, 360.T, 610.C. DELTRAN: **24.s** (0.75), 59.2 (1.00), 62.y (0.13), **69.m** (0.13), **94.y** (1.00), **126.k** (0.42).

Branch 17.—ACCTRAN: **24.y** (0.25), 51.a (0.25), **124.d** (0.88), 126.y (0.58), **130.y** (1.00). DELTRAN: **24.y** (0.25), **124.d** (0.88), **130.y** (1.00).

Branch 18.—ACCTRAN: **5.y** (0.75), **60.y** (0.79), **66.y** (1.00), 108.d (0.13), 19.T, 25.A, 55.–, 82.G, 121.T, 168.G, 187.A, 193.–, 196.A, 198.G, 305.C, 379.G, 396.C, 403.A, 476.G, 537.T, 538.A. DELTRAN: **5.y** (1.00), 59.2 (1.00), **60.u** (0.83), 62.w (0.04), **66.y** (1.00), 80.d (0.13), 126.f (0.21).

Branch 19.—ACCTRAN: 44.1 (1.00), 58.c (0.08), 69.f (0.17), **147.1** (1.00). DELTRAN: **147.1** (1.00), 19.T, 25.A, 55.–, 82.G, 193.–, 196.A, 198.G, 305.C, 360.A, 379.G, 396.C, 403.A, 476.G, 537.T, 538.A.

Branch 20.—ACCTRAN: **6.q** (0.04), 64.f (0.21), 80.d (0.17), **117.a** (0.13), **126.h** (0.04), 318.T. DELTRAN: **6.q** (0.04), 44.1 (1.00), 62.y (0.08), 108.d (0.13), **117.a** (0.13), **126.h** (0.08).

Branch 21.—ACCTRAN: **5.m** (0.50), **6.y** (0.33), 58.a (0.08), **88.u** (0.83), **90.w** (0.92), **96.y** (1.00), **97.y** (1.00), **108.r** (0.58), **116.0** (1.00), **126.y** (0.71). DELTRAN: **5.m** (0.50), **6 .y** (0.33), **88.u** (0.83), **90.w** (0.92), **96.y** (1.00), **97.y** (1.00), **108.r** (0.58), **116.0** (1.00), **126.y** (0.71).

Branch 22.—ACCTRAN: 72.d (0.13), **103.y** (1.00), **105.2** (1.00), **57.C**, 99.C, 122.A, 123.A, 157.T, **164.A**, **180.T**, 183.T, 319.C, 360.T, 402.A, 437.T, 508.A. DELTRAN: **103.y** (1.00), **105.2** (1.00), **57.C**, **164.A**, **180.T**.

Branch 23 (*Sator*).—ACCTRAN: **9.a** (1.00), **66.u** (0.83), 69.e (0.04), **76.y** (0.58), **117.e** (0.04), 125.y (1.00), 10.G, 12.C, 92.A, 123.C, 124.A, 146.A, 168.G, 204.–, 222.C, 338.A, 354.C, 401.A, 440.T, 443.T, 446.C, 539.C, 540.A, 551.C, 610.C, 664.T. DELTRAN: **9.a** (1.00), 62.e (0.17), **66.u** (0.83), **76.y** (0.83), **117.e** (0.04).

Branch 24 (*Sceloporus*).—ACCTRAN: 62.a (0.17), 67.h (0.29), **71.a** (1.00), 74.c (0.08), **91.y** (1.00), 127.y (1.00), 129.1 (1.00), 188.T, 357.A, 498.T, 499.A, 503.T, 558.C. DELTRAN: **71.a** (1.00), 72.c (0.08), **91.y** (1.00).

Branch 25.—ACCTRAN: **6.k** (0.42), **36.i** (0.33), **56.y** (1.00), 61.c (0.08), **67.v** (0.58), **68.k** (0.42), **76.a** (0.42), 90.m (0.50), **95.y** (1.00), **107.f** (0.21), **109.y** (1.00), 116.0 (1.00), 124.a (1.00). DELTRAN: **6.k** (0.42), **36.i** (0.33), **56.k** (0.42), **67.v** (0.88), **68.k** (0.42), **76.a** (0.17), **95.y** (1.00), **107.f** (0.21), **109.y** (1.00).

Branch 26.—ACCTRAN: **4.y** (1.00), **6.y** (0.58), **19.y** (1.00), **24.y** (1.00), **29.y** (1.00), **36.m** (0.17), **39.a** (1.00), **59.2** (1.00), **67.y** (0.13), **68.t** (0.38), **69.d** (0.08), **73.c** (0.08), **80.w** (0.92), **98.y** (1.00), **101.y** (1.00), **107.l** (0.25), **110.y** (1.00), **129.0** (1.00). DELTRAN: **4.y** (1.00), **6.y** (0.58), **19.y** (1.00), **24.y** (1.00), **29.y** (1.00), **36.m** (0.17), **39.a** (1.00), **59.2** (1.00), **67.y** (0.13), **68.t** (0.38), **69.d** (0.04), **73.c** (0.08), **80.w** (0.92), **98.y** (1.00), **101.y** (1.00), **107.l** (0.25), **110.y** (1.00), 116.0 (1.00), **129.0** (1.00).

Branch 27.—ACCTRAN: **5.q** (0.67), **37.a** (1.00), **59.1** (1.00), **117.a** (0.13). DELTRAN: **5.k** (0.42), **37.a** (1.00), **59.1** (1.00), 76.j (0.21), **117.a** (0.13), 124.u (0.83), 188.T, 313.A, 319.C, 498.T.

Branch 28.—ACCTRAN: **72.f** (0.08), **74.y** (0.92), **80.c** (0.08), **88.c** (0.08), **105.1** (1.00), **115.y** (1.00), **144.1** (1.00), 99.A, 106.C, 114.T, 157.C, 164.–, 226.A, 304.T, 314.A, 340.G, 342.C, 343.T, 345.C, 422.C, 550.T, 552.T, 561.T, 578.G, 592.C. DELTRAN: 67.h (0.29), **72.e** (0.08), **74.w** (0.92), **80.c** (0.08), **88.c** (0.08), **105.1** (1.00), **115.y** (1.00), **144.1** (1.00).

Branch 29.—ACCTRAN: **6.m** (0.50), **64.d** (0.13), **67.w** (0.63), **69.c** (0.13), 76.y (0.58), **77.y** (1.00). DELTRAN: **6.m** (0.50), **64.d** (0.13), **67.w** (0.63), **69.c** (0.08), **77.c** (0.08), 127.y (1.00).

Branch 30.—ACCTRAN: 5.a (0.67), 15.m (0.50), **56.y** (1.00), **64.u** (0.71), 67.y (0.08), 69.a (0.08), 72.e (0.04), 74.w (0.08), 79.c (0.08), **80.g** (0.17), **88.u** (0.75), **95.y** (1.00), **98.y** (1.00), **116.2** (1.00), 117.g (0.25). DELTRAN: **56.u** (0.83), **64.u** (0.71), **80.g** (0.17), **88.t** (0.71), **95.y** (1.00), **98.y** (1.00), **116.2** (1.00), 106.C, 114.T, 164.–, 183.T, 226.A, 304.T, 314.A, 340.G, 342.C, 345.C, 422.C, 437.T, 503.T, 550.T, 552.T, 561.T, 578.G, 592.C.

Branch 31.—ACCTRAN: **27.c** (0.08), **38.m** (0.50), **59.2** (1.00), **80.u** (0.58), **124.a** (1.00), **129.0** (1.00), **153.1** (1.00), 10.G, 12.C, 92.T, 107.T, 121.C, 191.T, 232.G, 327.T, 341.A, 404.T, 508.T, 543.T, 551.T, 558.T, 610.C. DELTRAN: **27.c** (0.08), **38.m** (0.50), **59.2** (1.00), 76.y (0.63), 77.y (0.92), **80.u** (0.58), **124.a** (0.83), **129.0** (1.00), **153.1** (1.00).

Branch 32.—ACCTRAN: **2.m** (0.50), **51.g** (0.25), 67.a (0.29), **69.l** (0.25), 72.c (0.04), 74.a (0.08), 79.s (0.75), **98.y** (1.00), **93.C**, **152.C**, **180.C**, 183.A, **228.A**, **306.T**, **341.T**, **360.A**, 437.A, **472.A**, **495.**–. DELTRAN: **2.k** (0.42), **51.g** (0.25), **69.i** (0.17), **98.y** (1.00), 124.y (0.17), 127.y (1.00), **93.C**, 99.C, **152.C**, 157.T, **180.C**, **228.A**, **306.T**, **341.T**, **360.A**, **472.A**, **495.**–.

Branch 33.—ACCTRAN: 20.u (0.83), 72.a (0.08), 76.w (0.50), **108.e** (0.17), 112.q (0.67), **152.1** (1.00), 117.A, 124.A, 146.A, 159.G, 188.A, 190.G, 191.T, 295.–, 327.T, 338.A, 359.T, 401.A, 503.C, 559.T, 666.A. DELTRAN: **108.e** (0.17), **152.1** (1.00).

Branch 34.—ACCTRAN: **5.y** (0.33), **20.y** (0.17), 67.c (0.08), 69.i (0.13), 79.a (0.75), 84.1 (1.00), **112.y** (0.33). DELTRAN: **5.y** (0.58), **20.y** (1.00), 76.s (0.38), **112.y** (1.00).

Branch 35.—ACCTRAN: 2.a (0.50), **58.y** (1.00), 59.2 (1.00), 60.y (1.00), **62.y** (1.00), 153.1 (1.00). DELTRAN: **58.y** (1.00), **62.y** (1.00).

Branch 36.—ACCTRAN: 5.k (0.25), 6.g (0.25), **34.y** (1.00), **36.y** (1.00), **107.q** (0.67), 108.m (0.33), **126.y** (1.00). DELTRAN: **34.y** (1.00), **36.y** (1.00), 69.l (0.13), 79.m (0.50), **107.q** (0.67), **126.y** (1.00).

Branch 37.—ACCTRAN: 2.k (0.08), **5.f** (0.21), 20.a (0.83), **51.k** (0.17), **69.y** (0.54), **72.d** (0.13), **76.y** (0.08), **77.y** (1.00), **101.y** (1.00), **107.y** (0.33), 112.a (0.67), **119.y** (1.00). DELTRAN: **5.f** (0.21), **51.k** (0.17), **69.y** (0.54), **72.d** (0.04), **76.y** (0.63), **77.y** (1.00), **101.y** (1.00), **107.y** (0.33), **119.y** (1.00).

Branch 38.—ACCTRAN: **15.i** (0.33), **47.m** (0.50), 51.i (0.08), **69.w** (0.46), **79.w** (0.17), **86.c** (0.08), 141.2 (1.00), **143.2** (1.00), **62.G**, **187.C**, **342.A**, **402.C**, **498.C**, **499.C**, 508.T, 533.T, **551.C**. DELTRAN: 2.m (0.08), **15.i** (0.33), **47.m** (0.50), **69.w** (0.58), **79.q** (0.67), **86.c** (0.08), **143.2** (1.00), **62.G**, **187.C**, **342.A**, **402.C**, **498.C**, **499.C**, **551.C**.

Branch 39.—ACCTRAN: 5.k (0.25), **15.y** (0.67), 72.d (0.04), 76.c (0.33), 86.f (0.13), **101.y** (1.00), 114.o (58), **129.3** (1.00), **141.5** (1.00), **12.C**, **305.C**, **313.G**, **504.G**, 558.T. DELTRAN: **15.u** (0.50), **101.y** (1.00), **129.3** (1.00), **141.5** (1.00), **12.C**, **305.C**, **313.G**, 503.T, **504.G**, 533.T.

Branch 40.—ACCTRAN: 2.p (0.13), 37.k (0.42), **51.a** (0.33), **76.a** (0.08), 79.q (0.25), **140.y** (1.00), 153.1 (1.00), **175.G**, **179.T**, 476.T, 519.T. DELTRAN: **51.a** (0.25), **76.a** (0.38), **140.y** (1.00), **175.G**, **179.T**.

Branch 41.—ACCTRAN: 47.y (0.50), 86.c (0.13), 114.a (0.58), **130.y** (1.00), **188.C**, 232. G, **476.C**. DELTRAN: 15.y (0.17), **130.y** (1.00), **188.C**, **476.C**.

Branch 42.—ACCTRAN: **5.a** (0.42), 51.q (0.33), **73.m** (0.50), **79.y** (0.08), 86.m (0.29), **114.y** (0.42), 117.c (0.08), **256.T**, 378.C, **610.C**. DELTRAN: **5.a** (0.42), 15.y (0.17), **73.c** (0.08), **79.y** (0.33), **114.y** (1.00), **256.T**, **610.C**.

Branch 43.—ACCTRAN: **72.y** (0.88), 76.q (0.58), **126.m** (0.50), 143.0 (1.00), **57.T**, 93.T, 473.T, **559.A**. DELTRAN: **72.y** (0.92), **126.m** (0.50), **57.T**, **559.A**.

Branch 44.—ACCTRAN: **2.u** (0.33), **47.y** (0.50), **51.a** (0.67), **69.r** (0.21), 73.c (0.42), 86.a (0.50), **128.m** (0.50), **187.T**, 378.T, **478.C**. DELTRAN: **2.u** (0.33), **47.y** (0.50), **51.a** (0.25), **69.r** (0.21), 117.c (0.08), **128.e** (0.17), **187.T**, 473.T, **478.C**.

Branch 45.—ACCTRAN: 2.y (0.17), **69.p** (.08), **76.a** (0.67), 108.e (0.17), **114.a** (1.00), 93.C, **147.T**, **519.T**, **538.A**, **552.C**, **558.C**. DELTRAN: **69.p** (0.08), **76.a** (0.38), **114.a** (1.00), **147.T**, **519.T**, **538.A**, **552.C**, **558.C**.

Branch 46.—ACCTRAN: 64.c (0.08), **72.a** (1.00), 73.a (0.08), **116.0** (1.00), **126.a** (0.50), 128.e, (0.33), 143.2 (1.00), **191.T**, **319.A**. DELTRAN: **72.a** (1.00), **116.0** (1.00), **126.a** (0.50), **191.T**, **319.A**.

Branch 47.—ACCTRAN: **51.i** (0.33), 79.r (0.29), 108.a (0.17), 128.d (0.04), **129.2** (1.00), 124.C, **503.C**. DELTRAN: **51.i** (0.33), 64.c (0.08), **129.2** (1.00), **503.C**.

Branch 48.—ACCTRAN: **47.q** (0.33), **51.m** (0.17), **64.f** (0.13), **112.g** (0.25), **117.a** (0.08), **498.T**, **504.A**, **656.C**. DELTRAN: 2.y (0.17), **47.q** (0.33), **51.m** (0.17), **64.f** (0.13), 73.a (0.08), 86.a (0.08), **112.g** (0.25), **117.a** (0.08), **498.T**, **504.A**, **656.C**.

Branch 49.—ACCTRAN: **15.q** (0.33), **67.c** (0.08), **108.g** (0.08), 499.A. DELTRAN: **15.q** (0.33), **67.c** (0.08), 73.a (0.08), 86.a (0.08), **108.g** (0.25).

Branch 50.—ACCTRAN: 2.p (0.38), **15.a** (0.67), 64.a (0.08), 108.h (0.04), **116.3** (1.00), 117.o (0.50), **140.y** (1.00), **141.3** (1.00), **143.1** (1.00), 508.A, **378.C**, **473.A**, 478.T, **499.T**. DELTRAN: **15.a** (0.67), **116.3** (1.00), **140.y** (1.00), **141.3** (1.00), **143.1** (1.00), **378.C**, **473.A**, **499.T**.

Branch 51.—ACCTRAN: **51.k** (0.42), 128.a (0.17), 207.C, **121.C**, 188.C, 222.T, **256.C**. DELTRAN: 2.p (0.21), **51.k** (0.42), **121.C**, **256.C**.

Branch 52.—ACCTRAN: **67.a** (0.08), 101.a (1.00), **116.1** (1.00), **117.a** (0.58), **170.G**, **171.T**, **183.G**, 503.A. DELTRAN: **67.a** (0.08), **116.1** (1.00), **117.a** (0.08), 128.a (0.17), 57.C, **170.G**, **171.T**, **183.G**.

Branch 53.—ACCTRAN: **6.d** (0.13), **38.g** (0.25), **69.y** (0.38), **78.r** (0.71), **108.a** (0.29), **112.y** (1.00), **127.u** (0.17), **129.1** (1.00), 140.a (1.00), 117.C, 159.G, 179.T, 232.T, 314.G, 401.A, 447.–, 503.C, 533.C. DELTRAN: **6.d** (0.13), **38.g** (0.25), **69.y** (0.38), **78.p** (0.63), **108.a** (0.25), **112.y** (1.00), **127.u** (0.17), **129.1** (1.00).

Branch 54.—ACCTRAN: **2.m** (0.13), **5.g** (0.25), **6.g** (0.13), **15.s** (0.75), **28.1** (1.00), **38.i** (0.08), **47.g** (0.75), **51.y** (0.58), **56.y** (1.00), **59.2** (1.00), **118.k** (0.42), **120.g** (0.25), **127.a** (0.83), **141.5** (1.00), **143.0** (1.00). DELTRAN: **2.m** (0.13), **5.g** (0.25), **6.g** (0.13), **15.s** (0.75), **28.1** (1.00), **38.i** (0.08), **47.g** (0.75), **51.y** (0.58), **56.y** (1.00), **59.2** (1.00), 101.a (1.00), **118.k** (0.42), **120.g** (0.25), **127.a** (0.83), **141.5** (1.00), **143.0** (1.00).

Branch 55.—ACCTRAN: **2.m** (0.13), **51.m** (0.08), **117.u** (0.25), **124.C**, **179.G**, **304.T**, **462.A**, **561.T**. DELTRAN: **2.m** (0.13), **51.m** (0.08), **117.u** (0.75), **124.C**, **179.G**, 222.T, **304.T**, 314.A, **462.A**, **561.T**.

Branch 56.—ACCTRAN: **69.c** (0.54), **76.c** (0.08), 79.w (0.08), 108.i (0.04), **153.C**, **507.A**, 528.G, **551.A**, 608.T, **664.T**. DELTRAN: **69.c** (0.54), **76.c** (0.08), 117.o (0.50), **153.C**, **507.A**, **551.A**, **664.T**.

Branch 57.—ACCTRAN: 2.a (0.63), 38.i (0.33), 47.a (1.00), 91.r (0.29), **117.y** (0.42), **175.G**, **232.G**, 314.G, 478.C, **531.A**. DELTRAN: **117.t** (0.21), **175.G**, **232.G**, **531.A**.

Branch 58.—ACCTRAN: 51.i (0.33), **61.r** (0.71), **108.m** (0.17), **12.T**, **511.T**. DELTRAN: **61.r** (0.71), 79.w (0.08), **108.m** (0.25), **12.T**, **511.T**, 608.T.

Uma notata.—ACCTRAN: 51.a (0.33), **78.d** (0.13), **121.y** (0.13), **53.–**, **59.–**, **82.G**, **157.T**, **164.A**, **189.T**, **341.T**, **399.T**, **403.C**, **472.A**, **508.A**, **511.T**, **512.T**, 551.A. DELTRAN: 27.y (0.17), 57.v (0.46), 61.h (0.04), **78.d** (0.13), 111.y (0.13), **121.y** (0.13), **53.–**, **59.–**, **82.G**, **157.T**, **164.A**, 168.T, 180.T, **189.T**, 190.T, **341.T**, **399.T**, **403.C**, **472.A**, **508.A**, **511.T**, **512.T**.

Callisaurus draconoides.—ACCTRAN: **20.y** (1.00), 27.u (0.17), **51.y** (0.67), **52.y** (1.00), 61.g (0.04), **103.c** (0.08), **108.j** (0.13), **116.1** (1.00), **117.c** (0.08), **129.3** (1.00), **59.T**, **92.A**, **99.T**, **147.T**, **168.C**, 190.A, **191.A**, **192.C**, **340.T**, **342.C**, **400.C**. DELTRAN:

20.y (1.00), **51.y** (0.75), **52.y** (1.00), **103.c** (0.08), **108.j** (0.13), **116.1** (1.00), **117.c** (0.08), 124.y (1.00), **129.3** (1.00), 155.0 (1.00), **59.T**, **92.A**, **99.T**, 112.T, 121.T, **147.T**, **168.C**, 180.T, **191.A**, **192.C**, 228.A, 327.T, **340.T**, **342.C**, **400.C**, 538.A.

Cophosaurus texanus.—ACCTRAN: **2.m** (0.29), 51.g (0.08), **61.y** (0.08), **65.y** (0.54), **121.r** (0.17), **63.G**, 112.C, 121.A, **147.A**, **166.C**, **176.G**, **183.C**, **190.C**, **204.–**, 228.G, **304.C**, **379.G**, **401.A**, **503.T**, **508.A**, **519.C**, 538.C, **539.–**. DELTRAN: **2.m** (0.29), **61.y** (0.08), **65.y** (0.54), **121.r** (0.17), 124.y (1.00), 155.0 (1.00), **63.G**, **147.A**, **166.C**, 168.T, **176.G**, **183.C**, **190.C**, **204.–**, **304.C**, 327.T, **379.G**, **401.A**, **503.T**, **508.A**, **519.C**, **539.–**.

Holbrookia maculata.—ACCTRAN: **29.g** (0.25), **45.f** (0.21), **47.m** (0.50), **74.f** (0.21), **102.f** (0.79), **111.a** (0.63), **121.y** (0.13), **123.a** (1.00), 124.a (1.00), **129.0** (1.00), 155.1 (1.00), **53.–**, **99.C**, **123.G**, **159.C**, 168.A, **180.C**, **189.G**, **191.T**, **295.–**, 327.C, **399.T**, **403.C**, **511.T**, **512.T**, **551.T**, **552.T**, **610.C**, **611.C**. DELTRAN: **29.g** (0.25), **45.f** (0.21), **47.m** (0.50), 51.i (0.08), **74.f** (0.21), **102.f** (0.79), **111.a** (0.63), **121.y** (0.13), **123.a** (1.00), **129.0** (1.00), **53.–**, **99.C**, 112.T, 121.T, **123.G**, **159.C**, 166.T, **180.C**, **189.G**, 190.T, **191.T**, 228.A, **295.–**, **399.T**, **403.C**, **511.T**, **512.T**, 538.A, **551.T**, **552.T**, **610.C**, **611.C**.

Phrynosoma asio.—ACCTRAN: 61.f (0.08), **100.y** (1.00), **104.y** (1.00), **106.y** (1.00), **109.y** (1.00), **10.G**, **107.T**, **112.T**, **165.A**, **183.C**, **228.A**, **327.T**, **343.T**, **345.A**, **379.T**, **396.C**, **477.T**, **519.T**, 531.G, **551.T**, **561.T**, **659.C**. DELTRAN: 26.y (1.00), 40.i (0.33), **100.y** (1.00), **104.y** (1.00), **106.y** (1.00), 108.y (0.33), **109.y** (1.00), 129.0 (1.00), **10.G**, **107.T**, **112.T**, **165.A**, **183.C**, 190.C, 191.T, **228.A**, **327.T**, **343.T**, **345.A**, **379.T**, **396.C**, **477.T**, 508.C, **519.T**, **551.T**, **561.T**, **659.C**.

Phrynosoma douglassii.—ACCTRAN: 26.a (1.00), 40.a (0.33), **61.w** (0.25), 108.q (0.33), 129.1 (1.00), **140.y** (1.00), **16.A**, **106.C**, **146.A**, **168.T**, **186.C**, **190.T**, **401.A**, **403.C**, **443.C**, **498.T**, **499.T**, **503.C**, **518.T**. DELTRAN: 31.y (0.33), **61.w** (0.71), 112.i (0.33), **140.y** (1.00), **16.A**, **106.C**, **146.A**, **168.T**, **186.C**, **190.T**, 191.T, 318.T, 399.T, **401.A**, **403.C**, **443.C**, **498.T**, **499.T**, **503.C**, 508.C, **518.T**, 540.A, 551.C, 666.A.

Phrynosoma cornutum.—ACCTRAN: 31.q (0.33), **40.y** (0.50), **61.d** (0.54), **100.y** (1.00), **104.y** (1.00), **106.f** (0.21), **107.y** (1.00), **109.i** (0.33), 112.a (0.33), **10.G**, **99.T**, **102.G**, **107.T**, **108.T**, **152.C**, **171.T**, **176.G**, **179.T**, **189.T**, 190.A, **191.–**, **232.T**, **256.T**, **319.C**, **327.T**, **341.T**, **400.T**, **511.T**, **519.T**, 540.T, 666.G. DELTRAN: 28.2 (1.00), **40.y** (0.50), **61.d** (0.08), **100.y** (1.00), **104.y** (1.00), **106.f** (0.21), **107.y** (1.00), **109.i** (0.33), **10.G**, **99.T**, **102.G**, **107.T**, **108.T**, **152.C**, **171.T**, **176.G**, **179.T**, **189.T**, **191.–**, **232.T**, **256.T**, 318.T, **319.C**, **327.T**, **341.T**, 399.T, **400.T**, **511.T**, **519.T**, 551.C,558.G.

Phrynosoma modestum.—ACCTRAN: **15.q** (0.33), **16.y** (1.00), **30.y** (1.00), **89.y** (1.00), **99.a** (1.00), **112.y** (0.67), **177.A**, **180.T**, **187.C**, **192.T**, **198.G**, 318.C, **360.C**, 399.A, **462.A**, **518.A**, 551.A, **558.C**. DELTRAN: **15.q** (0.33), **16.y** (1.00), **30.y** (1.00), 31.y (0.33), 61.q (0.46), **89.y** (1.00), **99.a** (1.00), 108.y (0.33), **112.y** (1.00), **177.A**, **180.T**, **187.C**, 190.C, **192.T**, **198.G**, **360.C**, **462.A**, **518.A**, 540.A, **588.C**, 666.A.

Uta palmeri.—ACCTRAN: **27.f** (0.21), **76.m** (0.08), **80.c** (0.08), **117.r** (0.25), **130.y** (1.00), **112.T**, **123.C**, **256.A**, **342.C**, 401.T, **519.T**. DELTRAN: **27.f** (0.21), **76.m** (0.33), **80.c** (0.08), **117.r** (0.25), **130.y** (1.00), 10.G, **112.T**, **123.C**, 232.T, **256.A**, **342.C**, **519.T**, 664.–.

Uta stansburiana.—ACCTRAN: **36.y** (0.67), **45.i** (0.33), **48.y** (0.67), **61.c** (0.08), 76.e (0.25), **121.y** (0.17), **92.T**, **122.T**, **167.T**, **168.C**, **403.T**, **561.T**. DELTRAN: **36.y** (0.67), **45.i** (0.33), **48.y** (0.67), **61.c** (0.08), **121.y** (0.17), **92.T**, **122.T**, **167.T**, **168.C**, 401.C, **403.T**, **561.T**.

Petrosaurus mearnsi.—ACCTRAN: **29.m** (0.50), **69.h** (0.08), **115.q** (0.67), **117.e** (0.04), **123.d** (0.13), 129.1 (1.00), **57.C**, **63.G**, **102.C**, **167.C**, **177.A**, **180.C**, **187.C**, **198.G**, **319.C**, **327.T**, **359.A**, **399.G**, **400.C**, **503.C**, **519.C**, **559.T**. DELTRAN: **29.m** (0.50), **69.h** (0.29), **115.q** (0.67), **117.e** (0.04), **123.d** (0.13), 124.y (1.00), **57.C**, **63.G**, **102.C**, **167.C**, **177.A**, **180.C**, **187.C**, **198.G**, 204.–, **319.C**, **327.T**, **359.A**, **399.G**, **400.C**, 499.C, **503.C**, **519.C**, **559.T**.

Petrosaurus thalassinus.—ACCTRAN: **49.y** (0.33), **67.i** (0.33), 69.a (0.21), **77.e** (0.17), **111.m** (0.50), 124.a (1.00), **10.G**, **93.C**, **159.G**, **166.T**, **171.T**, **183.T**, **189.T**, **222.T**, **227.G**, **232.G**, **295.–**, **304.T**, **314.–**, **342.C**, **401.A**, **498.G**, 499.A, **508.C**, **610.C**. DELTRAN: **49.y** (0.33), **67.i** (0.33), **77.e** (0.17), **111.m** (0.50), 129.3 (1.00), **10.G**, **93.C**, **159.G**, **166.T**, **171.T**, **183.T**, **189.T**, **222.T**, **227.G**, **232.G**, **295.–**, **304.T**, **314.–**, **342.C**, 400.G, **401.A**, **498.G**, **508.C**, **610.C**.

Urosaurus graciosus.—ACCTRAN: 5.a (0.25), **51.i** (0.08), 59.0 (1.00), 60.a (0.21), 62.v (0.13), **80.s** (0.46), 126.a (0.25), **93.C**, **400.C**, **402.C**, **437.G**, **513.G**, **538.T**. DELTRAN: **51.i** (0.33), **80.s** (0.75), **93.C**, 360.A, **400.C**, **402.C**, **437.G**, **513.G**, **538.T**.

Urosaurus ornatus.—ACCTRAN: **5.i** (0.08), **29.m** (0.50), **58.c** (0.08), **60.i** (0.13), **69.r** (0.04), **76.f** (0.21), **103.c** (0.08), **129.3** (1.00). DELTRAN: **5.i** (0.33), **29.m** (0.50), 31.i (0.33), 51.g (0.25), **58.c** (0.08), **60.i** (0.33), **69.r** (0.21), 72.c (0.08), **76.f** (0.21), 97.f (0.21), **103.c** (0.08), **129.3** (1.00), 92.T, 152.C, 191.T, 610.C.

Urosaurus auriculatus.—ACCTRAN: 5.a (0.25), 31.a (0.08), 60.a (0.21), 69.m (0.17), 72.a (0.08), **80.j** (0.38), **96.w** (0.08), 97.a (0.21), **102.y** (1.00), **128.i** (0.33). DELTRAN: **80.j** (0.38), **96.w** (0.08), **102.y** (1.00), 126.y (0.58), **128.i** (0.33).

Urosaurus clarionensis.—ACCTRAN: **31.m** (0.17), **88.f** (0.21), **97.y** (0.79), **124.a** (0.75). DELTRAN: 5.g (0.25), **31.m** (0.50), 60.f (0.21), 69.q (0.17), 72.c (0.08), **88.f** (0.21), **97.y** (1.00), **124.a** (0.13).

Urosaurus bicarinatus.—ACCTRAN: **5.a** (0.50), **25.i** (0.33), **27.d** (0.13), **31.s** (0.75), **40.m** (0.50), **51.g** (0.25), 60.u (0.17), **61.c** (0.08), 64.a (0.21), **66.s** (0.25), **67.g** (0.25), **68.g** (0.25), **69.a** (0.21), **80.c** (0.04), **90.y** (0.08), **94.y** (1.00). DELTRAN: **5.a** (0.50), **25.i** (0.33), **27.d** (0.13), **31.s** (0.75), **40.m** (0.50), **51.g** (0.25), **61.c** (0.08), **66.s** (0.25), **67.g** (0.25), **68.g** (0.25), **69.a** (0.21), **80.c** (0.04), **90.y** (0.08), **94.y** (1.00).

Urosaurus gadovi.—ACCTRAN: 69.k (0.21), **80.r** (0.58), **88.w** (0.08), **107.d** (0.13), **108.v** (0.17). DELTRAN: 60.y (0.17), 64.f (0.21), 69.k (0.21), **80.r** (0.58),

88.w (0.08), **107.d** (0.13), **108.v** (0.17).

Urosaurus nigricaudus.—ACCTRAN: **64.h** (0.08), **127.k** (0.42). DELTRAN: 58.c (0.08), 60.y (0.17), **64.h** (0.29), **127.k** (0.42), 121.T, 168.T, 187.A.

Urosaurus microscutatus.—ACCTRAN: **6.m** (0.13), **29.i** (0.33), 60.u (0.17), 62.w (0.08), 108.a (0.13), **117.l** (0.33), 126.f (0.04), **129.3** (1.00), **59.T**, **121.C**, **122.T**, **187.C**, **401.T**, **508.A**, **518.T**. DELTRAN: **6.m** (0.13), **29.i** (0.33), 58.c (0.08), 80.h (0.17), **117.l** (0.33), **129.3** (1.00), **59.T**, **121.C**, **122.T**, 168.G, **187.C**, **401.T**, **508.A**, **518.T**.

Urosaurus lahtelai.—ACCTRAN: **31.g** (0.25), **38.m** (0.50), **69.y** (0.63), **80.m** (0.21), **108.i** (0.21). DELTRAN: **31.g** (0.25), **38.m** (0.50), 60.y (0.17), 62.y (0.08), **69.y** (0.79), **80.m** (0.38), **108.i** (0.33), 126.g (0.04).

Sator angustus.—ACCTRAN: **27.g** (0.25), **34.y** (1.00), **62.k** (0.25), **66.y** (0.17), **69.a** (0.17), **72.e** (0.04), **111.y** (1.00), **117.i** (0.17). DELTRAN: **27.g** (0.25), **34.y** (1.00), **62.k** (0.25), **66.y** (0.17), **69.a** (0.17), **72.e** (0.17), **111.y** (1.00), **117.i** (0.17), 124.y (1.00), 125.y (1.00), 10.G, 12.C, 92.A, 99.C, 123.C, 124.A, 146.A, 157.T, 168.G, 183.T, 204.–, 222.C, 338.A, 354.C, 357.G, 401.A, 437.T, 440.T, 443.T, 446.C, 499.C, 508.A, 539.C, 540.A, 551.C, 610.C, 664.T.

Sator grandaevus.—ACCTRAN: **61.e** (0.17), 72.a (0.13), **105.1** (1.00), **107.i** (0.33), 124.a (1.00). DELTRAN: **61.e** (0.17), **105.1** (1.00), **107.i** (0.33), 129.0 (1.00).

Sceloporus merriami.—ACCTRAN: **66.c** (0.08), **69.c** (0.25), **71.p** (0.63), **76.y** (0.08), **77.h** (0.29), **91.a** (1.00), **98.a** (1.00), **105.1** (1.00), **123.f** (0.21), **142.3** (1.00). DELTRAN: 2.m (0.08), **66.c** (0.08), 67.c (0.08), **69.c** (0.25), **71.p** (0.63), 72.a (0.08), **76.y** (0.25), **77.h** (0.29), 84.1 (1.00), **91.a** (1.00), **98.a** (1.00), **105.1** (1.00), **123.f** (0.21), **142.3** (1.00), 117.A, 124.A, 146.A, 159.G, 188.A, 190.G, 191.T, 295.–, 327.T, 338.A, 359.T, 401.A, 503.C, 508.A, 558.C, 559.T, 666.A.

Sceloporus parvus.—ACCTRAN: **5.y** (0.33), **60.c** (0.08), **62.c** (0.08), **68.f** (0.21), **72.i** (0.13), 76.j (0.04), **112.y** (1.00), **114.f** (0.21), 124.u (0.17), 127.a (1.00). DELTRAN: **5.y** (0.58), **60.c** (0.08), **62.c** (0.08), **68.f** (0.21), 69.f (0.04), **72.i** (0.17), 74.y (0.08), **112.y** (1.00), **114.f** (0.21).

Sceloporus couchii.—ACCTRAN: **6.u** (0.33), **37.y** (1.00), **45.e** (0.17), **61.c** (0.08), **108.e** (0.17). DELTRAN: 5.q (0.25), **6.u** (0.33), **37.y** (1.00), **45.e** (0.17), **61.c** (0.08), 72.f (0.04), 74.y (0.08), 76.y (0.63), 77.y (0.92), **108.e** (0.17), 124.y (0.17).

Sceloporus variabilis.—ACCTRAN: **9.q** (0.33), **47.m** (0.50), **64.w** (0.08), **74.n** (0.38), **76.i** (0.67), 77.c (0.92), **79.e** (0.08), **88.y** (0.33), **128.k** (0.42), **108.T**, **167.T**, **171.T**, **192.T**, **256.–**, **319.A**, **343.C**, **344.T**, **436.C**, **440.A**, **446.G**, **447.G**, **472.T**, **477.T**, **499.T**, **518.T**, **559.T**, **664.T**. DELTRAN: 5.a (0.42), **9.q** (0.33), 15.m (0.50), **47.m** (0.50), 56.y (0.17), **64.w** (0.08), 67.y (0.08), 69.a (0.08), **74.n** (0.38), **76.i** (0.04), **79.e** (0.17), **88.y** (0.21), 117.g (0.25), 124.y (0.17), **128.k** (0.42), **108.T**, **167.T**, **171.T**, **192.T**, **256.–**, **319.A**, **343.C**, **344.T**, **436.C**, **440.A**, **446.G**, **447.G**, **472.T**, **477.T**, **499.T**, 508.A, **518.T**, 558.C, **559.T**, **664.T**.

Sceloporus chrysostictus.—ACCTRAN: **15.y** (0.50), **27.f** (0.13), **28.1** (1.00), **72.c** (0.08), **73.w** (0.92), **80.w** (0.08), **101.y** (1.00), **115.a** (1.00), 117.a (0.25). DELTRAN: 5.a (0.42), **15.y** (1.00), **27.f** (0.13), **28.1** (1.00), 56.y (0.17), 67.y (0.08), 69.a (0.08), **72.c** (0.08), **73.w** (0.92), 79.c (0.08), **80.w** (0.08), 88.u (0.04), **101.y** (1.00), **115.a** (1.00), 10.G, 12.C, 92.T, 107.T, 121.C, 191.T, 232.G, 327.T, 341.A, 343.T, 404.T, 543.T, 551.T, 610.C.

Sceloporus cozumelae.—ACCTRAN: **5.m** (0.50), **6.s** (0.25), 15.a (0.50), **33.m** (0.50), **51.m** (0.50), 56.u (0.17), **61.f** (0.21), **62.j** (0.38), **67.q** (0.33), 69.c (0.08), **72.h** (0.13), 79.a (0.08), 88.t (0.04), **117.p** (0.38). DELTRAN: **5.m** (0.08), **6.s** (0.25), **33.m** (0.50), **51.m** (0.50), **61.f** (0.21), **62.j** (0.38), **67.q** (0.25), **72.h** (0.13), **117.p** (0.63).

Sceloporus utiformis.—ACCTRAN: **9.u** (0.17), **45.y** (1.00), **47.a** (1.00), **61.d** (0.04), **69.o** (0.38), **74.y** (0.92), **79.h** (0.29), **90.y** (0.50), **108.g** (0.25), **116.2** (1.00), **123.o** (0.58), **152.1** (1.00), **153.1** (1.00). DELTRAN: **9.u** (0.17), **45.y** (1.00), **47.a** (1.00), 56.y (0.58), **61.d** (0.13), **69.o** (0.42), 72.d (0.04), **74.y** (1.00), **79.h** (0.29), **90.y** (1.00), **108.g** (0.25), **116.2** (1.00), **123.o** (0.58), **152.1** (1.00), **153.1** (1.00).

Sceloporus siniferus.—ACCTRAN: **38.m** (0.50), 56.k (0.58), **69.a** (0.13), **72.a** (0.13), **117.a** (0.13). DELTRAN: **38.m** (0.50), 61.c (0.08), **69.a** (0.13), **72.a** (0.08), 74.c (0.08), 90.m (0.50), **117.a** (0.13).

Sceloporus squamosus.—ACCTRAN: **51.m** (0.50), 61.a (0.08), **64.d** (0.13), **68.y** (0.21), **73.d** (0.04), 74.a (0.08), **78.y** (1.00), **80.y** (0.08), **86.d** (0.13), 90.a (0.50), **107.p** (0.17). DELTRAN: **51.m** (0.50), 56.y (0.58), **64.d** (0.13), **68.y** (0.21), 72.d (0.04), **73.d** (0.04), **78.y** (1.00), **80.y** (0.08), **86.d** (0.13), **107.p** (0.17).

Sceloporus jalapae.—ACCTRAN: **64.c** (0.08), 76.s (0.17), **80.c** (0.08), 84.0 (1.00), **108.a** (0.17), **127.u** (0.17). DELTRAN: 2.a (0.42), **64.c** (0.08), 67.c (0.08), 72.a (0.08), **80.c** (0.08), **108.a** (0.17), **127.u** (0.17), 153.1 (1.00).

Sceloporus maculosus.—ACCTRAN: 67.a (0.08), **69.p** (0.29), **72.f** (0.21), **107.o** (0.58), **108.i** (0.17), **115.y** (1.00), **117.m** (0.50), **128.i** (0.33), **141.2** (1.00). DELTRAN: 59.2 (1.00), 60.y (1.00), **69.p** (0.29), **72.f** (0.13), 76.w (0.17), 84.1 (1.00), **107.o** (0.58), **108.i** (0.17), **115.y** (1.00), **117.m** (0.50), **128.i** (0.33), **141.2** (1.00).

Sceloporus gadoviae.—ACCTRAN: **2.y** (0.50), **24.y** (1.00), **44.1** (1.00), **51.a** (0.25), **74.q** (0.67), **76.a** (0.92), **115.y** (1.00). DELTRAN: **2.y** (0.58), 6.g (0.25), 20.u (0.83), **24.y** (1.00), **44.1** (1.00), **51.a** (0.25), 72.a (0.08), **74.q** (0.67), **76.a** (0.38), 79.s (0.25), 108.m (0.33), 112.q (0.67), **115.y** (1.00).

Sceloporus nelsoni.—ACCTRAN: **2.i** (0.08), **5.a** (0.21), 6.a (0.25), **31.y** (1.00), **51.m** (0.08), **58.h** (0.29), **60.g** (0.25), **61.k** (0.42), **62.k** (0.42), **72.v** (0.75), **79.y** (0.25). DELTRAN: **2.i** (0.08), **5.a** (0.21), **31.y** (1.00), **51.m** (0.08), **58.h** (0.29), **60.g** (0.25), **61.k** (0.42), **62.k** (0.42), **72.v** (0.75), **79.y** (0.50).

Sceloporus pyrocephalus.—ACCTRAN: **6.q** (0.42), **15.k** (0.42), **25.q** (0.67), **37.g** (0.25), **38.f** (0.21), **56.d** (0.13), **73.k** (0.42), 79.m (0.25), **125.y** (1.00), **127.s** (0.25), **128.y** (1.00), **142.1** (1.00). DELTRAN: **6.q** (0.67), **15.k** (0.42), **25.q** (0.67), **37.g** (0.25), **38.f** (0.21), **56.d** (0.13), **73.k** (0.42), **125.y** (1.00), **127.s** (0.25), **128.y** (1.00), **142.1** (1.00).

Sceloporus pictus.—ACCTRAN: **2.v** (0.25), **30.k**

(0.42), **36.m** (0.50), **37.y** (1.00), **51.g** (0.17), **78.y** (0.29), **79.u** (0.17). DELTRAN: **2.v** (0.25), **30.k** (0.42), **36.m** (0.50), **37.y** (1.00), **51.g** (0.17), **78.y** (0.38), **79.u** (0.17), 140.a (1.00).

Sceloporus scalaris.—ACCTRAN: **5.i** (0.08), **6.i** (0.08), 9.u (0.17), **15.y** (0.25), **33.k** (0.42), **38.m** (0.17), **64.e** (0.17), **76.d** (0.13), 78.p (0.08), **118.w** (0.50). DELTRAN: **5.i** (0.08), **6.i** (0.08), **15.y** (0.25), **33.k** (0.42), **38.m** (0.17), **64.e** (0.17), **76.d** (0.13), 77.d (0.13), **118.w** (0.75), 140.a (1.00), 117.C, 159.G, 179.T, 188.C, 222.T, 232.T, 401.A, 447.–, 478.T, 503.C, 533.C.

Sceloporus aeneus.—ACCTRAN: **2.k** (0.08), **47.a** (0.25), **72.d** (0.13), **120.o** (0.33), 140.y (1.00). DELTRAN: **2.k** (0.08), **47.a** (0.25), **72.d** (0.13), 78.r (0.08), **120.o** (0.75).

Sceloporus graciosus.—ACCTRAN: **29.y** (1.00), **69.y** (0.08), **128.m** (0.50), **10.G**, **16.C**, **50.C**, **112.G**, **123.T**, **158.T**, **171.T**, **232.T**, **318.T**, **319.A**, **403.A**, **404.T**, **478.T**, 503.A, **530.G**, **533.C**, **537.T**, **538.A**, **543.T**, **608.T**. DELTRAN: 5.q (0.25), **29.y** (1.00), 51.i (0.08), **69.y** (0.08), 76.k (0.04), 79.w (0.25), **128.m** (0.50), 141.2 (1.00), **10.G**, **16.C**, **50.C**, **112.G**, **123.T**, **158.T**, **171.T**, **232.T**, **318.T**, **319.A**, **403.A**, **404.T**, **478.T**, **530.G**, **533.C**, **537.T**, **538.A**, **543.T**, 558.C, **608.T**.

Sceloporus magister.—ACCTRAN: **2.i** (0.17), **47.i** (0.17), **49.i** (0.33), **67.c** (0.08), **73.s** (0.25), **86.y** (0.50), 117.a (0.08), **126.p** (0.13), **141.4** (1.00), **142.1** (1.00), **99.A**, **107.T**, **112.G**, **121.C**, **146.A**, **171.T**, **176.G**, **179.G**, **180.T**, **186.C**, **188.C**, **193.G**, **228.C**, **319.A**, **343.T**, **401.A**, **407.T**, **499.A**, **508.A**, **543.T**, **611.C**. DELTRAN: **2.i** (0.17), **47.i** (0.17), **49.i** (0.33), 51.q (0.42), **67.c** (0.08), **73.s** (0.67), 76.q (0.29), **86.y** (0.92), **126.p** (0.13), **141.4** (1.00), **142.1** (1.00), 93.T, **99.A**, **107.T**, **112.G**, **121.C**, **146.A**, **171.T**, **176.G**, **179.G**, **180.T**, **186.C**, **188.C**, **193.G**, **228.C**, **319.A**, **343.T**, 378.C, **401.A**, **407.T**, **499.A**, **508.A**, **543.T**, **611.C**.

Sceloporus spinosus.—ACCTRAN: **6.k** (0.42), **51.r** (0.04), **64.d** (0.21), 72.c (0.04), **108.e** (0.17), **117.f** (0.13), **127.u** (0.17), **147.A**, **304.T**, **319.T**, **342.T**, **400.T**, **401.T**, **402.T**, **538.A**. DELTRAN: **6.k** (0.42), **51.r** (0.46), **64.d** (0.13), 73.m (0.42), 76.c (0.29), 86.m (0.42), **108.e** (0.17), **117.f** (0.21), **127.u** (0.17), **147.A**, **304.T**, **319.T**, **342.T**, 378.C, **400.T**, **401.T**, **402.T**, **538.A**.

Sceloporus clarki.—ACCTRAN: **6.m** (0.50), **34.i** (0.33), **61.c** (0.08), **69.m** (0.13), **73.y** (0.92), **78.c** (0.08), 86.c (0.08), **126.u** (0.33), **128.y** (0.50), **141.2** (1.00), **142.2** (1.00), **53.C**, **57.C**, **112.G**, **121.C**, **123.G**, **168.C**, **188.A**, **204.–**, **232.T**, **440.A**, **477.T**, **533.C**, **539.C**, **610.A**. DELTRAN: 2.y (0.17), **6.m** (0.50), **34.i** (0.33), **61.c** (0.08), **69.m** (0.13), **73.y** (0.92), **78.c** (0.08), 108.e (0.17), **126.u** (0.33), **128.y** (0.83), **141.2** (1.00), **142.2** (1.00), 143.0 (1.00), **53.C**, **57.C**, **112.G**, **121.C**, **123.G**, **168.C**, **188.A**, **204.–**, **232.T**, **440.A**, **477.T**, **533.C**, **539.C**, **610.A**.

Sceloporus orcutti.—ACCTRAN: **5.f** (0.21), **36.g** (0.25), **37.f** (0.21), **76.w** (0.25), **117.h** (0.21), **127.a** (1.00), **141.1** (1.00), **54.T**, **106.C**, **107.G**, **189.C**, **191.A**, **192.T**, **306.C**, **403.A**, **495.A**, **508.C**, **512.T**, **528.T**, **561.T**. DELTRAN: **5.f** (0.21), **36.g** (0.25), **37.f** (0.21), **76.w** (0.54), 86.a (0.08), **117.h** (0.21), **127.a** (1.00), 128.m (0.33), **141.1** (1.00), 143.0 (1.00), **54.T**, 93.T, **106.C**, **107.G**, **189.C**, **191.A**, **192.T**, **306.C**, **403.A**, **495.A**, **508.C**, **512.T**, **528.T**, **561.T**.

Sceloporus occidentalis.—ACCTRAN: **61.c** (0.08), **64.g** (0.17), **66.c** (0.08), **68.g** (0.25), **69.q** (0.04), **117.a** (0.08), **128.u** (0.67), **112.G**, **120.T**, **190.G**, **191.A**, **198.G**, **379.G**, **395.A**, **396.C**, **400.C**. DELTRAN: 2.y (0.13), **61.c** (0.08), **64.g** (0.25), **66.c** (0.08), **68.g** (0.25), **69.q** (0.04), **117.a** (0.08), **128.u** (0.67), **112.G**, **120.T**, **190.G**, **191.A**, **198.G**, **379.G**, **395.A**, **396.C**, **400.C**, 499.A.

Sceloporus olivaceus.—ACCTRAN: **2.a** (1.00), 73.c (0.08), **74.c** (0.08), 86.c (0.08), **114.y** (1.00), **117.f** (0.13), **127.i** (0.67), **57.C**, **93.A**, **113.C**, **123.G**, **188.C**, **190.G**, **227.G**, **228.T**, **229.C**, **305.T**, **344.G**, **400.G**, **473.A**, **508.C**, **519.A**, **530.G**, **539.C**. DELTRAN: **2.a** (0.83), **74.c** (0.08), 79.r (0.29), **114.y** (1.00), **117.f** (0.13), **127.i** (0.67), 128.d (0.04), **57.C**, **93.A**, **113.C**, **123.G**, 124.C, **188.C**, **190.G**, **227.G**, **228.T**, **229.C**, **305.T**, **344.G**, **400.G**, **473.A**, **508.C**, **519.A**, **530.G**, **539.C**.

Sceloporus undulatus.—ACCTRAN: **36.f** (0.21), **56.c** (0.08), **108.g** (0.25), **116.1** (1.00), **128.m** (0.38), 124.T, **189.C**, **191.A**, **327.T**, **345.C**, **401.A**, **403.A**, **610.A**. DELTRAN: **36.f** (0.21), **56.c** (0.08), 79.r (0.29), **108.g** (0.25), **116.1** (1.00), **128.m** (0.33), **189.C**, **191.A**, **327.T**, **345.C**, **401.A**, **403.A**, **610.A**.

Sceloporus virgatus.—ACCTRAN: **6.y** (1.00), **47.i** (0.33), **51.y** (0.50), **64.m** (0.29), **67.c** (0.08), **69.w** (0.29), 79.y (0.29), **85.c** (0.08), **95.c** (0.08), **112.j** (0.13), **124.a** (1.00), **128.a** (0.13), **148.A**, **158.T**, **176.T**, **179.G**, **183.G**, **256.C**, **362.G**, **396.C**, **499.A**, **552.T**, **558.T**. DELTRAN: **6.y** (1.00), **47.i** (0.33), **51.y** (0.50), **64.m** (0.29), **67.c** (0.08), **69.w** (0.29), **85.c** (0.08), **95.c** (0.08), **112.j** (0.13), **124.a** (1.00), **128.a** (0.17), **148.A**, **158.T**, **176.T**, **179.G**, **183.G**, **256.C**, **362.G**, **396.C**, **499.A**, **552.T**, **558.T**.

Sceloporus formosus.—ACCTRAN: **2.y** (0.38), **5.a** (0.42), 37.a (0.42), **38.m** (0.50), **69.y** (0.08), **72.a** (0.13), **86.a** (0.08), **99.T**, **180.T**, **187.A**, **189.T**, **304.T**, **306.C**, **314.A**, **319.T**, **512.T**, 519.A, **551.T**, **559.A**, **561.G**, **608.T**. DELTRAN: **2.y** (0.50), **5.a** (0.42), **38.m** (0.50), 47.y (0.50), **69.y** (0.08), **72.a** (0.08), **86.a** (0.08), 153.1 (1.00), **99.T**, **180.T**, **187.A**, **189.T**, **304.T**, **306.C**, **314.A**, **319.T**, **512.T**, **551.T**, **559.A**, **561.G**, **608.T**.

Sceloporus taeniocnemis.—ACCTRAN: **2.a** (0.63), **5.y** (0.58), **37.y** (0.58), **64.y** (1.00), **79.u** (0.17), **108.f** (0.21), **128.f** (0.21), **112.G**, **204.–**, **340.G**, **343.G**. DELTRAN: **2.a** (0.50), **5.y** (0.58), **37.y** (1.00), **64.y** (1.00), 72.d (0.04), **79.u** (0.17), **108.f** (0.21), **128.f** (0.21), **112.G**, **204.–**, 232.G, **340.G**, **343.G**, 519.T.

Sceloporus malachiticus.—ACCTRAN: 15.u (0.17), **29.m** (0.50), **47.a** (0.50), **69.u** (0.08), **72.f** (0.08), **74.g** (0.25), **78.y** (1.00), **79.j** (0.29), **85.c** (0.08), **117.C**, **176.G**, **359.T**, **400.T**, **403.A**, **440.A**, **539.C**. DELTRAN: 2.p (0.13), **29.m** (0.50), 37.k (0.42), **47.a** (0.42), **69.u** (0.08), **72.f** (0.13), **74.g** (0.25), **78.y** (1.00), **79.j** (0.29), **85.c** (0.08), 86.f (0.13), 114.o (0.58), **117.C**, **176.G**, **359.T**, **400.T**, **403.A**, **440.A**, 476.T, 519.T, **539.C**.

Sceloporus grammicus.—ACCTRAN: **34.q** (0.67), **71.c** (0.08), **76.c** (0.08), **77.c** (0.08), **130.f** (0.21), **59.T**, **93.T**, **99.A**, **121.T**, **168.G**, 188.T, **198.G**, 222.A, **228.G**, **379.G**, **396.C**, **400.C**, **478.A**, **508.C**, **518.A**, **519.C**, **531.T**, **558.T**, **664.A**. DELTRAN:

34.q (0.67), **71.c** (0.08), **76.c** (0.08), **77.c** (0.08), 108.h (0.04), **130.f** (0.21), **59.T**, **93.T**, **99.A**, **121.T**, **168.G**, **198.G**, **228.G**, 314.A, **379.G**, **396.C**, **400.C**, **478.A**, 503.A, **508.C**, **518.A**, **519.C**, **531.T**, **558.T**, **664.A**.

Sceloporus cyanogenys.—ACCTRAN: **5.i** (0.33), **76.f** (0.13), 79.y (0.08), **108.a** (0.33), **130.y** (1.00), **99.A**, **191.C**, **344.G**, **379.C**, **508.C**, 608.C, **610.A**. DELTRAN: 2.a (0.83), **5.i** (0.33), 38.i (0.33), 47.a (1.00), **76.f** (0.13), 91.r (0.29), **108.a** (0.25), 117.y (0.21), **130.y** (1.00), **99.A**, **191.C**, **344.G**, **379.C**, **508.C**, 528.G, **610.A**.

Sceloporus dugesii.—ACCTRAN: **2.y** (1.00), 38.a (0.33), **56.y** (1.00), **59.2** (1.00), **61.u** (0.13), **64.g** (0.25), **67.a** (0.08), **69.k** (0.33), **76.a** (0.08), **79.k** (0.50), **91.a** (0.71), **128.a** (0.17), **50.C**, **204.–**, **256.C**, **354.C**, **478.T**, **503.C**, **518.A**. DELTRAN: **2.y** (0.17), 47.a (1.00), **56.y** (1.00), **59.2** (1.00), **61.u** (0.13), **64.g** (0.25), **67.a** (0.08), **69.k** (0.33), **76.a** (0.08), **79.k** (0.50), **91.a** (1.00), 117.y (0.21), **128.a** (0.17), **50.C**, **204.–**, **256.C**, **354.C**, **478.T**, **503.C**, **518.A**, 528.G.

Sceloporus mucronatus.—ACCTRAN: **2.y** (0.38), **67.f** (0.13), **69.a** (0.08), **79.s** (0.17), **126.q** (0.67), **127.q** (0.33), **128.m** (0.33), **124.C**, **191.G**, **318.T**, **343.G**, **396.A**, **401.T**, **402.A**, **403.T**, **528.T**, **533.C**, **552.T**, **558.T**, **561.A**. DELTRAN: **2.y** (0.17), **67.f** (0.13), **69.a** (0.08), **79.s** (0.25), 108.i (0.08), **126.q** (0.67), **127.q** (0.33), **128.m** (0.33), **124.C**, **191.G**, 314.A, **318.T**, **343.G**, **396.A**, **401.T**, **402.A**, **403.T**, 478.T, **528.T**, **533.C**, **552.T**, **558.T**, **561.A**, 608.T.

Sceloporus jarrovii.—ACCTRAN: **69.c** (0.54), **74.c** (0.08), **91.p** (0.38), **108.p** (0.33), **117.w** (0.08), **124.m** (0.50), **127.m** (0.50), **128.m** (0.50), **129.0** (1.00), 57.T, **102.T**, **117.C**, **176.G**, **228.T**, **256.A**, **319.G**, **476.G**, 478.C, **499.C**, **558.T**. DELTRAN: **69.c** (0.54), **74.c** (0.08), **91.p** (0.38), **108.p** (0.38), **117.w** (0.08), **124.m** (0.50), **127.m** (0.50), **128.m** (0.33), **129.0** (1.00), **102.T**, **117.C**, **176.G**, **228.T**, **256.A**, **319.G**, **476.G**, **499.C**, **558.T**.

Sceloporus poinsetti.—ACCTRAN: **9.q** (0.33), **15.y** (1.00), **37.i** (0.33), 47.y (1.00), **67.o** (0.50), **69.a** (0.08), **86.c** (0.08), 91.y (0.29), **107.q** (0.67), **108.y** (0.50), 117.t (0.21), **128.v** (0.71), **154.0** (1.00), **191.A**, 528.A, **610.–**. DELTRAN: 2.a (0.83), **9.q** (0.33), **15.y** (1.00), **37.i** (0.33), 38.i (0.33), 51.i (0.33), **67.o** (0.50), **69.a** (0.08), **86.c** (0.08), **107.q** (0.67), **108.y** (0.50), **128.v** (0.71), **154.0** (1.00), **191.A**, **610.–**.

Sceloporus torquatus.—ACCTRAN: **2.i** (0.17), **6.e** (0.17), **15.m** (0.50), **30.e** (0.17), **33.e** (0.17), **37.e** (0.17), **47.i** (0.67), **49.f** (0.21), **51.u** (0.33), **61.o** (0.58), **64.d** (0.13), **69.r** (0.08), **73.c** (0.08), **86.t** (0.79), **108.a** (0.29), **112.f** (0.21), **154.0** (1.00), **122.C**, **123.C**, **159.G**, **180.T**, **225.G**, **318.T**, **345.C**, **550.C**. DELTRAN: **2.i** (0.17), **6.e** (0.17), **15.m** (0.50), **30.e** (0.17), **33.e** (0.17), **37.e** (0.17), **47.i** (0.67), **49.f** (0.21), **51.u** (0.33), **61.o** (0.58), **64.d** (0.13), **69.r** (0.08), **73.c** (0.08), **86.t** (0.79), **108.a** (0.25), **112.f** (0.21), 128.a (0.17), **154.0** (1.00), 57.C, **122.C**, **123.C**, **159.G**, **180.T**, 338.C, **225.G**, **318.T**, **345.C**, 712.T, **550.C**.