

## PHYLOGENY OF THE SPINY LIZARDS (*SCELOPORUS*) BASED ON MOLECULAR AND MORPHOLOGICAL EVIDENCE

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**ABSTRACT:** Relationships within the phrynosomatid lizard genus *Sceloporus* are estimated using parsimony analysis of molecular and morphological data. The data include DNA sequences from the mitochondrial 12S and 16S ribosomal RNA genes (262 informative characters) obtained for 64 ingroup taxa, and morphological characters (202 informative characters describing variation in osteology, squamation, coloration, karyology, and life history) scored for 109 ingroup taxa. The molecular data set includes representatives of all of Smith's species groups as well as the genus *Sator*, and the morphological data set includes *Sator* and nearly all the recognized species and distinctive subspecies of *Sceloporus*. The data sets are analyzed separately and in combination, and the single, fully resolved tree from the simultaneous analysis of all the taxa and characters is taken as the best estimate of phylogeny and the basis for a revised classification. The genus *Sator* is nested inside *Sceloporus* (as the sister taxon of the *utiformis* and *siniferus* species groups), and is classified within *Sceloporus* as the *angustus* species group. The traditional division of *Sceloporus* into large-scaled and small-scaled radiations is not supported; the small-scaled species form a graded series of lineages leading up to a clade of mostly large-scaled species, and this clade contains the putatively small-scaled *scalaris* species group. Most of the species groups recognized in Hobart Smith's 1939 monograph are upheld by this study (with or without minor modifications), but the polyphyletic "spinosus" species group is dismantled into six monophyletic groups. A general pattern of strong character support for the monophyly of species groups but weak support for the relationships between them occurs in the trees from the molecular, morphological, and combined data sets; this congruent pattern is most likely the result of rapid speciation.

**Key words:** *Sceloporus*; Phylogeny; Classification; Speciation; Molecular data; Mitochondrial rDNA; Morphological data

THE LIZARD GENUS *Sceloporus* is the largest genus of reptiles endemic to North America, with approximately 80 species currently recognized (Sites et al., 1992). *Sceloporus* occur from southern Canada to Panama, but are most diverse in the southwestern USA and Mexico. In most of the areas where they occur, *Sceloporus* are among the most abundant, conspicuous, and diverse vertebrates present. Seemingly because of this, *Sceloporus* has been the subject of intense and diverse biological research, including studies of behavioral ecology, hybrid zone dynamics, host-parasite interactions, life history evolution, cytogenetics, reproductive biology, biogeography, physiological ecology, and allometric engineering (recently reviewed by Sites et al., 1992).

Despite this immense body of research, however, the phylogenetic relationships of *Sceloporus* species have remained poorly known. Although there have been several important systematic studies (i.e., Hall, 1973; Smith, 1939), the only explicitly cladistic analysis addressed the relationships of only 19 species (Mindell et al., 1989). There have been no comprehensive analyses of the genus using modern systematic techniques, yet a phylogenetic framework is desperately needed to understand the biology of *Sceloporus* species in an evolutionary context (Sites et al., 1992).

The goal of this study is to provide the first comprehensive analysis of *Sceloporus* using phylogenetic methods. This study will address the relationships of almost all the currently recognized species using molecular data collected by Reeder, morphological data collected by Wiens, and data from the literature on karyology and life

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history. The molecular and nonmolecular data sets will be analyzed separately and in combination, and the tree based on the combined data will then be used to revise the taxonomy of the genus. Prior to this revision, the species-group taxonomy of Smith (1939), with modifications by Thomas and Dixon (1976), is used throughout. References to Hall's unpublished dissertation work are based on the summary of Sites et al. (1992), and are cited simply as Hall (1973).

## MATERIALS AND METHODS

### *Morphological Data*

*Sources of characters.*—Morphological characters were derived from two sources: external morphology and osteology. Many of the external characters were originally used by Smith (1939) to identify and diagnose species and species groups, whereas others were found during this study. External characters were examined and scored from alcohol-preserved museum specimens, which are listed in Appendix I. External characters mostly involved variation in squamation and coloration. Unless otherwise stated, all coloration characters apply to the coloration of ethanol-preserved specimens; this allowed all taxa to be scored consistently regardless of whether living individuals were seen. Observations on live, recently preserved, and older preserved *Sceloporus* suggest that the major features of coloration and pattern used here are not significantly altered by preservation. Terminology for external features generally follows Smith (1939).

Most of the osteological specimens used in this study were prepared by Wiens from preserved museum specimens. For most specimens, the skull was prepared as a dry skeleton (with flesh removed by dermestid beetles and/or picking with forceps) and the postcranial skeleton and hyoid apparatus were cleared and double-stained with Alizarin red and Alcian blue using a modified version of the technique of Dingerkus and Uhler (1977). For some specimens (mostly those prepared prior to the study) the whole skeleton was prepared as a dry skeleton or (rarely) as a cleared-

and-stained skeleton. Dry skeletons were scored for postcranial characters, but specimens often could not be scored for many characters because of damage to delicate features during preparation. Because of potential artifactual differences between cleared-and-stained and dry skull preparations, cleared-and-stained skulls were not scored. All osteological specimens examined are listed in Appendix II. Terminology for osteological features follows de Queiroz (1987), Etheridge (1964), and Oelrich (1956).

Hemipenial features have been used widely in squamate systematics, but few preparations were available and this character system was not investigated. However, limited observations of *Sceloporus* hemipenes suggest there is little obvious variation. Previous authors have examined *Sceloporus* species for variation in scale surface microstructure (Burstein et al., 1974) and myology (Secoy, 1971) without finding useful characters. These sources of evidence were not considered further.

*Character selection and definition.*—Characters were chosen and character states (traits or conditions) were defined so that the observed morphological variation could be described as unambiguously as possible. 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 non-random covariance (see below). Characters that could not be described unambiguously, such as those involving continuous variation in shape and size, were avoided. The morphological characters used in this study are described and illustrated in Appendix IV.

Characters were considered to be independent *a priori* if they did not show

identical distributions among taxa. Several characters involved variation in color patterns that were treated as independent in males and females. There seems to be strong evidence that these traits can evolve independently in the sexes, based on the different distributions of the traits in males and females in the data matrix. To minimize biases due to ontogenetic variation, only adults were scored for morphological characters in this study.

*Coding morphological variation.*—Most of the characters showed extensive intra-specific variation (see Appendix V). Wiens (1995) found that "discrete" intraspecifically variable characters can contain significant phylogenetic information, although levels of noise (homoplasy) may increase with increasing intraspecific variability. Wiens (1995) also found that a frequency approach may be the best method for treating polymorphic data, based on comparing eight parsimony methods for up to five optimality criteria using seven real data sets, and based on its unique ability to extract significant phylogenetic information from the polymorphic characters in all the data sets examined. Furthermore, results from computer simulations of polymorphic data suggest that the frequency method is the most accurate parsimony coding approach under almost all combinations of branch lengths, sample sizes, and numbers of characters, and that excluding polymorphic characters decreases accuracy under all conditions (Wiens and Servedio, 1997a,b). Based on these results, 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 organismal conditions (e.g., scale present or absent, binary in the usual sense of the term) were coded using the frequency-bins method described by Wiens (1993b, 1995). Each species was assigned a letter from "a" to "y" based on the observed frequency of the putative derived trait ( $a = 0\text{--}3\%$ ,  $b = 4\text{--}7\%$ , etc.; Wiens, 1995), and traits were ordered from trait absence to fixation ( $a \rightarrow y$ ). 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.

Characters with multiple conditions (i.e., three or more traits among taxa) could not be coded using the frequency-bins method (Appendix IV, characters 55, 106, 146, 160, 162, 163). To analyze frequency data with multiple conditions, Wiens (1995) employed a method (suggested by D. Hillis) using 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 (i.e., requires more than the maximum of 32 states allowed by PAUP and slows down tree searches to an unacceptably slow rate). Instead, these characters were simply coded 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, for a given data set, the set of shortest trees generated by the majority method consistently includes the shortest tree(s) produced by the frequency method. Character state transformations using 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.

A few potentially multistate characters (such as number of premaxillary teeth) were broken down into two characters when the variation involved obvious reductions and additions to the primitive condition (e.g., reduction from 6 to 5 premaxillary teeth or increase from 6 to 7). This allowed the extensive intraspecific variation in these characters to be coded in a relatively precise fashion, using the frequency-bins method for binary characters. The disadvantage of this approach is that these pairs of characters are not fully

independent (a potential problem in character weighting), yet their weighting is effectively the same as if they were ordered (i.e., a change from 5 to 7 premaxillary teeth entails two full steps using either procedure).

Individuals that were bilaterally variable or asymmetric were included in calculations of trait 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 logical unknown ("?", unobservable, rather than unobserved). Similarly, in species in which only certain specimens could be scored for a feature (e.g., color of the belly patch in a species which 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 the color of the belly patch if the species was polymorphic for the presence or absence of belly patches.

*Chromosomal, life history, and behavioral characters.*—Chromosomal and life history variation (i.e., parity mode) have played an important role in previous hypotheses of *Sceloporus* phylogeny (Hall, 1973; Smith, 1939). Relevant chromosomal and life history data were extracted from the literature and coded for phylogenetic analysis. Variation in microchromosome number was treated as a single multistate character, because the homologies of individual microchromosomes are unclear. This character was ordered, given the reasonable assumption that (for example) a change from 10 to 12 microchromosomes is "easier" than a change from 10 to 20. Homologies among macrochromosome pairs have been hypothesized, and variation in macrochromosome structure (i.e., centric fissions or pericentric inversions) was coded by treating each chromosome pair as a separate character (following Bo-

rowik, 1995, and others). The extensive variation in sex chromosomes was described using several seemingly independent characters. Chromosome characters were weighted by 24 to maintain comparable weights to the frequency coded data (e.g., chromosome change equals change in frequency from 0 to 100%). Because subspecies were often treated as separate terminal taxa in this analysis, and because authors often did not report which subspecies were sampled, putative conspecific subspecies were assumed to have the same chromosomal characteristics. The general lack of geographic variation in the chromosomal characters used here (although numerous localities were often sampled) and the general chromosomal homogeneity of putative close relatives (Sites et al., 1992: their Table 4) seem to validate this convention. Parity mode was coded as a standard binary morphological character using the frequency-bins method. Conspecific subspecies were treated as having the same parity mode (unless known otherwise). These characters are listed in Appendix IV.

A substantial data base is available in the literature on comparative display behavior within *Sceloporus* (summarized in Carpenter, 1978). Although it would be tempting to code and include these characters also (as done by Reeder and Wiens, 1996), serious concerns have been raised about these data, particularly about standardization of results, intraspecific variation, and whether or not the patterns reported are truly species-specific (Leslie, 1988). These data were excluded from the phylogenetic analysis.

#### DNA Sequence Data

Molecular data consisted of DNA sequences of the mitochondrial 12S and 16S ribosomal RNA (rRNA) genes, collected from 64 ingroup taxa (see Table 1). These data were collected by Tod Reeder and, except where noted, methods of DNA isolation, amplification, and sequencing are described in Reeder (1995). For more recently sequenced taxa (those not included in Reeder, 1995), the following molecular methods were used. PCR cycle parameters

TABLE 1.—*Sceloporus* used as terminal taxa in this study. All taxa were scored for some or all external characters; other types of data scored are marked by an "X" (Chrom. = chromosomal characters). Species marked as being scored for a given data type often could not be scored for every character of that type. Deviations from standard or current taxonomy are discussed in the taxonomic accounts.

Species	Oste- ology	Chrom.	mtDNA	Species	Oste- ology	Chrom.	mtDNA
<i>acanthinus</i>	X			<i>merriami</i>	X	X	X
<i>adleri</i>	X	X	X	<i>mucronatus aureolus</i>		X	
<i>aeneus</i>	X	X		<i>m. mucronatus</i>	X	X	
<i>arenicolus</i>	X	X	X	<i>m. omiltemanus</i>	X	X	X
<i>asper</i>	X	X		<i>nelsoni</i>	X	X	
<i>bicanthalis</i>	X	X	X	<i>occidentalis</i>	X	X	X
<i>bulleri</i>	X	X		<i>ochoterenae</i>	X	X	X
<i>carinatus</i>	X			<i>olivaceus</i>	X	X	X
<i>cautus</i>	X			<i>orcutti</i>	X	X	X
<i>chaneyi</i>	X	X	X	<i>ornatus caeruleus</i>	X	X	X
<i>chrysostictus</i>	X	X	X	<i>o. ornatus</i>	X	X	
<i>clarkii</i>	X	X	X	<i>palaciosi</i>		X	
<i>couchii</i>	X	X	X	<i>parvus</i>	X	X	X
<i>cozumelae</i>	X	X	X	<i>pictus</i>	X	X	X
<i>cryptus</i>	X	X	X	<i>poinsettii</i>	X	X	X
<i>cupreus</i>	X			<i>prezygus</i>	X		
<i>cyanogenys</i>	X	X	X	<i>pyrocephalus</i>	X	X	X
<i>dugesii dugesii</i>	X	X	X	<i>salvini</i>			
<i>d. intermedius</i>	X	X		<i>scalaris samcolemani</i>		X	
<i>edwardtaylori</i>	X	X		<i>s. scalaris</i>	X	X	
<i>exsul</i>		X		<i>s. slevini</i>	X	X	X
<i>formosus formosus</i>	X	X	X	<i>s. unicanthalis</i>		X	
<i>f. scitulus</i>	X	X		<i>serrifer</i>	X	X	
<i>gadoviae</i>	X	X	X	<i>shannonorum</i>	X	X	
<i>goldmani</i>		X		<i>siniferus</i>	X	X	X
<i>graciosus</i>	X	X	X	<i>smaragdinus</i>	X		X
<i>grammicus</i>	X	X	X	<i>smithi</i>	X	X	X
<i>heterolepis</i>	X	X	X	<i>spinosus caeruleopunctatus</i>	X	X	X
<i>horridus albiventris</i>	X	X		<i>s. spinosus</i>	X	X	X
<i>h. horridus</i>	X	X	X	<i>squamosus</i>	X		
<i>hunsakeri</i>	X	X	X	<i>stejnegeri</i>		X	X
<i>insignis</i>	X			<i>subniger</i>	X		
<i>internasalis</i>	X			<i>subpictus</i>	X	X	X
<i>jalapae</i>	X	X	X	<i>taeniocnemis</i>	X	X	X
<i>jarrovi cyanostictus</i>		X	X	<i>tanneri</i>			
<i>j. erythrocyaneus</i>		X		<i>teapensis</i>	X	X	
<i>j. immucronatus</i>	X	X		<i>torquatus binocularis</i>	X	X	X
<i>j. jarrovii</i>	X	X	X	<i>t. melanogaster</i>	X	X	X
<i>j. minor</i>	X	X	X	<i>t. torquatus</i>	X	X	
<i>j. oberon</i>		X		<i>undulatus consobrinus</i>	X	X	X
<i>j. sugillatus</i>		X		<i>u. elongatus</i>	X	X	
<i>licki</i>	X	X	X	<i>u. erythrocheilus</i>	X	X	X
<i>lineatulus</i>	X			<i>u. garmani</i>	X	X	
<i>lineolateralis</i>	X			<i>u. hyacinthinus</i>	X	X	
<i>lunaei</i>	X			<i>u. tristichus</i>	X	X	
<i>lundelli</i>	X	X		<i>u. undulatus</i>	X	X	X
<i>macdougalli</i>			X	<i>utiformis</i>	X	X	X
<i>maculosus</i>	X	X	X	<i>vandenburgianus</i>	X	X	X
<i>magister</i>	X	X	X	<i>variabilis marmoratus</i>	X	X	X
<i>malachiticus</i>	X	X	X	<i>v. variabilis</i>	X	X	
<i>megalepidurus halli</i>		X		<i>virgatus</i>	X	X	X
<i>m. megalepidurus</i>	X	X	X	<i>woodi</i>	X	X	X
<i>melanorhinus melanorhinus</i>	X	X	X	<i>zosteromus</i>	X	X	X
<i>m. stuarti</i>	X	X					

for the 16SaR–16Sd fragment were: 94 C for 45 s, 45 C for 1 min, 72 C for 45 s (35 cycles). Before sequencing the PCR products, unincorporated nucleotides and primers were removed either using the silica matrix/NaI GeneClean™ protocol (Bio101, Inc.) or through PEG (20% PEG 8000/2.5 M NaCl) precipitation. The DNA pellet resulting from PEG precipitation was washed with 100 µl of 80% ethanol, followed by an additional wash with 100 µl of 95% ethanol. The DNA pellet was dried and resuspended in sterile distilled water. DNA templates were sequenced using a dye-labeled dideoxy terminator cycle sequencing kit (Applied Biosystems, Inc.) and ABI 373A automated DNA sequencer (Applied Biosystems, Inc.) as described in Caporale and Kocher (1994), with the following modifications. DMSO (final concentration 5%) was added to cycle sequencing reactions. Cycle parameters were: 96 C for 30 s, 45 C (16S) or 55 C (12S) for 20 s, 60 C for 3.5 min (35 cycles). Sequences were analyzed and edited using the computer software program Sequencher™. Specimens used in the molecular analyses are listed in Appendix III.

Interspecific length variation is a common feature of rDNA sequences (Kjer, 1995). The presence of insertions/deletions requires that gaps be placed in the sequences during alignment and the placement of gaps may be sensitive to gap cost, making nucleotide positional homologies ambiguous (Gatesy et al., 1993). We aligned the mitochondrial rDNA sequences under varying gap costs using the multiple sequence alignment program Clustal W (Thompson et al., 1994). The “Slow/Accurate” alignment option (versus Fast/Approximate) was employed. The initial pairwise alignment parameters for guide tree estimation were held constant during all alignments (Gap Open Penalty = 10; Gap Extension Penalty = 0.1). The following multiple alignment parameters were held constant during all alignments: Gap Extension Penalty = 0.05, Delay Divergent Sequences = 40%, and Transitions = unweighted. The main multiple alignment parameter that varied between alignments was Gap Opening Penalty (6, 8, 10, and

12). Regions of sequence were considered alignment-ambiguous if nucleotide positional homologies differed among the different gap cost (= Gap Opening Penalty) alignments (Gatesy et al., 1993). Ambiguously aligned regions were not included in the phylogenetic analyses.

Recent studies have advocated using rRNA secondary structure as an aid in aligning rRNA gene sequences (e.g., Kjer, 1995; Titus and Frost, 1996). Secondary structure information was taken into account following the general approach outlined by Titus and Frost (1996). Titus and Frost (1996) used the multiple sequence alignment program MALIGN (Wheeler and Gladstein, 1994) to constrain homologous stem regions to align to one another while optimally placing gaps (via specified gap costs) into other regions (i.e., loops and nonstem regions) of the rDNA sequence. Whereas MALIGN has the desirable option of allowing the enforcement of constraints during sequence alignment (no such option in Clustal W), the large number of taxa in this study made the implementation of MALIGN impractical (Reeder, personal experience). However, the placement of an identical 10-mer sequence (“GATCATCTAG”) before and after stem regions in all species sequences (before alignment) forced homologous stem regions to align to one another during the Clustal alignments.

In this study, the 12S rRNA secondary structural model of Van de Peer et al. (1994) and the 16S rRNA model of Gutell and Fox (1988) were used to identify stem regions constrained in the DNA sequence alignments. Stem locations in our sequence alignment can be found in Appendix V, with 12S stem designations following Van de Peer (1994) and 16S stem designations shown in Figure 1.

Because of the close relationship between *Sceloporus* and the outgroups, most nucleotide positions were alignment-invariant for the gap costs used in this study. In all, 985 nucleotide positions were aligned (345 12S and 640 16S; Appendix V), with only 47 positions being excluded from phylogenetic analysis. All DNA sequences are deposited in GenBank (acces-

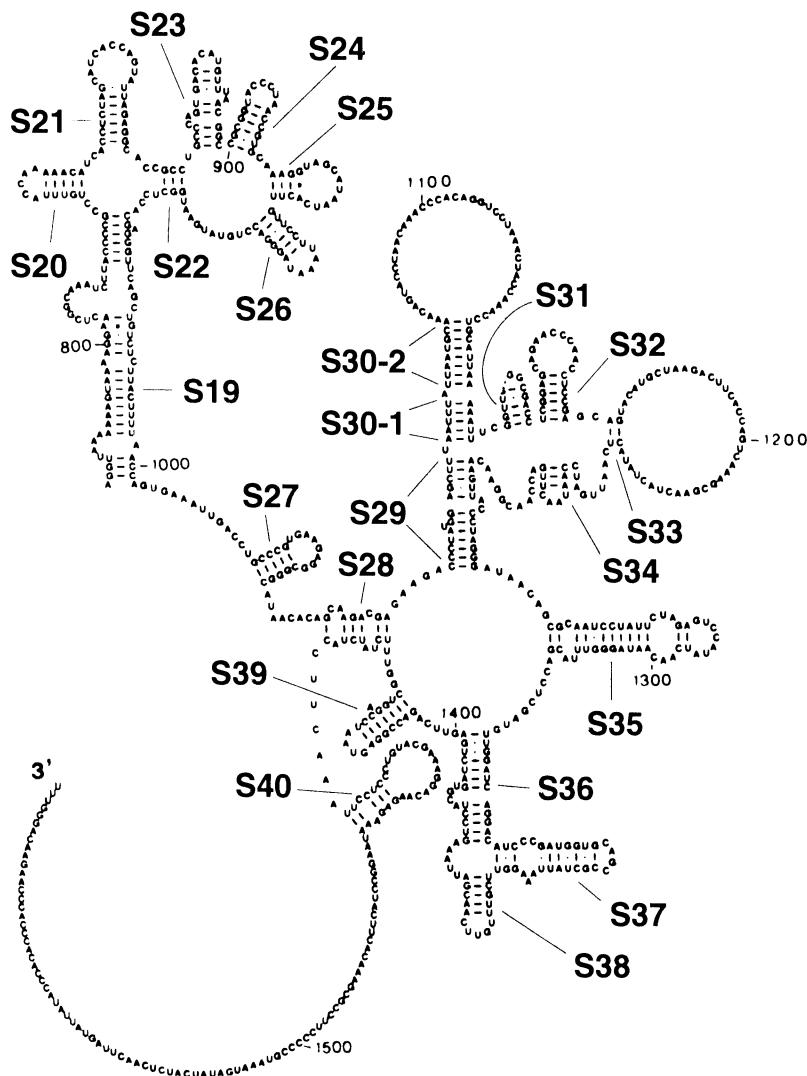


FIG. 1.—Secondary structure of 3' half of the 16S ribosomal RNA in humans (Gutell and Fox, 1988). Numbers preceded by "S" indicate sequence of stems. Figure modified from Gutell and Fox (1988).

sion numbers L40436–L40458, 41416–41489, AF000789–AF000897).

Nucleotide positions containing gaps were included in the phylogenetic analysis, with gaps (-) generally regarded as a fifth nucleotide character state. However, in some situations, such a coding scheme can obscure potential additional phylogenetic information. For example, a given clade could be defined by the presence of a DNA insertion (e.g., gap → G). However, this putative synapomorphy may be erased by subsequent nucleotide substitution (=

character transformation; e.g., G → A) in some taxa of the clade. In our study, nucleotide positions exhibiting gaps and multiple nucleotide bases were recoded to maximize the potential amount of phylogenetic information in such characters. This was done by splitting such characters into two characters. In the first character, all gaps were converted to missing data (i.e., gap → ?) and the nucleotide bases were left in their observed state (i.e., G, A, T, or C). The second character was coded as the presence/absence of gaps (i.e.,

gap [deletion] = 0; nucleotide base [insertion] = 1). Out of 18 phylogenetically informative nucleotide positions possessing gaps, only 8 required recoding. Seven of the 10 positions not recoded exhibited gaps and only a single nucleotide base (e.g., gap and A), effectively making them binary insertion/deletion characters. At the three remaining gap positions, the gaps were autapomorphic.

A variety of weighting and noise-reduction schemes have been applied to DNA data in phylogeny estimation (see Hillis et al., 1993, for a review). However, most reasonable weighting schemes are inapplicable to this study. Transition-transversion weighting may be inappropriate for phrynosomatid mitochondrial rDNA because there does not appear to be a significant transition bias and transitions and transversions appear to have similar phylogenetic information content in this group (Reeder, 1995). More sophisticated weighting schemes using step matrices to weight characters based on the observed frequency of different classes of substitutions have been used (e.g., Arevalo et al., 1994; Knight and Mindell, 1993; Wheeler, 1990). However, such step matrices would make effective tree searches difficult or impossible. Thus, as a default, all DNA characters and nucleotide substitutions were weighted equally.

#### *Phylogenetic Analysis*

*Choice of phylogenetic method.*—Parsimony analyses were performed using PAUP\* 4.0d52 (Swofford, 1996). Parsimony was used because of its intuitive appeal (i.e., the obvious relationship of character evidence to estimated trees), because it has been shown to accurately estimate phylogeny in computer simulations under a wide variety of realistic conditions (Hillis et al., 1994; Wiens and Hillis, 1996), and because current implementations of other phylogenetic methods (e.g., distance and likelihood) are problematic for combining data and including incomplete taxa (e.g., Felsenstein, 1995). The combined data matrix, including all taxa and characters, is given in Appendix V.

*Choice of taxa.*—We attempted to in-

clude all likely evolutionary species (*sensu* Frost and Hillis, 1990) of *Sceloporus*, regardless of whether or not they are currently recognized as such. Numerous subspecies have been recognized throughout the history of *Sceloporus* systematics (e.g., Smith, 1939); over 50 are currently recognized. These include many taxa that appear to be morphologically diagnosable and potentially allopatric to other putative conspecifics, and that may represent evolutionary species. Subspecies that are morphologically diagnosable and potentially allopatric and those that are clearly allopatric (based on Smith, 1939) were treated as separate terminal taxa in the phylogenetic analysis (Table 1). It is unlikely that all of these represent different evolutionary species, but we considered it more conservative to err on the side of treating conspecific populations as potentially different rather than lumping trait frequencies from more than one species. With this in mind, we also treated several species of questionable status (i.e., *S. bicanthalis*, *S. cyanogenys*, *S. internasalis*, *S. lineolateralis*, *S. pictus*, *S. prezygus*, *S. salvini*, *S. shannonorum*, *S. subniger*, and *S. teapensis*) as distinct species in the analysis (the literature on these controversial taxa was reviewed recently by Sites et al., 1992). Some subspecies of *Sceloporus* are seemingly not geographically separated and have overlapping morphological variation (e.g., the subspecies of *S. lundelli* and of *S. parvus*). These subspecies were either not sampled or were combined with conspecific samples. Some subspecies currently assigned to *S. undulatus* and *S. jarrovii* were treated as different terminal taxa although there is little evidence for geographical or morphological separation (e.g., *S. u. undulatus* and *S. u. hyacinthinus*, and *S. j. minor* and *S. jarrovii immucronatus*). This was done because of the difficulty of deciding exactly which taxa to combine with which in these problematic complexes. Possible taxonomic changes suggested by the resulting phylogenetic trees are discussed in the systematic accounts of the species groups. Finally, a few potentially distinctive taxa were not included because well-preserved adult specimens were not

available at the time: *S. anahuacus*, *S. occidentalis becki*, *S. spinosus apicalis*, and *S. torquatus mikeprestoni*. A total of 107 taxa of *Sceloporus* were included in the morphological data set.

**Rooting of trees.**—Outgroup relationships of *Sceloporus* are currently well resolved, if not strongly supported (Reeder and Wiens, 1996). We accepted the inter- and intrageneric relationships found by Reeder and Wiens (1996), based on combined molecular, morphological, and behavioral data, with *Urosaurus*, *Petrosaurus*, and *Uta* forming successive first, second, and third outgroups of the *Sator* + *Sceloporus* clade. Rather than going through a laborious optimization for each character (e.g., Maddison et al., 1984), we simply constrained the species relationships of the outgroup species sampled to the combined, all-taxa tree of Reeder and Wiens (1996). This was done using the constraints option of PAUP, such that trees were only retained if they met the constraint of the assumed outgroup relationships. Note that the unrooted outgroup topology we used (*Uta*, *Petrosaurus* (*Urosaurus* (*Sator* + *Sceloporus*))) is consistent with the novel placement of *Petrosaurus* and *Uta* posited by Reeder and Wiens (1996) and the more traditional arrangements (with *Uta* as the sister group of the clade of *Urosaurus* and *Sceloporus* + *Sator*) suggested by Etheridge and de Queiroz (1988) and Wiens (1993a).

Monophyly of *Sceloporus* has been a contentious issue, with several authors arguing that *Sator* is likely nested inside *Sceloporus* (Etheridge and de Queiroz, 1988; Frost and Etheridge, 1989; Reeder, 1995; Wyles and Gorman, 1978) and others suggesting that *Sator* is the sister group of a monophyletic *Sceloporus* (Reeder and Wiens, 1996; Wiens, 1993a). To further test the monophyly of *Sceloporus*, the two species of *Sator* were included as ingroup taxa, bringing the total number of ingroup taxa to 109.

**Evaluation of signal, support, and confidence.**—Given a large number of characters relative to the number of taxa, it is possible to generate a single most parsimonious tree from a data set even when

the characters show levels of noise (homoplasy) comparable to random data (Hillis and Huelsenbeck, 1992). To guard against this possibility, each data set (molecular, morphological, and the two combined data sets) was examined to see if it contained levels of covariation among characters significantly greater than expected for random data using the  $g_1$  statistic (Hillis, 1991; Hillis and Huelsenbeck, 1992; Huelsenbeck, 1991). Critical values for random data were extrapolated from Tables 1 and 2 of Hillis and Huelsenbeck (1992). Although it would be preferable to generate critical values from randomization of each data set (e.g., Reeder, 1995; Wiens, 1995), the data sets used in this study were too large to make such an analysis tractable and our observed  $g_1$  values were never close to the published critical values. The large number of taxa also made it necessary to estimate the tree length frequency distribution using a random sample of 10,000 trees (from the set of all trees) from each data set, rather than examining the length of every tree (i.e., through an exhaustive search). For each data set,  $g_1$  values were calculated with the outgroup taxa deleted, so that the test evaluated signal within the ingroup only. The  $g_1$  statistic was used as the primary test of whether or not each data set contained useable levels of phylogenetic information relative to random noise; values of the consistency index (Kluge and Farris, 1969) and retention index (Farris, 1989) are reported for each data set but are not interpreted. The  $g_1$  statistic has been criticized by Källersjö et al. (1992), but these authors did not rigorously address the ability of this index to distinguish data sets with significant phylogenetic signal from those containing only random noise (see instead Hillis, 1991; Hillis and Huelsenbeck, 1992; Huelsenbeck, 1991).

To examine the stability of individual clades we examined trees slightly longer (one full step, or the length from a to y) than the shortest tree found for each data set (molecular, morphological, and combined) to see if the recovered nodes were present among the near-shortest trees, following Bremer (1988) and Hillis and Dix-

on (1989). The decay index (Donoghue et al., 1992) is somewhat problematic in that the significance of different decay values are unclear in terms of accuracy (i.e., is a clade with a decay index value of two steps probably right or probably wrong?; see also Hillis and Huelsenbeck, 1992). We considered clades not present in near-shortest (one step longer) trees to be only weakly supported, but did not necessarily consider clades present in the near-shortest trees to be well supported. Nonparametric bootstrapping (Felsenstein, 1985) was difficult for data sets with 109 taxa (given this number of taxa, it is difficult to find the shortest tree even once, but to find the shortest tree in each of 100 pseudoreplicates would likely be impossible). Bootstrapping analyses were performed on the molecular data and the reduced, combined data set (including only those taxa scored for molecular and morphological data, see below) and for analyses with all the taxa but with some topological constraints applied. The constrained analyses applied to each data set are described in their respective sections. The constraints were used because of the large number of taxa, but in some cases they may make bootstrap values less conservative. For each bootstrapping analysis, 100 pseudoreplicated data sets were analyzed, with two replicated heuristic searches (with TBR branch swapping) for each pseudoreplicate. Hillis and Bull (1993) found that bootstrap values of 70% or greater generally correspond to a 95% or greater probability of a clade being correctly resolved (based on simulated and experimental phylogenies), given that conditions are otherwise amenable to accurate phylogeny reconstruction using parsimony (e.g., "safe" branch lengths). For these reasons we consider clades with bootstrap values  $\geq 70\%$  to be strongly supported, but with the caveat that the relationship between bootstrap values and accuracy will be less conservative under some conditions (Hillis and Bull, 1993). In many cases, we consider it unlikely that our heuristic searches for shortest trees from the bootstrap-resampled data matrices actually found the shortest tree. However, this should make

the analysis more conservative (because a well-supported clade will tend to be found more often than a weakly supported clade among the suboptimal trees).

*Separate and combined analysis of data sets.*—The molecular and nonmolecular data sets were analyzed separately and then combined. For each analysis, at least 200 replicated searches were used, each using TBR (tree–bisection–reconnection) branch swapping. In the combined analyses, all characters were weighted equivalently. Thus, all DNA characters were weighted by 24 so that a nucleotide change was equal in weight to a change in the frequency of a morphological trait from 0 to 100%.

The tree from the combined data was taken as the best estimate of the species phylogeny because (1) the combined analysis uses the largest number of characters, and accuracy generally increases with increasing numbers of characters; and (2) any misleading sets of characters should be outnumbered by those representing the true phylogeny in the combined analysis, because the phylogenetic history shared by most sets of characters should be the true species phylogeny (Wiens and Chippindale, 1994). Bull et al. (1993b) and de Queiroz (1993) argued that if the underlying phylogenetic histories of the data sets differ (e.g., if the ribosomal 12S gene tree did not match the species tree), then the combined-data estimate may be incorrect, especially if the misleading data set has more characters. However, such arguments are based (implicitly or explicitly) on trees with a small number of taxa, where the estimated phylogeny is either right or wrong. Given a data set with a large number of taxa, where the phylogenetic histories of the data sets may differ in only part of the tree, the part of the phylogeny where the histories differ may be incorrectly estimated in the combined analysis, but combining data may nevertheless increase accuracy when the entire tree is considered by using a larger number of characters (Wiens, unpubl. data). Given this perspective, we take an approach that uses the advantages of combined analysis while taking into account

the possibility that areas of strongly supported conflict between trees from the separate data sets may be indicative of different phylogenetic histories (Bull et al., 1993b; de Queiroz, 1993). In this study we (1) partition the total data available to maximize detection of possible gene tree-species tree mismatch (dividing the total data into one data set consisting of the two linked mitochondrial genes and a second consisting of the nonmitochondrial data); (2) perform both separate and combined analyses of the data sets, and evaluate support for individual clades in each (using the bootstrap); and (3) take the tree(s) from the combined data as the best estimate of phylogeny, but consider questionable those parts of the tree that are in strongly supported conflict between the separately analyzed data sets. These questionable parts of the phylogeny can be considered decisively resolved when a majority of unlinked data sets support one resolution over the other.

The number of ingroup taxa scored for the morphological characters ( $n = 109$ ) greatly exceeded the number available for molecular analysis ( $n = 64$ ). 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. 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) and the tree based on all 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. Furthermore, they found that similar decreases were also possible for adding complete taxa. In this study we performed two analyses of the combined data sets: one that included only those species scored for both data sets and another including all the species. The final hypothesis included all the species, but the placement of incomplete taxa was considered tentative, and more confidence was

placed in relationships insensitive to their inclusion or exclusion. It should also be noted that species varied greatly in their level of completeness, with even relatively complete species often missing (1) osteological data (because specimens were unavailable for preparation as skeletons), (2) karyological and life history characters (for poorly known taxa), and (3) some external characters (because of inapplicability of characters). The general types of data available for each terminal taxon are given in Table 1.

## RESULTS

### *Molecular Data*

The molecular data set consists of 945 aligned nucleotide positions from the mitochondrial ribosomal 12S and 16S rRNA genes (993 sequenced, 48 excluded because of ambiguous alignment). The data set contains a minimum of 262 parsimony-informative characters. This is a minimal estimate because the outgroup taxa were deleted to determine the number informative within the ingroup, but any characters that are found in only one species in the ingroup and also one or more outgroup species are not counted. Molecular data were obtained for a total of 64 ingroup taxa.

Analysis of the lengths of 10,000 randomly sampled trees resulted in a  $g_1$  index of  $-0.592$  for these data (outgroup taxa excluded). The critical  $g_1$  value for random data for 25 or more taxa for a four-state character (such as DNA sequences) for 250 characters is  $-0.08$  ( $P = 0.05$ ) or  $-0.09$  ( $P = 0.01$ ), based on Table 1 of Hillis and Huelsenbeck (1992). The more negative  $g_1$  value observed suggests that the molecular data do contain significant phylogenetic information.

Analysis of the molecular data alone with 500 replicated searches with TBR branch swapping resulted in 44 shortest trees (Fig. 2) of length 1731. The trees each have a consistency index of 0.29 (excluding uninformative characters) and a retention index of 0.52. Parsimony analysis retaining trees up to one step longer than the shortest tree resulted in 1376 trees (after 100 replicated searches).

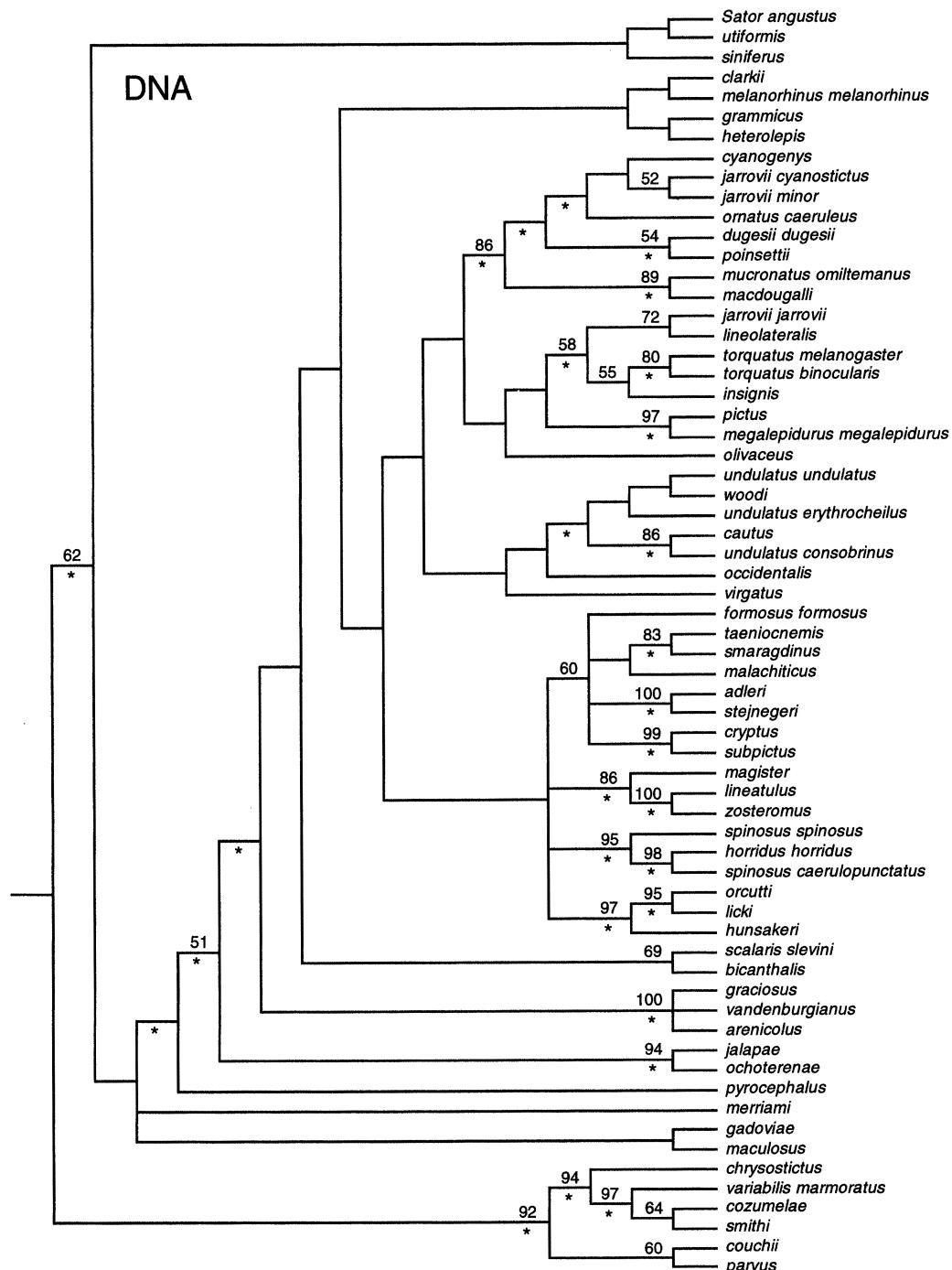


FIG. 2.—Strict consensus tree of 44 shortest trees from the analysis of the DNA data alone. Numbers correspond to bootstrap values. Asterisks correspond to clades supported in an analysis of trees up to one step longer than the shortest tree (i.e., a decay index of one or greater). Nodes with no bootstrap values listed have P-values less than 50%, and clades with no asterisks are not supported in slightly longer trees.

The shortest molecular trees (Fig. 2) support a monophyletic *variabilis* species group (including *S. chrysostictus*, per Cole, 1978) as the sister taxon of all other *Sceloporus* (including *Sator*). Within the *variabilis* group, *S. couchii* and *S. parvus* make up the sister group of the remaining species. Above the *variabilis* group, a clade consisting of *S. utiformis* and the representatives of the *siniferus* group (*S. siniferus*) and *Sator* is the sister taxon of the remaining *Sceloporus* species. These trees also place *S. utiformis* and *Sator* as sister taxa, as suggested by Wyles and Gorman (1978; based on immunological and allozyme similarity) and subsequent authors. *Sator* is placed well within *Sceloporus* by these data, despite previous morphological results (Reeder and Wiens, 1996; Wiens, 1993a). Above the *Sator-utiformis-siniferus* clade is a polytomy consisting *S. merriami*, the *S. gadoviae* + *S. maculosus* clade, and a clade containing the remaining species of *Sceloporus*. *Sceloporus pyrocephalus* is the next taxon up the tree. The failure of *S. gadoviae* to cluster with *S. pyrocephalus* rejects the monophyly of Smith's (1939) *pyrocephalus* group. However, the relationships among these species are only weakly supported by the molecular data (Fig. 2). Above *S. pyrocephalus*, the monophyletic *jalapae* group of Thomas and Dixon (1976; *S. jalapae* and *S. ochoterenae*) is the sister group of the remaining species. The *graciosus* group (*S. arenicolus*, *S. graciosus*, and *S. vandenburgianus*) is immediately above the *jalapae* group, and the representatives of the *scalaris* group (*S. bicarinatus* and *S. scalaris slevini*) are above the *graciosus* group. Above the *scalaris* group is a clade containing the representatives of Smith's large-scaled, large-bodied "radiation," exclusive of the *graciosus* group. Thus, the molecular data agree in general with Smith's (1939) tree (rooted with *Uta*, *Urosaurus*, and *Petrosaurus* as parts of "Uta"), with the small-scaled radiation as a paraphyletic series of lineages leading up to a large-scaled radiation, although the *scalaris* group (considered to be small-scaled by Smith) is placed among the large-scaled lineages. The first clade above the *scalaris*

group consists of *S. clarkii* + *S. melanorhinus* (of Smith's "spinosus" group) and the two representatives of the *grammicus* group (*S. grammicus* and *S. heterolepis*).

Above this clade, the large-scaled species are divided into two weakly supported clades, one containing representatives of the *undulatus*, *torquatus*, and *megalepidurus* groups (and also one species of the "spinosus" group), and the other clade containing representatives of the *formosus* and "spinosus" groups. Within the first clade, a monophyletic *undulatus* group is the sister taxon of the remaining species. The molecular trees suggest that *S. caudatus* and *S. woodi* are nested within *S. undulatus*, and that *S. virgatus* and *S. occidentalis* are outside of this clade. The sister taxon of the *undulatus* group is a clade containing mostly species of the *torquatus* group. Although well supported by morphology (see below), the molecular data do not support the monophyly of the *torquatus* group. Instead they suggest that the *torquatus* group is divided into two clades, with *S. olivaceus* (of Smith's "spinosus" group) and the monophyletic *megalepidurus* group (represented by *S. pictus* and *S. megalepidurus*) more closely related to one of these clades than are other species of the *torquatus* group. However, the nonmonophyly of the *torquatus* group is not strongly supported by bootstrapping (Fig. 2). The composition of and relationships within the two *torquatus* group clades are not particularly intuitive; some species are supported as monophyletic (*S. torquatus*) whereas others are not (*S. jarrovii* *jarrovii* is in one clade, *S. jarrovii minor* and *S. jarrovii cyanostictus* are in the other). Smith's (1939) division of the *torquatus* group into small and large scaled species is not supported.

The other major clade within the putative large-scaled radiation contains species of the *formosus* and "spinosus" groups. Relationships within this lineage are not well resolved, but four main clades are supported. One clade contains the monophyletic *magister* complex (*S. lineatulus*, *S. magister*, and *S. zosteromus*) and another clade contains the monophyletic *orcuttii* complex (*S. hunsakeri*, *S. laticauda*, and *S. or-*

*cutti*), following the terminology of Murphy (1983). A third clade contains *S. spinosus* + *S. horridus* and the fourth contains the representatives of the *formosus* group. The *formosus* group clade includes *S. cryptus* and *S. subpictus*, two species that were classified in the *megalepidurus* group in their original descriptions (Smith and Lynch, 1967, and Lynch and Smith, 1965, respectively) but were transferred to the *formosus* group by Hall (1973). Relationships within the *formosus* group are poorly resolved. One clade contains *S. cryptus* and *S. subpictus* (two cryptic species found sympatrically with *S. formosus* in different parts of its range), another contains the representatives of the *malachiticus* complex (sensu Sites et al., 1992; *S. malachiticus*, *S. smaragdinus*, and *S. tenuiocnemis*), and a third contains two species endemic to Guerrero (*S. adleri* and *S. stejnegeri*).

In summary, the molecular data support the monophyly of the following species groups: *variabilis* (sensu Cole, 1978), *jalapae* (sensu Thomas and Dixon, 1976), *scalaris*, *undulatus*, *megalepidurus* (sensu Hall, 1973), *grammicus*, *graciosus*, and *formosus* (sensu Hall, 1973). All but the *grammicus* and *undulatus* groups appear to be strongly supported by bootstrapping (Fig. 2). The molecular data provide weak evidence against the monophyly of the *pyrocephalus*, *spinosus*, and *torquatus* species groups. Relationships among the species groups are only weakly supported (Fig. 2).

#### Morphological Data

The morphological data set consists of 209 variable characters, of which 202 are phylogenetically informative. These data are relatively diverse, and can be grouped as follows (numbers in parentheses are the numbers of characters that are informative, if this differs from the total number): osteology = 50, scalation = 88 (87), coloration = 58 (53), life history (parity mode) = 1, and karyology = 12 (11). These characters are described and illustrated in Appendix IV.

The  $g_1$  value for the morphological data is -0.324. The critical  $g_1$  value for random

data for 25 or more taxa for a two or four-state character for 250 characters is -0.08 ( $P = 0.05$ ) or -0.09 ( $P = 0.01$ ), based on Table 1 of Hillis and Huelsenbeck (1992). The more negative  $g_1$  value suggests that the morphological data also contain significant levels of phylogenetic information. These morphological data are different in some ways from the random data sets generated by Hillis and Huelsenbeck (1992) in that they are mostly frequency data coded using 24 ordered character states. However, Hillis and Huelsenbeck (1992) found few differences in  $g_1$  values due to number of character states, and Wiens (1995) performed randomizations of a subset of these data (from a larger analysis of phrynosomatid relationships; Reeder and Wiens, 1996) and found significant phylogenetic signal in the frequency-coded morphological data using the  $g_1$  index.

Parsimony analysis of the morphological data resulted in a single shortest tree of length 1673.0 (Figs. 3, 4). The shortest tree was not found in 500 replicated searches, but only after a search retaining near-shortest trees. The shortest tree has a consistency index of 0.13 (excluding uninformative characters) and a retention index of 0.58. An analysis retaining trees up to a full step longer resulted in more than 20,000 trees. The search was stopped after 20,000 trees were found because of time and memory limitations. Because the analysis did not run to completion, clades that survived in the consensus trees should not necessarily be interpreted as strongly supported. Several constrained bootstrap analyses were performed to assess confidence within and between various groups. The first analysis examined the basal relationships of the genus. For this analysis, relationships within the 22-chromosome clade and the 32-chromosome clade (see Fig. 3 and discussion below) were constrained, and the rest of the ingroup tree was left unconstrained. Two more analyses examined the relationships within each of these two clades, constraining the relationships of the other taxa to the shortest morphology tree. The 22- and 32-chromosome clades were used because they conveniently divide up *Sceloporus* into large clades,

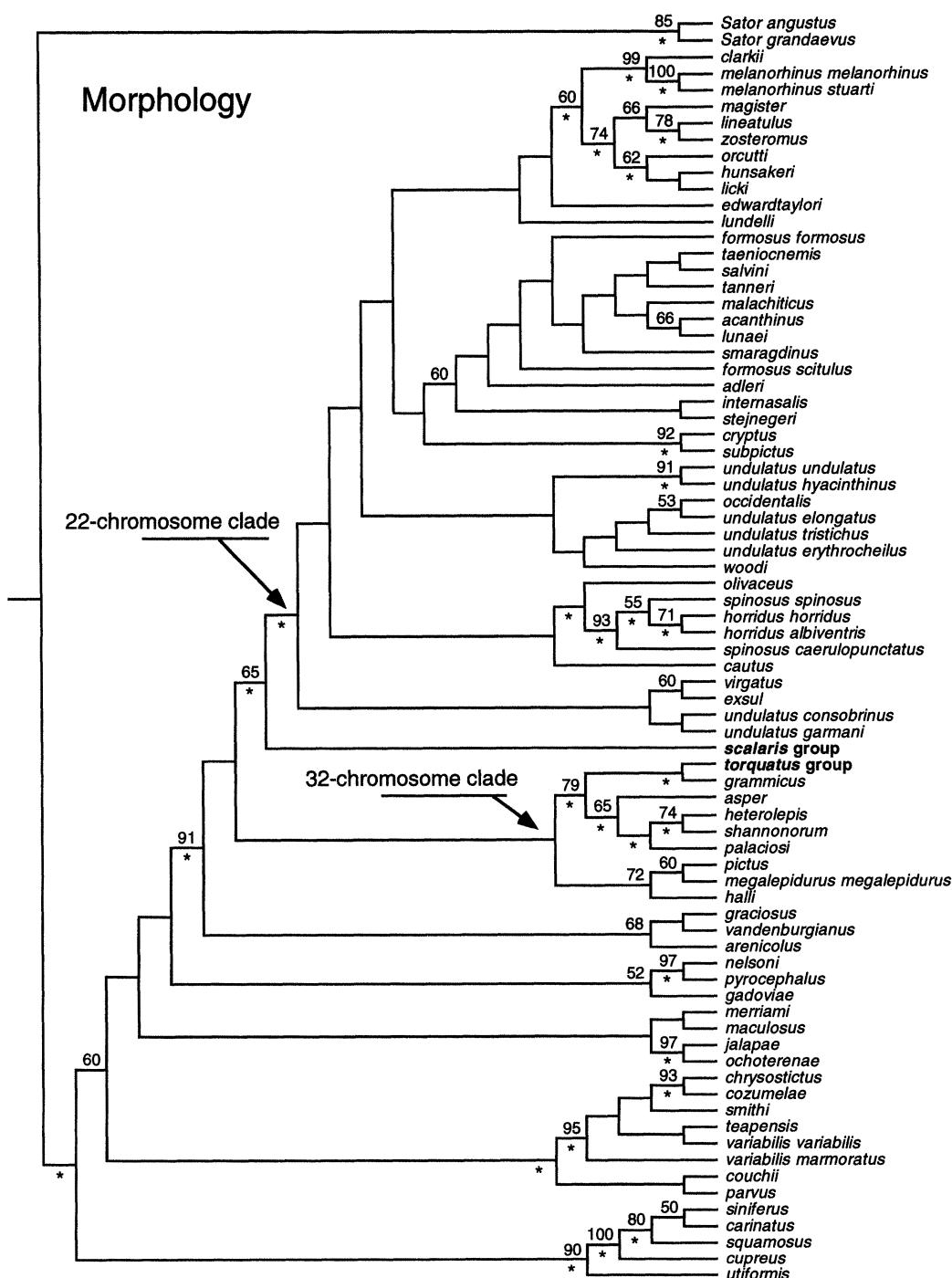


FIG. 3.—Shortest tree from the analysis of the morphological data alone. Relationships within the *scalaris* and *torquatus* species groups are shown in Figure 4. Numbers correspond to bootstrap values. Asterisks correspond to clades supported in an analysis of trees up to one step longer than the shortest tree (i.e., a decay index of one or greater). Nodes with no bootstrap values listed have *P*-values less than 50%, and clades with no asterisks are not supported in slightly longer trees.

## Morphology

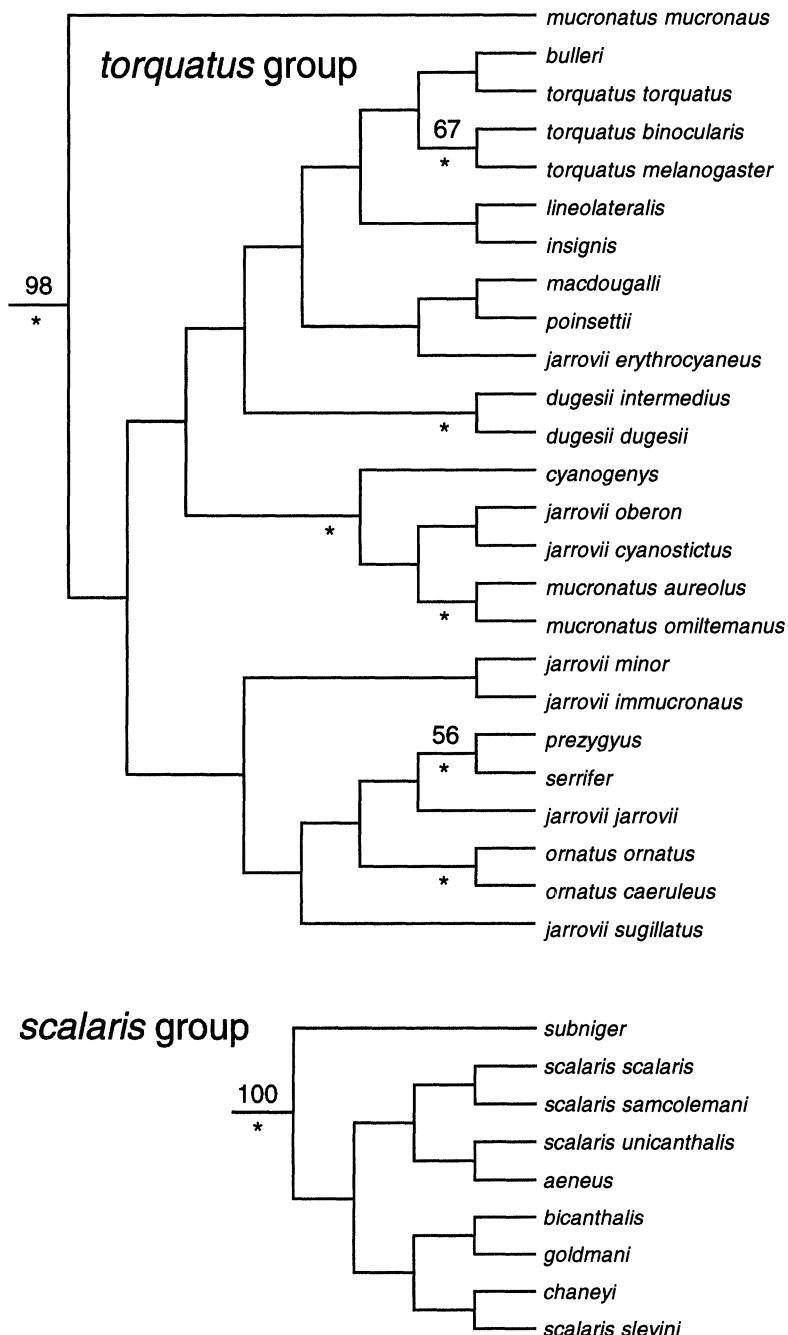


FIG. 4.—Relationships within the *scalaris* and *torquatus* species groups based on morphological data alone. Numbers correspond to bootstrap values. Asterisks correspond to clades supported in an analysis of trees up to one step longer than the shortest tree (i.e., a decay index of one or greater). Nodes with no bootstrap values listed have *P*-values less than 50%, and clades with no asterisks are not supported in slightly longer trees.

not because they are particularly well-supported groups.

The shortest tree from the morphological data is described below. The morphological data alone suggest that *Sator* is the sister group of *Sceloporus*, not nested inside of it. This is supported by previous morphological studies (Reeder and Wiens, 1996; Wiens, 1993a) but rejected by the molecular data of this and previous studies. The monotypic *utiformis* group and the monophyletic *siniferus* group together make up the sister taxon of all other *Sceloporus*. Above the *utiformis*–*siniferus* group clade, the *variabilis* group is the sister taxon of the remaining species. As in the molecular trees, the *variabilis* group is monophyletic if *S. chrysostictus* is included, and within the *variabilis* group, *S. couchii* and *S. parvus* are the sister group of the other species. Within the latter clade, the Yucatan species, *S. chrysostictus* and *S. cozumelae*, are sister taxa, whereas the *variabilis* complex (the current or former *S. variabilis* subspecies, *marmoratus*, *smithi*, *teapensis*, and *variabilis*) is not monophyletic.

Above the *variabilis* group, a clade containing the *jalapae*, *merriami*, and *maculosus* species groups is the sister taxon of the remaining species. The monotypic *merriami* and *maculosus* groups are sister taxa, both are small, rock-dwelling species from the Chihuahuan desert. The *jalapae* group of Thomas and Dixon (1976) is supported as monophyletic (*S. jalapae* and *S. ochoterenae*).

Above this clade is the *pyrocephalus* group (including *S. gadoviae*, *S. nelsoni*, and *S. pyrocephalus*). Smith's (1939) concept of the monophyly of and relationships within this group is supported by these data, whereas Hall's (1973) placement of the *pyrocephalus* group in his *orcutti* group (including *S. pyrocephalus*, *S. nelsoni*, *S. orcutti*, *S. licti*, and *S. hunsakeri* and excluding *S. gadoviae*) is rejected. Above the *pyrocephalus* group is a clade corresponding to the large-scaled radiation of Smith (1939), but including the *scalaris* group (as in the molecular trees).

The *graciosus* group (*S. arenicolus*, *S. graciosus*, and *S. vandenburgianus*) is the

sister taxon of the other members of this speciose clade. Above the *graciosus* group, the large-scaled species (including the *scalaris* group) can be divided into three main clades: (1) the *scalaris* group, (2) a group we term the 32-chromosome clade (those species with a diploid chromosome number of 32, including the *torquatus*, *grammicus*, *asper*, and *megalepidurus* groups of previous authors), and (3) the 22-chromosome clade (the primitive members of which have a diploid chromosome number of 22, including the *formosus*, *undulatus*, and “*spinosus*” groups of Smith, 1939). The *scalaris* group and 22-chromosome clade are sister taxa.

Within the 32-chromosome clade, a clade consisting of *S. megalepidurus* *megalepidurus*, *S. megalepidurus halli*, and *S. pictus* is the sister taxon of the remaining species. This grouping also is congruent with the molecular trees (molecular data lacking for *S. m. halli*) and is consistent with Hall's (1973) formulation of the *megalepidurus* group (based on chromosomal data), although Lynch and Smith (1965) and Smith and Lynch (1967) placed *S. cryptus* and *S. subpictus* in this group also. Above the *megalepidurus* group is a clade consisting of *S. asper* and three species of the *grammicus* group (*S. palaciosi*, *S. heterolepis*, and *S. shannonorum*). One other species of the *grammicus* group, *S. grammicus*, does not cluster with other species of the group, and is instead the sister taxon of the *torquatus* group. We consider this unusual placement of *S. grammicus* to be spurious, as the combined data place it with the other members of the *grammicus* group (see below). Because of the polytypic nature of *S. grammicus* (see Sites et al., 1992, for a review) only representatives of the S race of *grammicus* (and only from Oaxaca and Guerrero) were scored, in order to ensure that the molecular and morphological data pertained to the same species. However, these populations are not necessarily typical of the “species” as a whole, and lack some of the unusual features seen in other populations and in other species of the *grammicus* group (e.g., light throat stripe in males, posteriorly convergent nuchal collar). *Sceloporus as-*

*per* is the sister taxon of the *grammicus* group species exclusive of *S. grammicus*. Smith (1939) placed *S. asper* in the *formosus* group, whereas Hall (1973) placed it in its own species group close to the *grammicus* group. The latter hypothesis is supported in this morphological analysis.

Although monophyly of the *torquatus* group is supported by several morphological synapomorphies (see below) and has very strong bootstrap support, relationships within this group are very unstable (Fig. 4). The seeming polyphyly of many species (i.e., *S. jarrovii*, *S. mucronatus*, and *S. torquatus*) suggests that much additional work on both phylogenetics and geographic variation in this species group will be required. Smith's (1939) division of the *torquatus* group into large and small-scaled species is not supported by the morphological data.

Relationships within the *scalaris* group (Fig. 4) are weakly supported and do not support the traditional species-level taxonomy for the genus (i.e., the subspecies of *S. scalaris* do not form a monophyletic group, nor do the former subspecies of *S. aeneus*: *S. aeneus*, *S. bicanthalis*, and *S. subniger*).

Within the 22-chromosome clade, a clade of four taxa of the *undulatus* group (*S. exsul*, *S. virgatus*, *S. undulatus consobrinus*, and *S. undulatus garmani*) is weakly supported as the sister taxon of the remaining species. Above this clade is a clade consisting of *S. caurus* of the *undulatus* group and three species of the "spinosus" group (*S. olivaceus*, *S. horridus*, and *S. spinosus*). The *spinosus* + *horridus* clade is strongly supported, as is the clade uniting the two subspecies of *S. horridus* sampled. The next clade within the 22-chromosome group contains the remaining taxa of the *undulatus* group (*S. occidentalis*, *S. woodi*, and the other subspecies of *S. undulatus*). The next clade within the 22-chromosome group consists of two groups: one containing the species of the *formosus* group (including *S. cryptus* and *S. subpictus*) and the other containing the remaining species of the "spinosus" group. *Sceloporus cryptus* and *S. subpictus* together make up the sister tax-

on of the *formosus* group. Lynch and Smith (1965) and Smith and Lynch (1967) placed *S. cryptus* and *S. subpictus* in the *megalepidurus* group, whereas Hall (1973) placed these two species in the *formosus* group. The *formosus* group of Smith (1939) is supported as monophyletic, except that *S. asper* is clearly outside of it (as suggested by Hall, 1973). Relationships within the *formosus* group are generally not well supported, although there is moderate support for the clade *S. acanthinus* + *S. lunaei* (suggested by Smith, 1939).

Within the "spinosus" group clade, *S. lundelli* and *S. edwardtaylori* are successive outgroups of the remaining species. *Sceloporus clarkii* and *S. melanorhinus* are strongly supported as sister taxa, a grouping supported by the molecular data and consistent with Hall's (1973) *clarkii* group. Above the *clarkii* + *melanorhinus* clade is a clade containing the monophyletic *magister* complex (*S. lineatulus*, *S. magister*, and *S. zosteromus*) and *orcitti* complex (*S. hunsakeri*, *S. licki*, and *S. orcutti*), following Murphy's (1983) terminology. The monophyly and relationships of these two clades are identical in the molecular trees, except that the positions of *S. orcutti* and *S. hunsakeri* are reversed.

In summary, the morphological data support the monophyly of the following species groups: *graciosus*, *formosus* (sensu Hall, 1973), *jalapae* (sensu Thomas and Dixon, 1976), *scalaris*, *siniferus*, *megalepidurus* (sensu Hall, 1973), *pyrocephalus*, *torquatus*, and *variabilis* (sensu Cole, 1978). The morphological data reject the monophyly of the *grammicus*, *spinosus*, and *undulatus* groups. Support is generally weak for the relationships among these groups.

#### Congruence between Molecular and Morphological Trees

Many of the clades found in the mt-DNA trees are also found in the trees based on morphology. To illustrate the taxonomic congruence between the data sets, a strict consensus of the fundamental trees from the separate analyses is shown in Figure 5. As found by Reeder and Wiens (1996), many of the clades present in the

taxonomic congruence tree appear to be strongly supported by one or both data sets. For example, the *variabilis*, *jalapae*, *megalepidurus*, *scalaris*, and *graciosus* groups, the *magister* and *orcuttii* complexes, the *chrysostictus* + *cozumelae* + *variabilis* complex clade, the *cryptus* + *subpictus* clade, and the *spinulosus* + *horridus* clade are all strongly supported by bootstrapping in the molecular data set. Among these clades, all except the *megalepidurus* and *graciosus* groups are also present in the near-shortest morphological trees and are strongly or moderately well supported by bootstrapping. Most of the clades that are in conflict between the two data sets are not strongly supported by the molecular data, and/or appear to be only weakly supported by the morphological data. This is consistent with the results of Reeder and Wiens (1996), who found that none of the clades in conflict between their molecular and morphological data sets were strongly supported by both. However, there appears to be one strongly supported conflict between the molecular and morphological data sets within the *variabilis* group; the morphological data strongly support *S. chrysostictus* and *S. cozumelae* as sister taxa (bootstrap value = 97%), whereas the molecular data strongly support a clade that includes *S. cozumelae*, *S. smithi*, and *S. variabilis marmoratus* but excludes *S. chrysostictus* (bootstrap value = 94%).

#### Combined Data—All Taxa

The combined data set includes 109 ingroup taxa and at least 464 phylogenetically informative characters. The combined data have a  $g_1$  value of -0.415. The critical values for two and four state characters for 25 or more taxa for 500 characters is -0.08 and -0.07 ( $P = 0.05$ ) and -0.08 and -0.09 ( $P = 0.01$ ), suggesting that the combined data do have significant phylogenetic signal.

A search using 200 different starting trees and TBR branch swapping resulted in a single shortest tree of length 3465.0 (Figs. 6, 7). Extensive swapping on near-shortest trees failed to find a more parsimonious tree. The shortest tree has a con-

sistency index of 0.21 and a retention index of 0.55. An analysis retaining trees up to a full step longer resulted in more than 20,000 equally parsimonious trees. The search was stopped after 20,000 trees were found because of time and memory limitations. Because the analysis did not run to completion, clades that survived in the consensus trees should not necessarily be interpreted as strongly supported. Several constrained bootstrap analyses were performed to better assess support within and between various groups. The first analysis examined the basal relationships of the genus. Relationships within the 22-chromosome clade and the 32-chromosome clade (see Fig. 6 and discussion below) were again constrained, and the rest of the ingroup tree was left unconstrained. Two more analyses examined the relationships within each of these two clades, constraining the relationships of the other taxa to those of the shortest combined-data tree.

The major results of the combined analysis are described below. Character support for this tree is summarized in a later section of the Results, and is described in detail in Appendix VI. In the tree from the combined data, many of the conflicts between the trees from the separately analyzed molecular and morphological data sets are resolved in favor of the molecular data among the basal lineages of *Sceloporus* (i.e., the small-scaled species) whereas conflicts are often resolved in favor of the morphological data among the large-scaled species.

The molecular data place the *variabilis* group (including *S. chrysostictus*) as the sister taxon to all other *Sceloporus*, and this is supported in the combined tree including all the taxa. The *variabilis* group is placed above *Sator* and the *siniferus* + *utiformis* groups in the morphology tree. As in the trees from the separate analyses, the *couchii* + *parvus* clade is the sister taxon of the remaining species in the *variabilis* group. *Sceloporus chrysostictus* and *S. cozumelae* are supported as sister taxa in the morphology tree, but are not in the molecular and combined trees. In contrast to the morphological analysis but in accord with the molecular trees, the combined

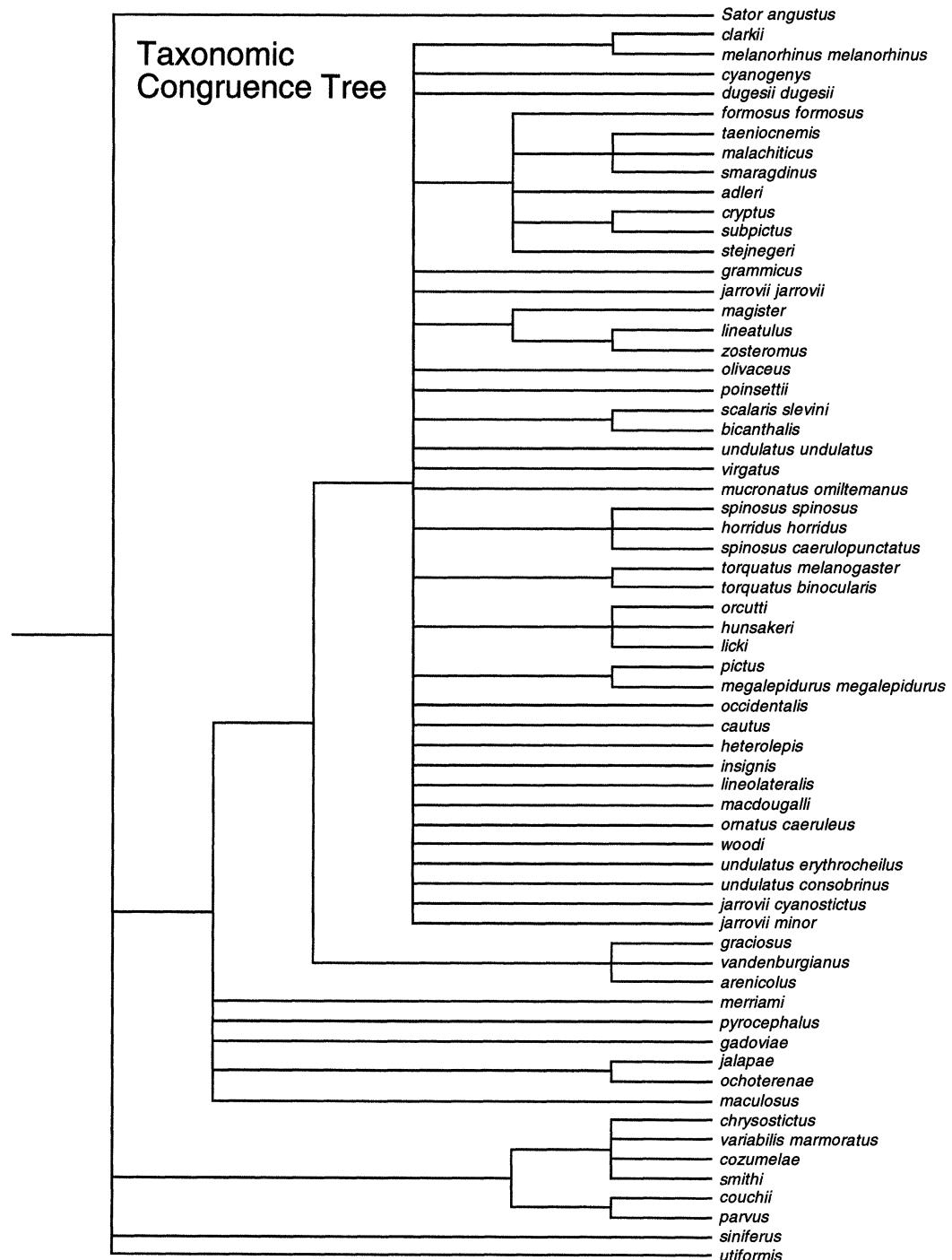


FIG. 5.—Taxonomic congruence tree, showing only those clades present in all the shortest trees from the separate analyses of the molecular and morphological data sets. Taxa scored only for morphological data were pruned from the morphological tree.

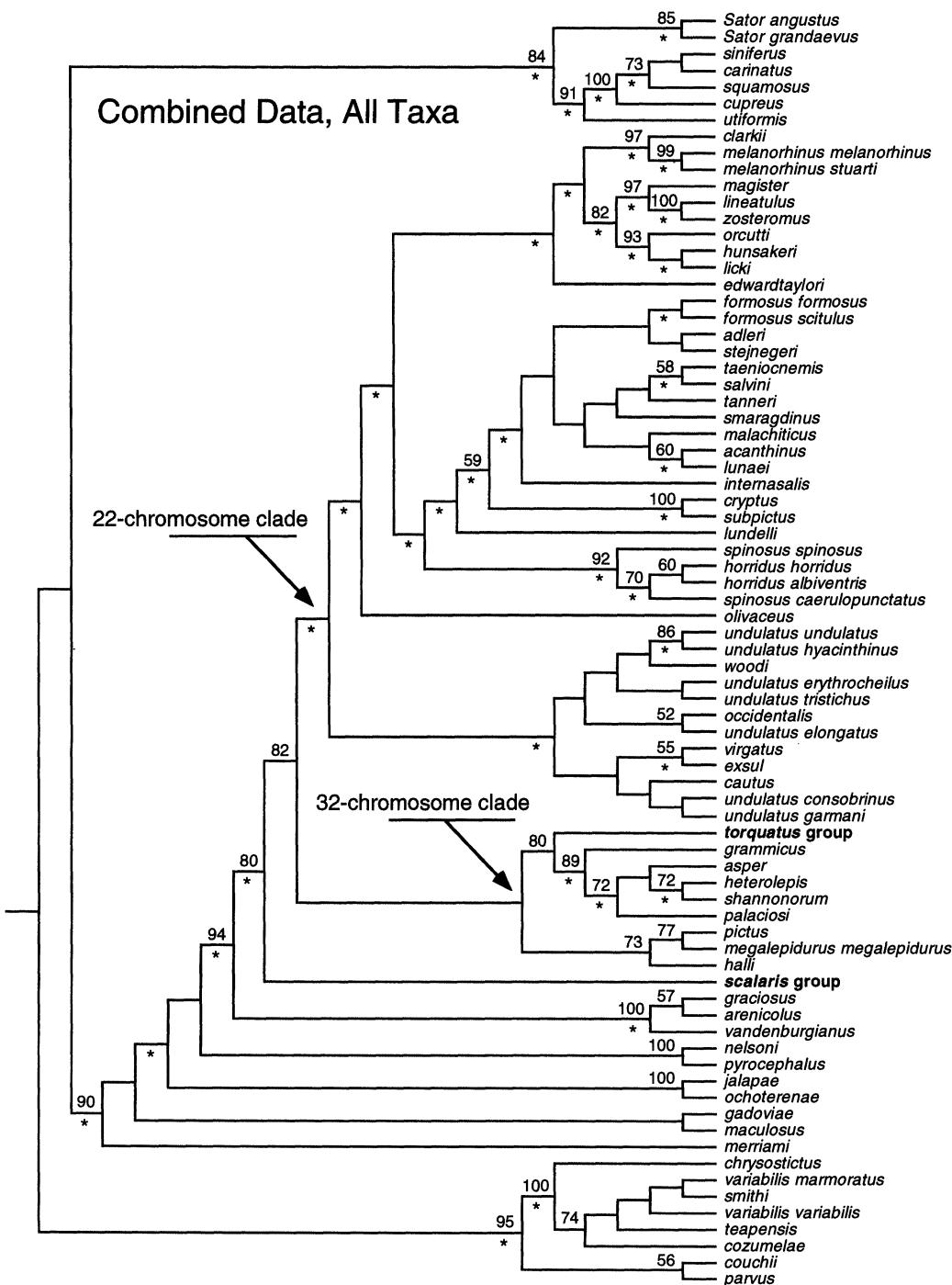


FIG. 6.—Shortest tree from combined analysis, including all taxa. Numbers correspond to bootstrap values. Asterisks correspond to clades supported in an analysis of trees up to one step longer than the shortest tree (i.e., a decay index of one or greater). Nodes with no bootstrap values listed have *P*-values less than 50%, and clades with no asterisks are not supported in slightly longer trees.

## Combined Data

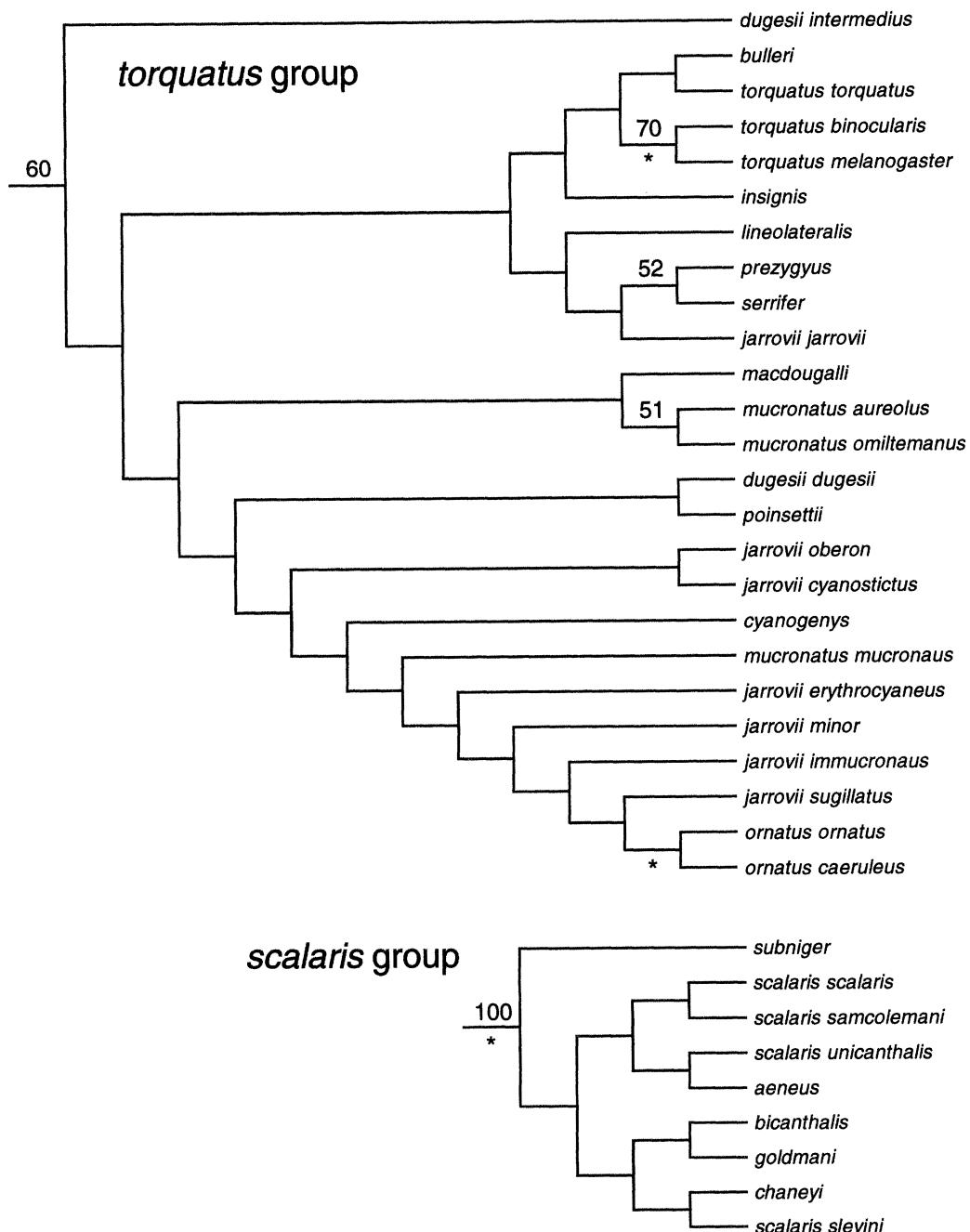


FIG. 7.—Relationships within the *scalaris* and *torquatus* groups based on the combined analysis including all the taxa. Numbers correspond to bootstrap values. Asterisks correspond to clades supported in an analysis of trees up to one step longer than the shortest tree (i.e., a decay index of one or greater). Nodes with no bootstrap values listed have *P*-values less than 50%, and clades with no asterisks are not supported in slightly longer trees.

analysis does not support the monophyly of *Sceloporus*. Instead of being the sister group of *Sceloporus*, *Sator* is the sister group of a clade containing *S. uniformis* and the *siniferus* group. Together these three lineages make up the sister group of the rest of *Sceloporus*.

The clade containing the *jalapae*, *merriami*, and *maculosus* groups found in the morphology tree is contradicted by the molecular data, and is not supported in the combined analysis. However, the trees from all three analyses agree on the generally basal position of these species within the genus. Above the *Sator* + *siniferus* group + *uniformis* clade is *S. merriami*, above *S. merriami* is a clade consisting of *S. maculosus* and *S. gadoviae*, and above the latter clade is the *jalapae* group. The next clade up the tree consists of *S. nelsoni* and *S. pyrocephalus* of the *pyrocephalus* group. The next two clades above the *pyrocephalus* group are the *graciosus* group and the *scalaris* group, respectively. Resolution within the *scalaris* group is the same as in the morphology tree, but again these relationships are only weakly supported.

The clade above the *scalaris* group contains all the species of Smith's (1939) large-scaled, large-bodied radiation, except for the *graciosus* group. These species are divided into two large clades, corresponding to the 32-chromosome clade (the *megalepidurus*, *grammicus*, and *torquatus* groups) and the 22-chromosome clade (the *undulatus*, *formosus*, and "spinosus" groups) from the morphology tree. Within the 32-chromosome clade, the *megalepidurus* group is the sister taxon of the remaining species. Although supported by both molecular and morphological data sets, the monophyly of the group appears as weakly supported in the combined analysis, presumably because of missing data in the poorly known *S. megalepidurus halii*. Above the *megalepidurus* group, the *grammicus* + *asper* groups together make up the sister taxon of the *torquatus* group. The unusual placement of *S. grammicus* in the morphology tree is overruled by the molecular data in the combined analysis. The combined tree shows that *S. asper*

(placed in the *formosus* group by Smith and in a monotypic species group by Hall) is nested inside the *grammicus* group; this taxonomic problem is easily remedied by considering *S. asper* to be a member of the *grammicus* group. Although the molecular data suggest the diphyley of the *torquatus* group, its monophyly is supported in the combined analysis. Relationships within the *torquatus* group are again only weakly supported. The subspecific taxon *Sceloporus dugesii intermedius* appears as the sister taxon of the rest of the group, supported in part by the primitive, reticulate gular pattern (character 163.1) in males of this subspecies. The combined tree also suggests the polyphyly of the subspecies of *S. jarrovii* and *S. mucronatus* found in the morphology trees, but many of these subspecies are missing both molecular and osteological data.

Within the 22-chromosome clade, the monophyletic *undulatus* group is the sister taxon of the remaining species. As in the trees from the separate data sets, the subspecies of *S. undulatus* do not form a monophyletic group. Above the *undulatus* group, *S. olivaceus* is the sister taxon of the other species in the 22-chromosome clade. The remaining species can be divided into two clades. One of these contains *spinosis* + *horridus*, *S. lundelli*, and the monophyletic *formosus* group (including *S. cryptus* and *S. subpictus* and excluding *S. asper*, as suggested by Hall). The *spinosis* + *horridus* clade is the sister taxon of the *S. lundelli* + *formosus* group clade. Relationships within the *formosus* group are weakly supported, except for the basal placement of the *cryptus* + *subpictus* clade. At least some of the poor support within the *formosus* group is likely caused by the inclusion of several rare and poorly known species (*S. internasalis*, *S. salvini*, *S. stejnegeri*, and *S. tanneri*). The molecular, morphological, and combined analyses agree that *S. spinosis* and *S. horridus* are closely related, and that *S. horridus* is likely monophyletic but that *S. spinosis* is not. The other major grouping in the 22-chromosome clade is similar in content and relationships to the "spinosus" group clade in the morphology trees, except that *S. lundelli* is the sister tax-

on of the *formosus* group in the combined tree. Thus, *S. edwardtaylori* is the sister taxon of the remaining species, with the *clarkii* + *melanorhinus* clade as the sister taxon of a clade containing the *orcuttii* and *magister* complexes.

In summary the combined data support the monophyly of the following species groups: *variabilis* (sensu Cole, 1978), *jalapae* (sensu Thomas and Dixon, 1976), *scalaris*, *siniferus*, *megalepidurus*, *graciosus*, *formosus* (sensu Hall, 1973), *undulatus*, and *torquatus*. The combined data reject the monophyly of the *grammicus*, *spinosis*, and *pyrocephalus* groups.

#### Combined Data—Complete Taxa Only

A combined analysis was also performed in which those taxa lacking molecular data were excluded. This analysis included 64 ingroup taxa, for which there are at least 262 informative molecular characters and 195 informative morphological characters. This analysis was undertaken to (1) evaluate the sensitivity of the combined tree to the inclusion of incomplete taxa, and (2) assess support using a more manageable number of taxa and excluding potentially problematic incomplete taxa. Unfortunately, the exclusion of many morphology-only taxa may also have an adverse effect on these results, and this should be taken into consideration.

The combined data set with the “complete” taxa only has a  $g_1$  value of  $-0.415$ . The critical values for two- and four-state characters for 25 or more taxa for 500 characters are  $-0.08$  and  $-0.07$  ( $P = 0.05$ ) and  $-0.08$  and  $-0.09$  ( $P = 0.01$ ), suggesting that the reduced combined data set has significant phylogenetic signal.

Parsimony analysis (500 replicated searches) resulted in a single shortest tree of length 2962.3 (Fig. 8). This tree has a consistency index of 0.28 (excluding uninformative characters) and a retention index of 0.52. An analysis (100 replicated searches) retaining trees up to one full step longer than the shortest tree resulted in only 14 trees.

In general, the combined tree with complete taxa only is very similar to the combined tree including all taxa. This sug-

gests that most of the relationships based on the combined data are insensitive to the addition of incomplete taxa. There are some differences, however, including the following: (1) the positions of *S. pyrocephalus* and the *jalapae* group (*jalapae* + *ochoterenae*) are reversed in the complete-only tree relative to the all-taxa combined tree; (2) the 32-chromosome clade is paraphyletic in the complete-only tree but monophyletic in the all-taxa combined tree; and (3) within the 22-chromosome clade, *S. olivaceus* and the *undulatus* group are allied with the clade (*formosus* group + (*spinosis* + *horridus*)) in the complete-only tree but are the basal lineages within the 22-chromosome clade in the all-taxa combined tree. These differences between trees further demonstrate that the inclusion of incomplete taxa scored for only one data set can affect the placement of complete taxa scored for both data sets (Reeder and Wiens, 1996; Wiens and Reeder, 1995).

In general, bootstrapping of the combined, complete-only data set shows strong support for the monophyly of almost all of the species groups including the *formosus*, *graciosus*, *grammicus*, *jalapae*, *megalepidurus*, *scalaris*, *torquatus*, and *variabilis* groups. Furthermore, many of the relationships within these groups are strongly supported, particularly in the *formosus*, *torquatus*, and *variabilis* groups. There is also strong support for many of the subgroups within the non-monophyletic “*spinosis*” group, such as the *clarkii* + *melanorhinus* clade, the *spinosis* + *horridus* clade, and the *magister* + *orcuttii* complexes. Most of the relationships among the species groups of *Sceloporus* are only weakly supported by bootstrapping, although many are supported in trees at least one step longer than the shortest tree.

#### Character Support for Combined Tree (All Taxa)

This section briefly describes some of the characters unambiguously supporting major groups within *Sceloporus*, based on the combined molecular and morphological data and including all the taxa (Figs.

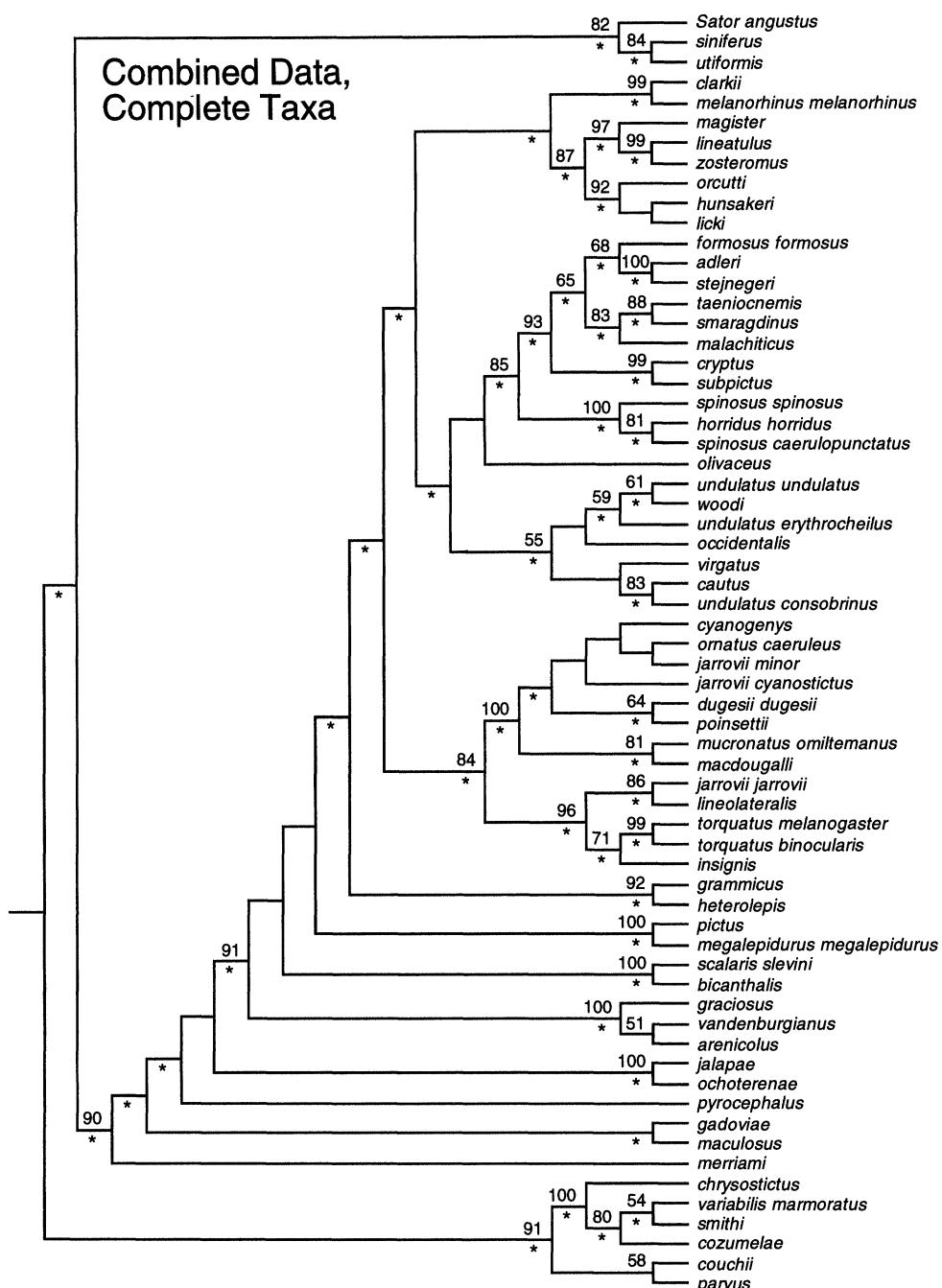


FIG. 8.—Shortest tree from the analysis of the combined data, including only those taxa scored for both DNA and morphological data. Numbers correspond to bootstrap values. Asterisks correspond to clades supported in an analysis of trees up to one step longer than the shortest tree (i.e., a decay index of one or greater). Nodes with no bootstrap values listed have *P*-values less than 50%, and clades with no asterisks are not supported in slightly longer trees.

9, 10). Characters are mentioned only if they are unambiguously placed at the stem in question (independent of optimization routine), and morphological characters are listed only if they involve a large, unambiguously optimized change in frequency. Herein, a large change in frequency is arbitrarily chosen to be 0.75 steps (roughly 75%). Use of this cut-off emphasizes frequency changes with similar weight to DNA sequence changes, but nevertheless includes many polymorphic characters. Small changes in frequency are more subject to sampling error and provide weaker evidence of relationships, although they clearly play an important part in determining and supporting the final tree, as do changes of ambiguous optimization. Many molecular synapomorphies are ambiguously optimized on this tree because of missing data in nearly half of the species; to a lesser extent this is also true for many of the osteological characters. The optimized changes in all the characters for all the branches of the all-taxa combined tree are listed in Appendix VI. In the section that follows, the numbers in parentheses correspond to the character numbers in Appendix IV, and the letter or number following the decimal point indicates the derived state at that node.

The monophyly of the *Sceloporus + Sator* clade was not tested in this study, but several changes are reconstructed as occurring along this branch (stem 1). These include imbrication of the gular scales (104.y), smooth (nongranular) skin between scales (123.a), and seven DNA synapomorphies.

Support for the *variabilis* group (including *S. chrysostictus*; stem 102) includes the dark margin on the male belly patch extending dorsally to posterior to the insertion of the forelimb (187.y) and 10 DNA synapomorphies. Within the *variabilis* group, *S. couchii* and *S. parvus* share a black bordered light stripe anterior to the insertion of the hindlimb (158.y) and five DNA synapomorphies. The clade containing the remaining species of the *variabilis* group (stem 103) is supported by the rounded dorsal process of the squamosal (11.y), rugose cephalic scales (51.y),

reduced preauricular fringe (107.x), distinct posterior lateral dorsals (118.y), imbricate posterior lateral scales (119.y), dark nuchal collar as dark spot dorsal to forelimb insertion (146.2), brown male gular coloration (163.2), and 10 DNA synapomorphies. Many of these morphological synapomorphies are shared with the *utiformis + siniferus* group clade (stem 5, including 11.y, 51.y, 107.y, 118.y, 119.y, 146.2). *Sceloporus* above the *variabilis* group (stem 2) are united by characters including the loss of the gular fold (106.2), the presence of a secondary constriction near the centromere of the large microchromosome (209.1), and seven DNA synapomorphies.

Support for the clade of *Sator*, *S. utiformis*, and the *siniferus* group (stem 3) includes penultimate and ultimate supralabials broadly overlapping (94.y), male belly patches arranged as transverse bars (177.y) and four DNA synapomorphies. The belly-patch character is problematic because *Sator grandaevis* and the *siniferus* group lack belly patches, and the faint, transverse ventrolateral stripes in male *S. utiformis* are only tentatively considered to be homologous to the distinct belly patches seen in other species. Synapomorphies for the *utiformis + siniferus* group clade (stem 5) include the rounded tip of the dorsal process of the squamosal (11.y), more ventral articulation of the squamosal on the supratemporal (12.y), large V-shaped gap in supraoccipital posterior to posterior border of parietal (16.y), rugose cephalic scales (51.w), one or both frontal scales divided sagittally (67.v), reduced preauricular fringe (107.y), distinct posterior lateral dorsal scales (118.y), keeled preanal scales in females (129.y), dark nuchal collar as dark spot dorsal to forelimb insertion (146.2), and three DNA synapomorphies. Synapomorphies for the *siniferus* group (stem 6) include the fused Meckel's groove on the lower jaw (20.y), expanded cusps of posterior dentary teeth (23.y), reduction to two postrostral scales (55.2), suture between rostral-supralabial scales overlapping (96.v), imbricate posterior lateral scales (119.y), and male belly patches absent (176.a). Evidence for the monophyly

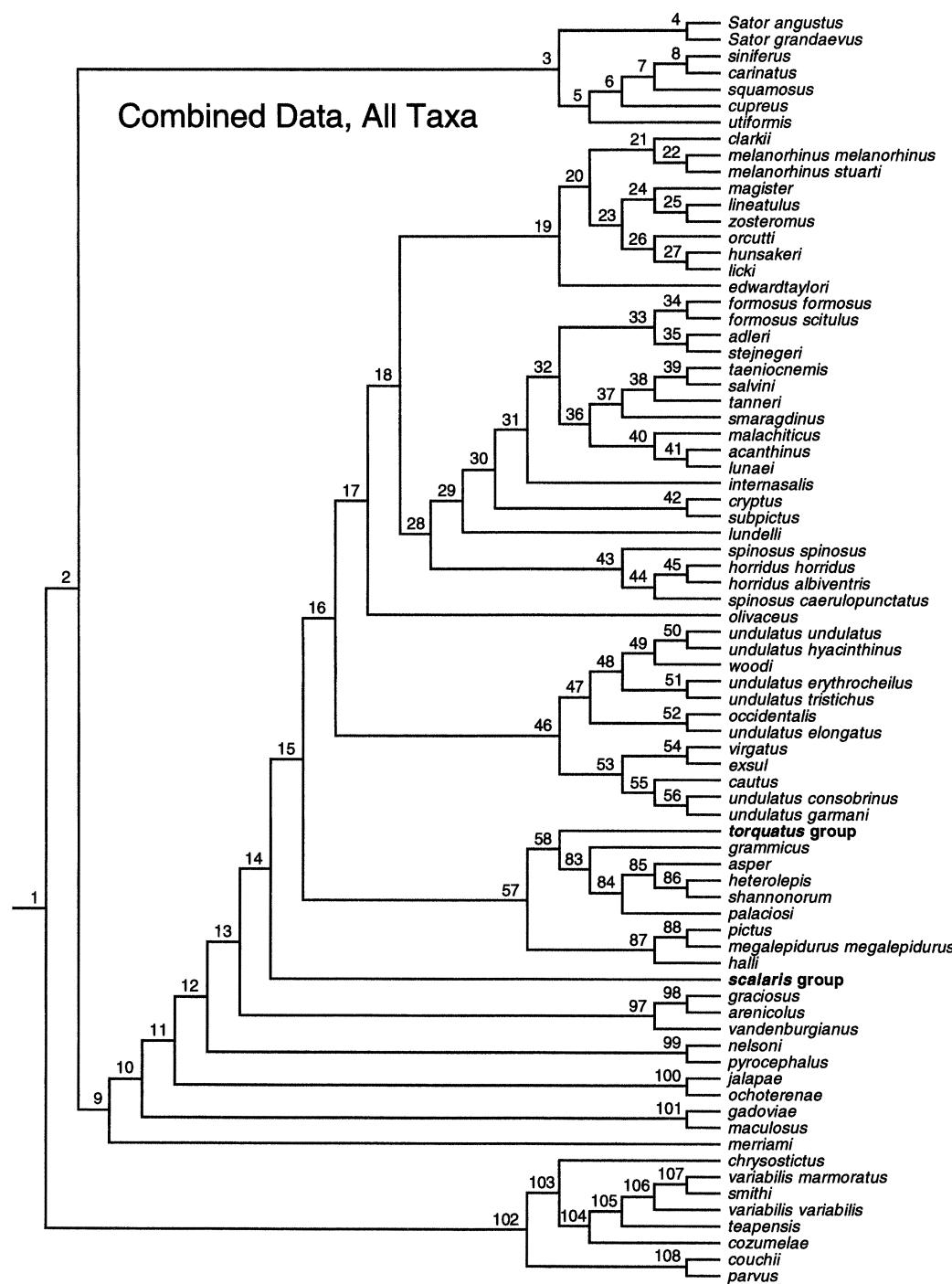


FIG. 9.—Shortest tree from combined analysis, including all taxa. Character state changes supporting the numbered stems are listed in Appendix VI.

## Combined Data

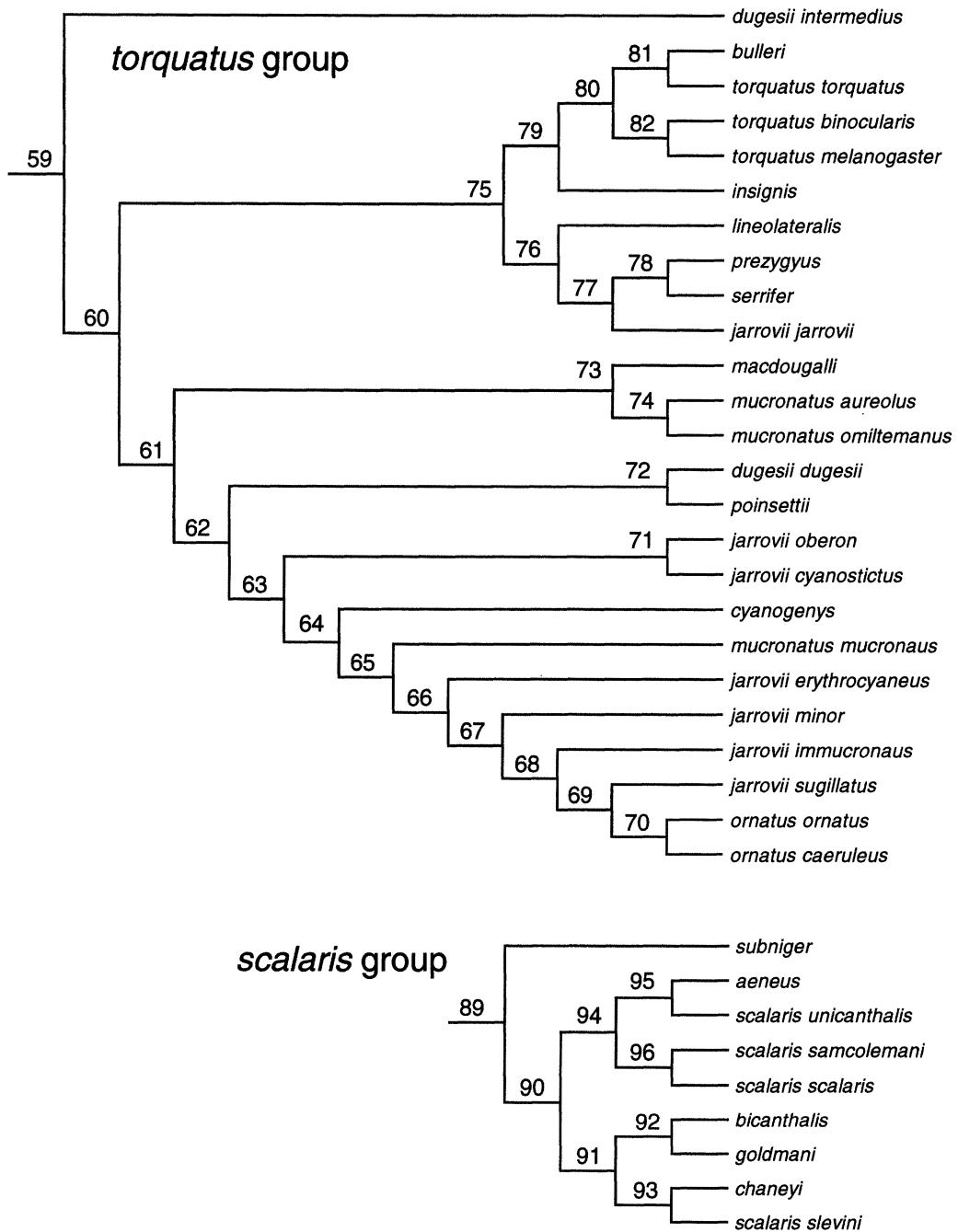


FIG. 10.—Relationships within the *scalaris* and *torquatus* groups based on the combined analysis including all taxa. Character state changes supporting the numbered stems are listed in Appendix VI.

of *Sator* (stem 4) includes fusion of the frontal scales (66.y).

*Sceloporus* above the *Sator + utiformis + siniferus* group clade (stem 9) are united by at least 16 DNA synapomorphies. *Sceloporus* above *S. merriami* (stem 10) are united by imbricate posterior lateral scales (119.w) and three DNA synapomorphies. The *S. gadoviae + S. maculosus* clade (stem 101) is supported by the fusion of the Meckel's groove on the lower jaw (20.y) and six DNA synapomorphies. *Sceloporus* above the *gadoviae + maculosus* clade (stem 11) are united by three DNA synapomorphies. Evidence for the *jalapae* group (stem 100) includes widely separated ceratobranchials (26.y), rostral–nasal scale contact present (54.y), postrostral scales absent (56.y), supranasal scales contacting medially (59.w), rostral–supralabial scale suture overlapping (96.x), three keels on ultimate subdigital lamella of fourth finger of forelimb (125.a), dark margin of male belly patch incomplete posteriorly (186.a), and 12 DNA synapomorphies. The clade of *Sceloporus* above the *jalapae* group (stem 12) is supported by characters including the loss of the antehumeral fold (114.y) and four DNA synapomorphies. *Sceloporus nelsoni* and *S. pyrocephalus* are united by numerous morphological synapomorphies, including laterally compressed tail in males (33.y), loss of anterior frontonasal scales (63.v), fusion of canthal and subnasal scales (85.y), keeled posterior thigh scales (124.y), reduction of enlarged male postanal scales (126.y), presence of a black interparietal spot (141.y), medial fusion of male belly patches (178.u), and distinct belly patches in females (190.y). *Sceloporus* above *S. nelsoni* and *S. pyrocephalus* (stem 13) are united by blue belly patches in males (rather than lavender; 179.a), a reduction from 20 to 18 microchromosomes (198.1), the enlargement of the Y-chromosome (205.1), the loss of X and Y chromosome heteromorphism (207.1), and six DNA synapomorphies. Evidence for the monophyly of the *graciosus* group (stem 97) includes 15 DNA synapomorphies. Within the *graciosus* group, *S. graciosus* and *S. arenicolus* are united by six DNA synapomorphies.

Monophyly of those *Sceloporus* above the *graciosus* group (stem 14) is supported by the loss of the glandular appearance of the male preanal scales (135.a) and 10 DNA synapomorphies. The monophyly of the *scalaris* group (stem 89) is strongly supported by morphological characters, including the loss of the hypoischiac foramen of the pelvic girdle (48.y), rugose cephalic scales (51.y), reduction to two postrostral scales (55.2), overlapping suture of rostral and supralabial scales (96.y), mental scale deeply indented by infralabials (99.y), midbody lateral scales parallel to dorsals (120.u), three keels on the ultimate subdigital lamella of the fourth finger of the forelimb (125.a), presence of four or fewer interfemoral scales (133.y), presence of a blue spot in the male dark nuchal collar (149.y), and black gular coloration in males (163.1).

Support for the clade of *Sceloporus* above the *scalaris* group (stem 15) includes keeled posterior thigh scales (124.y) and four DNA synapomorphies. Evidence for the monophyly of the 22-chromosome clade (stem 16; the *formosus*, *undulatus*, and “*spinosis*” groups) includes the presence of a black bar on the posterior surface of the thigh (160.2), paired gular blotches in males (162.2; modified subsequently), restriction of the gular patch(es) to the posterior gular region only (167.a), reduction to 10 microchromosomes (total of 22 diploid chromosomes, 198.5), and one DNA synapomorphy. Monophyly of the *undulatus* group (stem 46) is supported by the presence of paired gular blotches in females (172.2) and three DNA synapomorphies.

The clade consisting of the “*spinosis*” and *formosus* groups (stem 17; members of the 22-chromosome clade above the *undulatus* group) is supported by the expansion of the preauricular scales to cover the upper portion of the auricular opening (108.w), the presence of distinct pores on the preanal scales of males (134.y), and three DNA synapomorphies. Members of the clade above *S. olivaceus* (stem 18) share the presence of a single gular blotch in males (162.3) and four DNA synapomorphies. The clade consisting of the *spi-*

*nosus* + *horridus* clade, *S. lundelli*, and the *formosus* group (stem 28) is supported by nine DNA synapomorphies, although DNA data were unavailable for *S. lundelli*. The *spinosis* + *horridus* clade (stem 43) is united by characters including a posterior shelf on the raised anterolateral process of the parietal (11.y), male gular blotch with dark longitudinal stripes (168.y), and seven DNA synapomorphies. The clade of *S. lundelli* + *formosus* group (stem 29) is supported by the absence of pores on the male preanal scales (134.a; a reversal). The species of the *formosus* group (stem 30), including *S. cryptus* and *S. subpictus* (following Hall, 1973), share the presence of three or more rows of supraoculars (79.a) and the reduction of the preauricular scales so as not to cover the upper part of auricular opening (108.a). The *formosus* group may be supported by several DNA synapomorphies, but their placement at this node is rendered ambiguous by missing data in *S. lundelli*. The *S. cryptus* + *S. subpictus* clade is supported by the shortened posterolateral process of the basisphenoid (15.a), loss of anterior frontonasal scales (63.y), presence of three keels on ultimate subdigital lamella of fourth finger of forelimb (125.a), reduction to four or fewer interfemoral scales (133.s), and seven DNA synapomorphies. The *formosus* group above *S. cryptus* and *S. subpictus* (stem 89) is united by green ("malachite") dorsal coloration in males (157.y) and viviparity (197.y). Evidence that *S. cryptus* and *S. subpictus* actually lack these synapomorphies is not overwhelming (Lynch and Smith, 1965; Smith and Lynch, 1967); further study may show that they actually apply to the entire *formosus* group.

The clade containing the remaining species in the 22-chromosome clade (stem 19; all of which were in Smith's "*spinosis*" group) is supported by the absence of posterior circumorbital scales (76.s) and presence of supraocular-parietal scale contact (78.y). The clade containing the *clarkii* + *melanorhinus* clade and the *orcitti* and *magister* complexes (the species above *S. edwardtaylori*; stem 20) is supported by an increase in the number of microchromo-

somes from 10 to 18 (198.1). Because it is ordered, this character change has the same weight as four fixed-character state changes. The clade uniting the *magister* and *orcitti* complexes (stem 23) is supported by changes including the presence of black gular coloration in males (163.1) and two DNA synapomorphies. Monophyly of the *orcitti* complex (stem 26) is supported by a further increase in the number of microchromosomes from 18 to 20 (198.0), a minute Y-chromosome (205.0), and five DNA synapomorphies. Within the *orcitti* complex, *S. hunsakeri* and *S. licki* share a notch in the base of the dorsal process of the premaxilla (3.y), absence of anterior frontonasal scales (63.w), loss of denticulate margins on dorsal and lateral scales (122.a), and two DNA synapomorphies. Support for the *magister* complex (stem 24) includes the presence of contact between the mental and sublabial scales (98.s), extensive black pigment on male hindlimbs (194.y), and seven DNA synapomorphies. Within the *magister* complex, the *lineatus* + *zosteromus* clade is supported by the supranasal extending anteromedial to the nasal (60.x), an increase to three or more rows of supraoculars (79.a), female gular coloration as a single blotch (172.3), and 11 DNA synapomorphies. *Sceloporus clarkii* and *S. melanorhinus* (stem 21) share the loss of pores on the male preanal scales (134.a), presence of a black border on the anterior margin of the male gular blotch (169.u), macrochromosome pairs 1, 3, 4, and 5 acrocentric (199.1, 201.1, 202.1, 203.1), Em9 chromosomal mutation (208.1), and four DNA synapomorphies. The subspecies of *S. melanorhinus* share a reduction to four or fewer interfemoral scales (133.s), the "*melanorhinus*" color pattern (dark snout and dark middorsal nuchal blotch; 140.w), presence of a white, dark-bordered mental spot (170.u), and Y-autosomal fusion to an acrocentric autosome (206.2).

Support for the monophyly of the 32-chromosome clade (stem 57; including the *megalolepidurus*, *grammicus*, and *torquatus* species groups) includes Y-autosomal fusion to a metacentric autosome (206.1), the concomitant reacquisition of

heteromorphic sex chromosomes (207.0), and one DNA synapomorphy. Monophyly of the *megalepidurus* group (stem 87) is supported by reduction to a single canthal scale (86.x). The *grammicus* group (including *S. asper*) and *torquatus* group form a clade (stem 58) united by the supranasal extending anteromedial to the nasal (61.x), viviparity (197.y), and one DNA synapomorphy. Support for the *grammicus* group (including *S. asper*; stem 83) includes projecting lateral nuchal scales (111.x) and eight DNA synapomorphies. Within the *grammicus* group, the species above *S. grammicus* (stem 84) are united by the loss of the light border of the male nuchal collar (148.a), the presence of a median light stripe in the male gular coloration (166.y), and the dark margin of the male belly patch incomplete posteriorly (186.a). Support for the *torquatus* group (stem 59) includes the pointed process on the crista interfenestralis of the exoccipital (17.y), denticulate scale margins (122.y), granular skin between lateral scales (123.y), mid-dorsally complete nuchal collar in males (146.3), and loss of distinct pattern on the posterior surface of the thigh (160.3). The clade of species above the basal *S. dugesii intermedius* (stem 60) is supported by the modification of the reticulate male gular coloration to form a single blotch (162.3). This clade is divided into two subclades (stem 61 and 75), each united by at least nine DNA synapomorphies. Most other clades within the *torquatus* group are only weakly supported.

## DISCUSSION

### *Comparison with Previous Hypotheses*

In general, the similarity between many of the clades discovered in this analysis and the species groups recognized by Smith (1939) is striking. The best explanation for this congruence is that many of the external characters Smith used for identifying and delimiting species groups actually diagnose real evolutionary groups. Many of his characters were included in the present analysis, and additional sources of evidence not used by Smith (i.e., osteology, chromosomes, mtDNA)

lend support to most of his groupings. However, Smith's tree diagrams show that he did not believe some of them to be monophyletic (*formosus*, *siniferus*, and *variabilis* groups), and many of the intergroup and intragroup relationships differ substantially.

Most of the incongruities between Smith's taxonomy and the combined-data phylogeny of this study were corrected (or suggested) by Thomas and Dixon (1976), Cole (1978), and Hall (1973). These include: (1) placement of *S. jalapae* and *S. ochoterenae* in the *jalapae* group rather than in the *scalaris* and *siniferus* groups, respectively (Thomas and Dixon, 1976); (2) placement of *S. asper* with the *grammicus* group rather than in the *formosus* group (Hall, 1973); (3) placement of *S. chrysostictus* in the *variabilis* group (Cole, 1978); (4) placement of *S. cryptus* and *S. subpictus* in the *formosus* group rather than in the *megalepidurus* group (Hall, 1973; placement of these species in the *megalepidurus* group actually follows Lynch and Smith, 1965, and Smith and Lynch, 1967, rather than Smith, 1939); and (5) dismantling of the "spinosus" group (Hall, 1973). With the exception of the first case listed, all of these changes were based on chromosomal data. Some of these changes were also suggested independently by Carpenter (1978) on the basis of similarity of behavioral display patterns, in particular, removal of *S. cryptus* from the *megalepidurus* group and placement of *S. chrysostictus* with the *variabilis* group.

The division of *Sceloporus* into large-scaled and small-scaled radiations suggested by Smith (1939) and Hall (1973) is not supported by this analysis. The incongruity is due to the placement of the *scalaris* group among the large-scaled species (which are otherwise a monophyletic group) and the paraphyly of the small-scaled radiation. Interestingly, Smith's tree shows *Uta* (at that time containing *Uta*, *Petrosaurus*, and *Urosaurus*) as nested inside the small-scaled lineage. If Smith's tree is rooted using these closely related genera (rather than between the two radiations of *Sceloporus*) it also suggests monophyly of

the large-scaled radiation and paraphyly of the small-scaled radiation. Hall's (1973) tree depicts both radiations as monophyletic. The paraphyly of the small-scaled, small-bodied "radiation" is not particularly surprising; the outgroups of *Sceloporus* (i.e., *Uta* and *Urosaurus*) are clearly small-scaled and small-bodied. Many of the small-scaled species of *Sceloporus* have an undeniable similarity to *Petrosaurus*, *Urosaurus*, and *Uta* (i.e., *S. couchii*, *S. merriami*, and *S. utiformis*), whereas other small-scaled species have the enlarged lateral scales and reduced chromosome number characteristic of the large-scaled species of *Sceloporus* (i.e., the *scalaris* group).

Many of Hall's (1973) changes to Smith's taxonomy were based on chromosomal data unavailable to Smith, and were supported by this analysis. However, several changes were made among karyotypically homogeneous species without any clear character support. These changes are rejected by this analysis. The nonmonophyletic groups in Hall's (1973) taxonomy are (1) the *variabilis* group, because of the nontraditional removal of *S. couchii* and *S. parvus* and the traditional exclusion of *S. chrysostictus*; (2) the *jalapae* group, because of the nontraditional inclusion of *S. parvus* from Smith's *variabilis* group and *S. gadoviae* from the *pyrocephalus* group (although the latter change is not entirely inconsistent with the results of this study); (3) the *orcutti* group (placed in Hall's large-scaled radiation), because of the inclusion of *S. pyrocephalus* and *S. nelsoni* of the *pyrocephalus* group (placed by Smith in the small-scaled radiation) with the species of the *orcutti* complex (*S. hustakeri*, *S. licki*, and *S. orcutti*); and (4) the *horridus* group, containing some members of Smith's nonmonophyletic "*spinosus*" group as well as the monophyletic *undulatus* group. Hall's tree was only arguably based on an explicit phylogenetic analysis, and seemingly emphasized a more limited set of characters than did Smith's tree (i.e., in this analysis there are over 140 external morphological characters but only 11 informative chromosomal characters).

Two other hypotheses bear mentioning. Larsen and Tanner (1974, 1975) examined

the relationships of virtually all *Sceloporus* species using a phenetic analysis of cranial and external measurements, and also including a few characters of karyology, behavior, and geographic distribution. In general, the phenogram they generated is dissimilar to the combined-data tree of this study. However the results agree on the monophyly of certain groups proposed by Smith (i.e., *scalaris*, *siniferus*, *torquatus*, and *undulatus*) and on a few others (Larsen and Tanner's *jalapae*, *pyrocephalus*, and *magister* groups). As might be expected, the points of agreement between their phenogram and our hypothesis generally involve groups that appear to be very strongly supported in this study.

The previously most recent and only explicit cladistic analysis of *Sceloporus* relationships was that of Mindell et al. (1989). These authors performed a phylogenetic analysis of variation at 23 allozyme loci from two individuals of each of 19 species of *Sceloporus*. Aside from problems of subsampling taxa, individuals, and characters, the analysis suffered from two flaws: (1) no outgroup taxa were sampled, and the tree was rooted using the relatively derived *S. merriami*, and (2) the presence/absence of individual alleles at a locus were treated as independent characters. This coding method has been criticized (i.e., Buth, 1984), in large part because the frequency, presence, and absence of alleles at a locus are not independent of each other, and because ancestors can be reconstructed with the impossible condition of having no alleles at a locus. Furthermore, this coding method involves treating all the states of a character as if they are independently derived. (By analogy to morphology, presence of legs would be a synapomorphy for tetrapods and absence of legs would simultaneously be a synapomorphy of fish!) Moreover, the data matrix contains a number of errors, such that many species appear to have no alleles at a locus, and the original data have been lost (Mindell, pers. comm.). Although some points of congruence are interesting (i.e., monophyly of the *undulatus* and *variabilis* groups and most of the *torquatus*

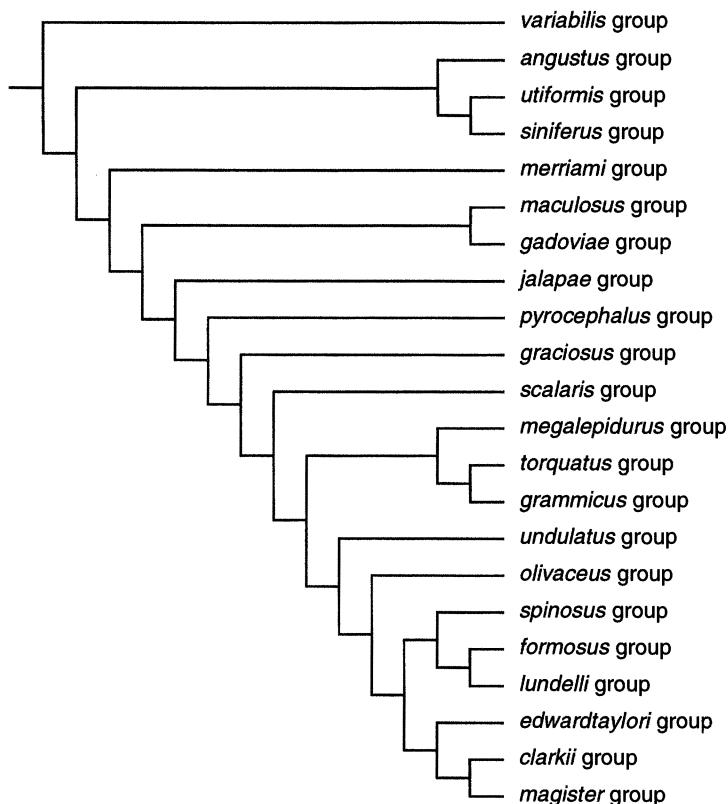


FIG. 11.—Relationships among the species groups of *Sceloporus* recognized in this study, based on the simultaneous analysis of all characters and taxa.

group), the analysis is problematic and reanalysis is not possible.

The analysis of higher-level phrynosomatid relationships by Reeder and Wiens (1996) also hypothesized relationships for many species of *Sceloporus* based on molecular and morphological data. However, that analysis used a subset of the taxa and characters used here, and therefore does not represent a separate phylogenetic study of *Sceloporus*.

#### *Proposed Taxonomic Changes*

Given that Smith's (1939) taxonomy is highly congruent with the results of this study, and because Smith's classification is the oldest and generally most widely used, the phylogenetic classification proposed here involves only minor modifications to Smith's (1939). The changes made are listed and justified below. A phylogeny summarizing the relationships among the new

species groups (based on the combined data for all the taxa) is shown in Figure 11.

*Sator* is placed in the synonymy of *Sceloporus* to maintain the monophyly of the older genus. Although this synonymy has been either suggested or implemented by previous authors (i.e., Etheridge and de Queiroz, 1988; Frost and Etheridge, 1989; Wyles and Gorman, 1978), this study represents the first to demonstrate nesting of *Sator* inside *Sceloporus* with an explicit phylogenetic analysis. The monophyly of *Sceloporus* (exclusive of *Sator*) was weakly supported by morphological data by Wiens (1993b) and this study, but the molecular and combined analyses strongly suggest that *Sator* is nested inside *Sceloporus*. If this result is later shown to be wrong, then synonymy of *Sator* will not make *Sceloporus* paraphyletic, unless *Sator* is actually outside the putative *Sator* + *Sceloporus* clade.

The two former species of *Sator* make up the newly erected *angustus* species group of *Sceloporus*. Other taxonomic options, such as expanding *Sator* or the *siniferus* or *utiformis* groups to include the entire clade are rejected in favor of maintaining the stability of currently recognized groups as much as possible.

Following Cole (1978), the monotypic *chrysostictus* group is subsumed into the *variabilis* group. Evidence that *S. chrysostictus* is nested inside the *variabilis* group is very strong (e.g., Figs. 2, 3, 6, 8), and this change avoids paraphyly of the *variabilis* group.

*Sceloporus gadoviae* is removed from the *pyrocephalus* group and placed in its own monotypic species group. Although the morphological data support Smith's (1939) concept of the *pyrocephalus* group, the combined and molecular analyses place *S. gadoviae* and *S. maculosus* as sister taxa. Because of our uncertainty about its position, we erect a monotypic species group for *S. gadoviae* (which is consistent with both the molecular and morphological trees) rather than adding it to the monotypic *maculosus* group.

*Sceloporus asper* is placed in the *grammicus* group. This analysis shows *S. asper* to be nested deep inside the *grammicus* group, and this change is therefore necessary to avoid the paraphyly of the *grammicus* group.

Smith's "spinosus" group is dismantled. Following Hall (1973), we recognize a *clarkii* group for the strongly supported *clarkii* + *melanorhinus* clade. We also recognize a *magister* group, containing both the *magister* and *orcutti* complexes. The *spinosus* group is restricted to the *spinosus* + *horridus* clade. Each of these species groups is supported as monophyletic by separate and combined analyses of the morphological and molecular data. The three "leftovers" of the former "spinosus" group (*S. edwardtaylori*, *S. lundelli*, and *S. olivaceus*) are each placed in a monotypic species group. Although monotypic species groups are not desirable (they convey little or no phylogenetic information), they are proposed for these species to avoid drastically altering previous concepts of

the species groups (i.e., synonymizing the "spinosus" and *formosus* groups) or recognizing many clades that are not strongly supported.

No formal higher-level taxa within *Sceloporus* are recognized above the level of species groups. This is because few of the relationships among the species groups are strongly supported, and we do not wish to name new taxa for which there is only weak evidence. However, many changes are suggested at the alpha-taxonomic level by this analysis. In particular, many species appear to be nonmonophyletic when their constituent subspecies are treated as separate terminal taxa in the phylogenetic analyses. We consider nonmonophyly to be a justification for recognizing populations as separate species only if there is other evidence that they are distinct lineages (i.e., significant frequency differences between large, geographically adjacent samples and/or demonstrated allopatry of the populations). The only subspecies that meets this criterion is *S. megalepidurus halli*, a clearly allopatric taxon that appears as the sister taxon of the clade *S. megalepidurus megalepidurus* + *S. pictus*. This taxon is recognized as *Sceloporus halli*. However, it seems that many other subspecies will need to be recognized as separate species after rigorous study of their geographic variation and distribution. Other species-level problems are discussed in the Comments section of the species group accounts.

#### Separate Versus Simultaneous Analysis

Several of the clades discovered in the combined analysis are absent in the trees from the separate data sets. For example, neither molecular nor morphological data sets place the *angustus* group (the former *Sator*) as the sister taxon of the *siniferus* group + *utiformis* clade, nor do they place the 22- and 32-chromosome clades as sister taxa. These results show the ability of combined analyses to discover relationships that would be missed if only separate analyses were performed (Barrett et al., 1991; Chippindale and Wiens, 1994). The combined analysis also demonstrates that the position of taxa scored for only one

data set can be affected by the characters of the other data set (Reeder and Wiens, 1996; Wiens and Reeder, 1995). For example, *S. lundelli* lacks DNA data and in the morphology trees is the sister taxon of a clade of various “*spinosus*” group species (*sensu* Smith, 1939). In the combined analysis, *S. lundelli* is the sister taxon of the *formosus* group. This further illustrates the potential dangers of attempting to map (*a posteriori*) taxa scored for only one data set onto a combined tree without including them in the analysis.

We found very little strongly supported incongruence between the trees from the separately analyzed molecular and morphological data sets. In general, most clades found in the separate analyses were (1) incongruent but weakly supported by one or both data sets, or (2) congruent and well supported by one or both data sets. We found only one case of strongly supported incongruence between the data sets. This involved the relationships within the clade containing *S. chrysostictus*, *S. cozumelae*, and the members of the *variabilis* complex: *S. chrysostictus* and *S. cozumelae* are strongly supported as sister taxa by the morphological data whereas the molecular data strongly support placement of *S. chrysostictus* as the basal taxon within the clade. The source of this incongruence is unclear. A variety of seemingly unlinked morphological characters unite *S. chrysostictus* and *S. cozumelae*, including the fusion of the canthal and subnasal scales (85.x), the loss of the antehumeral fold (114.y), male gular coloration brown (163.2), and loss of male belly patches (176.a). The molecular synapomorphies that reject this clade come from numerous positions in a roughly 600-bp segment of the 12S rRNA gene (between characters 300 and 900 in the data matrix). Given that the molecular characters are linked (i.e., from the same gene) and the morphological characters appear not to be, it may be that the 12S rRNA gene tree does not match the species tree for these taxa. Given this possibility, the combined tree (which supports the molecular results in a basal placement for *S. chrysostictus*) may not be an accurate estimate of the species

tree for these taxa (Bull et al., 1993b; de Queiroz, 1993). Although we take the combined tree as our best estimate of phylogeny, we consider the relationships among these taxa to be weakly supported until further (unlinked) characters can be found to support one hypothesis over the other.

These results have interesting implications for the debate over whether not to combine data sets for phylogenetic analysis. Some authors have argued that data sets that show strongly supported incongruence should not be combined (Bull et al., 1993b; de Queiroz, 1993; Hulsenbeck et al., 1996). The molecular and morphological data sets analyzed in this study do show strongly supported incongruence, and by this argument should not be combined. Yet this incongruence is restricted to a very small clade. Clearly, the accuracy of our estimation of clades outside of the *variabilis* group would suffer from subsampling of characters if the molecular and morphological data were not combined (e.g., the monophyly of the 22-chromosome clade, the *undulatus* group, and the *torquatus* group would not be supported; Fig. 4). It is possible that a statistical test of heterogeneity would show these data sets to be “combinable,” despite the incongruence within the *variabilis* group. Yet, with this coarse approach, no provision is made for those parts of the tree where combined analysis may be misled, once the initial decision to allow combination has been made. Our results underscore the benefits of approaches that always allow combined analysis, without ignoring the possibility that data sets may have different underlying phylogenetic histories (e.g., de Queiroz et al., 1995).

#### Rapid Speciation and *Sceloporus* Phylogeny

Examination of the bootstrap results and near-shortest trees from the molecular, morphological, and combined data sets suggests a common pattern. Some parts of the phylogeny of *Sceloporus* appear to be “difficult” and others are relatively “easy.” The parts that are easy are strongly supported by the separate and/or combined

analyses (such as many of the species groups), whereas other parts of the phylogeny are weakly supported by the separate and combined analyses and are in conflict between the data sets (such as the relationships among many of the species groups). The fact that areas of weak support are shared between the data sets suggests some underlying cause that is intrinsic to the actual phylogeny rather than the characters used to estimate it. Rapid speciation, such that lineages separate before they can accumulate a large number of synapomorphies, may be the cause of this shared pattern. We suggest that there was rapid speciation at some points in the evolution of *Sceloporus*, particularly above the level of the *angustus–siniferus–utiformis* group clade and the *variabilis* group, and among the large-scaled species groups. Rapid speciation has been implicated for a lack of resolution and/or strong support in certain parts of trees in several molecular phylogenetic analyses (e.g., Kraus and Miyamoto, 1991; Lanyon, 1988; reviewed by Donoghue and Sanderson, 1992). However, this explanation is made much more compelling by the presence of congruent areas of weak and strong support in trees from diverse, separately analyzed data sets (as in this study). A similar phenomenon was postulated for the higher-level relationships of phrynosomatid lizards (Reeder and Wiens, 1996), where both molecular and morphological data sets provide strong support for the monophyly of most genera, but weak support for many of the relationships between them. The best way to test this hypothesis may be through parametric bootstrapping (e.g., Bull et al., 1993a), by simulating data sets with the hypothesized short and long branch lengths and determining if the trees estimated from these data sets display the expected patterns of support and congruence. We suspect that this phenomenon of rapid speciation may be quite common, and may explain why molecular data sets often do not prove to be an immediate panacea for phylogenetic problems that have vexed morphologists (e.g., the hominid trichotomy; Patterson et al., 1993).

## SUMMARY AND PROSPECTUS

This study represents the first comprehensive analysis of *Sceloporus* relationships using modern phylogenetic methodology. The end result is a phylogenetic hypothesis for almost all taxa in the genus based on diverse types of data (Figs. 6, 7). This phylogeny is completely resolved and is strongly supported in some parts but not in others (Figs. 6, 7).

Overall, the results of this study are both encouraging and discouraging. First, it is encouraging that so many of the groups recognized by previous authors (particularly Smith) are upheld by the combination of traditional and nontraditional data in this study. This finding simultaneously increases confidence in the data and methods of analysis used in the present study, and in the idea that previous notions of *Sceloporus* phylogeny have not been grossly incorrect. The results are discouraging in that application of close to 500 phylogenetically informative characters to the problem of *Sceloporus* phylogeny failed to yield strongly supported results in many crucial parts of the tree. This problem may be due to rapid speciation, and the solution may require the acquisition of extensive DNA sequence data from many (relatively) slow-evolving genes (Kraus and Miyamoto, 1991).

Because the combined data in this study include a large number of diverse and independent characters and character systems and incorporates information from many previous studies (i.e., Hall, 1973; Reeder, 1995; Smith, 1939), it is hoped that future studies of *Sceloporus* phylogeny will utilize the actual character data from this study in comparing their results to these results (i.e., using combined analysis), rather than simply comparing trees based on newly acquired data sets to the trees from this study. Comparison of the trees alone ignores the strength of support for different hypotheses and hides potential congruence among characters hidden in the shortest trees from the separately analyzed data sets (see Chippindale and Wiens, 1994, for a review). This study further illustrates the ability of combined

analyses to discover novel clades not present in trees from separate analyses.

Sites et al. (1992) recently reviewed the literature on *Sceloporus* phylogeny and discussed the potential of *Sceloporus* as a model system for many kinds of evolutionary questions, given a well-supported phylogenetic context. The present study has provided a preliminary hypothesis for virtually all the species of *Sceloporus*, a monophyletic higher-level classification, and strong support for many parts of the tree. The results of this study also suggest that a strongly supported phylogeny for the entire genus may be a long time coming. Nevertheless, this should not be a deterrent for those wanting to study evolutionary questions within the genus. Methods are now becoming available that take into account uncertain or unresolved relationships among the taxa of interest (i.e., DeBry, 1993; Losos, 1994; Purvis and Garland, 1993). Furthermore, a strongly supported phylogeny for the entire genus may be unnecessary in many cases, because comparative studies often have data for only a small portion of the species (e.g., Martins, 1993). Overall, the results of this study should further encourage evolutionary biologists to undertake comparative studies using *Sceloporus* as a model system.

#### CONTENT OF SPECIES GROUPS

The following systematic accounts are intended to provide easy reference to the contents of each of the species groups in the new classification, and to serve as a springboard for discussing some of the potential alpha-taxonomic problems discovered in the course of the study. Species groups are listed in alphabetical order. Unless otherwise noted, all species groups were originally recognized by Smith (1939). Species groups are diagnosed in the phylogenetic sense, and the diagnosis for each species group is considered to be the apomorphies that support the stem subtending the species group. To avoid redundancy, the diagnoses merely point the reader to the appropriate clade in Figures 9 and 10 and the corresponding list of character support in Appendix VI. (We

leave it to the reader to extract all comparative statements from Appendix VI.) Diagnosing (in the nonphylogenetic sense) a species without reference to the tree may be problematic because character state differences between groups may appear at all cladistic levels between them, and many of the apomorphies of the species groups are neither unique to a given group nor universal among the species within them. Some of the fixed (or nearly fixed) autapomorphies of the monotypic species groups are listed also; this information is not presented elsewhere.

#### *Angustus* Group

**Diagnosis.**—See support for stem 4 (Fig. 9) in Appendix VI.

**Content.**—*Sceloporus angustus* and *S. grandaeus*.

**Comment.**—This new species group contains the two species previously recognized as the genus *Sator*.

#### *Clarkii* Group

**Diagnosis.**—See support for stem 21 (Fig. 9) in Appendix VI.

**Content.**—*Sceloporus clarkii* and *S. melanorhinus*.

**Comment.**—Same as the *clarkii* group of Hall (1973). *Sceloporus melanorhinus stuarti* is apparently isolated from other conspecific populations and should probably be recognized as a distinct species (Smith and Taylor, 1950).

#### *Edwardtaylori* Group

**Diagnosis.**—Secondary coracoid fenestra present (40.y), contact between superciliary and supraoculars present (81.y), contact between superciliaries and supraoculars extensive (82.y), low nuchal collar (147.y), male gular blotch completely covers gular area (167.y), and loss of male belly patches (176.y).

**Content.**—*Sceloporus edwardtaylori*.

**Comment.**—A new species group for a species formerly placed in the “*spinulosus*” group (Smith, 1939).

#### *Formosus* Group

**Diagnosis.**—See support for stem 30 (Fig. 9) in Appendix VI.

**Content.**—*Sceloporus acanthinus*, *S. adleri*, *S. cryptus*, *S. formosus*, *S. internasalis*, *S. lunaei*, *S. malachiticus*, *S. salvini*, *S. smaragdinus*, *S. stejnegeri*, *S. subpictus*, *S. taeniocnemis*, and *S. tanneri*.

**Comment.**—In general, the distribution and systematic status of taxa in the *formosus* group are poorly known and desperately in need of study (Sites et al., 1992). The two subspecies of *S. formosus* are easily diagnosable (male *S. f. scitulus* have light spots on the head) and seemingly allopatric; they are probably distinct species. Smith and Perez-Higareda (1992) recently placed *S. internasalis* in the synonymy of *S. salvini*. This change is not supported by this analysis, as these allopatric and geographically distant populations do not appear to be closely related. Furthermore, the taxonomic status of the isolated population in the Los Tuxtlas mountains of coastal Veracruz, considered to be *S. salvini* by Smith and Perez-Higareda (1992), should be investigated thoroughly; it most likely represents another distinct species.

#### Gadoviae Group

**Diagnosis.**—Meckel's groove fused (21.y), tail laterally compressed in males (34.y), seven to eight superciliary scales (84.u), continuous black ventral collar in males (166.y), and male belly patches fused medially (179.y).

**Content.**—*Sceloporus gadoviae*.

**Comment.**—A new species group recognized for a species formerly placed in the likely nonmonophyletic *pyrocephalus* group of Smith (1939).

#### Graciosus Group

**Diagnosis.**—See support for stem 97 (Fig. 9) in Appendix VI.

**Content.**—*Sceloporus arenicolus*, *S. graciosus*, and *S. vandenburgianus*.

**Comment.**—*Sceloporus arenicolus* and *S. vandenburgianus* were elevated from subspecific status within *S. graciosus* by Collins (1991), but without presenting any evidence beyond that in Stebbins (1985). *Sceloporus arenicolus* is clearly allopatric and diagnosable, whereas *S. vandenburgianus* may be distinct but is more mor-

phologically similar and geographically close to *S. graciosus* (Censky, 1986).

#### Grammicus Group

**Diagnosis.**—See support for stem 83 (Fig. 9) in Appendix VI.

**Content.**—*Sceloporus anahuacus*, *S. asper*, *S. grammicus*, *S. heterolepis*, *S. palaciosi*, and *S. shannonorum*.

**Comment.**—In this classification, the *grammicus* group is expanded to include *S. asper*. The number of evolutionary species hiding under the name *S. grammicus* remains unresolved; see Sites et al. (1992) and Arevalo et al. (1994) for recent reviews. Sites et al. (1988) questioned the validity of *S. anahuacus* (not included in this analysis), although they found some fixed allozyme differences separating it from the other *grammicus* complex taxa they sampled.

#### Jalapae Group

**Diagnosis.**—See support for stem 100 (Fig. 9) in Appendix VI.

**Content.**—*Sceloporus jalapae* and *S. ochoterenae*.

**Comment.**—Content follows Thomas and Dixon (1976) rather than Hall (1973).

#### Lundelli Group

**Diagnosis.**—Reduced lateral mite pocket (113.y), male gular coloration extending onto chest (164.y), lavender belly patches in male (179.y), and sex chromosomes heteromorphic (207.0).

**Content.**—*Sceloporus lundelli*.

**Comment.**—A new species group for a species formerly placed in the *spinulosus* group (Smith, 1939). *Sceloporus lundelli* contains two subspecies that do not appear to be allopatric or diagnosable from each other (Smith, 1939).

#### Maculosus Group

**Diagnosis.**—Rostral-nasal contact present (54.y), reduction to two postrostrals (55.2), median postrostral scales separated medially (57.y), supranasal scales contacting medially (59.y), internasal scales absent (61.y), subocular scale reduced (91.y), first sublabial scale contacts second infralabial (97.y), deep postfemoral dermal pocket

present (138.y), extensive black pigment on underside of hindlimb in males (194.y), reduction to 18 microchromosomes (198.1), and Y-autosomal fusion to metacentric autosome (206.1).

*Content.*—*Sceloporus maculosus.*

*Magister* Group

*Diagnosis.*—See support for stem 23 (Fig. 9) in Appendix VI.

*Content.*—*Sceloporus hunsakeri*, *S. licki*, *S. lineatulus*, *S. magister*, *S. orcutti*, and *S. zosteromus*.

*Comment.*—First recognized by Hall (1973). In this classification the alpha taxonomy of the *magister* complex follows Grismer and McGuire (1996) in that *S. monserratus* and *S. rufidorsum* are considered conspecific with *S. zosteromus* and that *S. lineatulus* and *S. zosteromus* are considered specifically distinct from each other and *S. magister*.

*Megalepidurus* Group

*Diagnosis.*—See support for stem 87 (Fig. 9) in Appendix VI.

*Content.*—*Sceloporus halli*, *S. megalepidurus*, and *S. pictus*.

*Comment.*—The isolated *S. megalepidurus halli* Dasmann and Smith, 1974, from Oaxaca is considered to be a distinct species. Sites et al. (1992) questioned the distinctness of *S. megalepidurus* and *S. pictus* on the basis of morphological similarity, ability to interbreed, and presence of intermediates/hybrids at one locality. However, there appear to be important morphological, chromosomal, and ecological differences between these taxa (Sites et al., 1992; Smith, 1939; pers. obs.) and we tentatively consider them to be separate species pending further resolution.

*Merriami* Group

*Diagnosis.*—Posterodorsal corner of squamosal rounded (11.y), anteromedial process on ceratohyal with acuminate posterior process (27.y), reduced subocular scale (91.y), first sublabial scale contacts second infralabial (97.w), remnant of gular fold present laterally, interrupted medially (106.1), skin between scales granular (123.u), male gular pattern distinctly

darker posteriorly (171.y), and macrochromosome pairs 1–6 acrocentric, presumably via centric fission (199.1, 200.1, 201.1, 202.1, 203.1, 204.1)

*Content.*—*Sceloporus merriami.*

*Comment.*—Four subspecies of *S. merriami* are currently recognized, all of which appear to intergrade (Olson, 1979). However the apparent disjunction between *S. merriami* populations in the Big Bend region of Texas and those in southern Chihuahua and Coahuila (Olson, 1979) should be investigated.

*Olivaceus* Group

*Diagnosis.*—Dark margin of belly patch reduced, if present (185.y).

*Content.*—*Sceloporus olivaceus.*

*Comment.*—A new species group for a species formerly placed in the “*spinosis*” group of Smith (1939).

*Pyrocephalus* Group

*Diagnosis.*—See support for stem 99 (Fig. 9) in Appendix VI.

*Content.*—*Sceloporus nelsoni* and *S. pyrocephalus*.

*Comment.*—*S. gadoviae* is removed from the *pyrocephalus* group of Smith (1939).

*Scalaris* Group

*Diagnosis.*—See support for stem 89 (Fig. 10) in Appendix VI.

*Content.*—*Sceloporus aeneus*, *S. bicanthalis*, *S. cheneyi*, *S. goldmani*, *S. scalaris*, and *S. subniger*.

*Comment.*—This analysis lends some support to the recognition of *S. bicanthalis* and *S. subniger* as distinct from *S. aeneus*; the three putative subspecies do not form a monophyletic group. The apparent non-monophyly of the subspecies of *S. scalaris* also requires further study. Mink and Sites (1996) recently analyzed the taxonomy and relationships of some of the taxa within the *scalaris* group using allozyme and morphological data, and supported the distinctness of *S. aeneus* from *S. bicanthalis* but not from *S. subniger*. Many of the relationships posited by Mink and Sites (1996) clash with the results of this study, but our phylogenetic hypothesis within the *scalaris*

group is only weakly supported. Unfortunately, this paper appeared too recently for us to incorporate the data in our analysis.

#### *Siniferus* Group

**Diagnosis.**—See support for stem 6 (Fig. 9) in Appendix VI.

**Content.**—*Sceloporus carinatus*, *S. cupreus*, *S. siniferus*, and *S. squamosus*.

**Comment.**—The results of this study suggest that *S. cupreus* and *S. siniferus* are only distantly related within the *siniferus* group, although Smith and Taylor (1950) tentatively considered them to be conspecific.

#### *Spinosus* Group

**Diagnosis.**—See support for stem 43 (Fig. 9) in Appendix VI.

**Content.**—*Sceloporus horridus* and *S. spinosus*.

**Comment.**—The polyphyletic “*spinosus*” group of Smith (1939) is here restricted to the *spinosus* + *horridus* clade. The subspecies of *S. spinosus* (*apicalis* [not seen], *caeruleopunctatus*, and *spinosus*) are likely different species, and this analysis suggests that *S. spinosus* is not monophyletic.

#### *Torquatus* Group

**Diagnosis.**—See support for stem 59 (Fig. 10) in Appendix VI.

**Content.**—*S. bulleri*, *S. cyanogenys*, *S. dugesii*, *S. insignis*, *S. jarrovii*, *S. lineolateralis*, *S. macdougalli*, *S. mucronatus*, *S. ornatus*, *S. poinsettii*, *S. prezygus*, *S. serrifer*, and *S. torquatus*.

**Comment.**—This analysis suggests that much more phylogenetic and alpha taxonomic work is needed in the *torquatus* group; the subspecies of *S. dugesii*, *S. jarrovii*, and *S. mucronatus* do not appear to be closely related to their nominally conspecific populations. This may be due in part simply to poor support and spurious resolution within the group caused by missing data (osteological and molecular), few informative characters, and homoplasy. The nonmonophyly of the distinctive *S. mucronatus* and *S. dugesii* seems unlikely. Olson (1987) considered *S. serrifer* and *S. cyanogenys* to be conspecific based on pu-

tative intergrades found in Tamaulipas. These taxa do not appear to be closely related based on the results of our study, but again this could be an artifact of weak support. The two subspecies *S. dugesii* appear to be allopatric (Smith, 1939) and diagnosable and probably represent different species. The taxonomic status of the seven subspecies of *S. jarrovii* is being investigated further by Wiens, Nieto, and Reed. *Sceloporus jarrovii cyanostictus* appear to be both allopatric and diagnosable (Axtell and Axtell, 1971), as is *S. j. sugillatus* (Chrapliwy, 1964); they are most likely distinct species. Webb and Axtell (1994) recently raised *S. jarrovii minor* to a full species, based on the distinctness of *S. j. minor* in eastern Zacatecas from *S. j. jarrovii* in western Zacatecas. However, they did not compare *minor* to other subspecies of *S. jarrovii* occurring in the Sierra Madre Oriental. According to Chrapliwy (1964), *minor* and *immucronatus* intergrade extensively, whereas the taxonomy of Webb and Axtell (1994) seemingly treats these taxa as different species. Although we concur that *S. j. minor* and *S. j. jarrovii* are not conspecific, this taxonomic change is not followed here pending resolution of the taxonomic status of the problematic eastern *S. jarrovii* populations.

#### *Undulatus* Group

**Diagnosis.**—See support for stem 46 (Fig. 9) in Appendix VI.

**Content.**—*Sceloporus cautus*, *S. exsul*, *S. occidentalis*, *S. undulatus*, *S. virgatus*, and *S. woodi*.

**Comment.**—The taxonomy of *S. undulatus* is in desperate need of revision, and the number of evolutionary species it contains remains unclear. Although not included in this analysis *S. occidentalis becki* appears to be allopatric (on the Channel Islands) and diagnosable (Stebbins, 1985) and should probably be recognized as a distinct species.

#### *Utiformis* Group

**Diagnosis.**—Elongate posterolateral processes of basisphenoid (15.y) and seven superciliary scales (83.x). See also characters on more basal stems.

*Content.*—*Sceloporus uniformis*.

*Variabilis* Group

*Diagnosis.*—See support for stem 102 (Fig. 9) in Appendix VI.

*Content.*—*Sceloporus chrysostictus*, *S. couchii*, *S. cozumelae*, *S. parvus*, *S. smithi*, *S. teapensis*, and *S. variabilis*.

*Comment.*—Includes *S. chrysostictus*, formerly placed in the monotypic *chrysostictus* group (Hall, 1973; Smith, 1939). Many unresolved species-level questions remain in the *variabilis* group. For example, the island and mainland populations of *S. cozumelae* (not treated separately here) have long been considered to be potentially distinct (i.e., Smith, 1939), and the status of *S. teapensis* has been contentious (reviewed by Sites et al., 1992).

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## APPENDIX I

*Specimens Scored for External Morphological Characters*

Abbreviations follow Leviton et al. (1985) except for JJW (John J. Wiens field series) and MZFC (Museo de Zoología, Facultad de Ciencias, Universidad Nacional Autónoma de México). *Sceloporus* and the other genera are listed separately. Sample sizes for each species are given after the species name. Some specimens used only in preparing illustrations are not listed.

*Sceloporus acanthinus* ( $n = 10$ ): UMMZ 84067 (6 specimens); UTA 20310–11, 29047, 29050. *Sceloporus adleri* ( $n = 12$ ): KU 182555, 182559–61, 182563, 182567, 182571, 182591; UTA 4125, 4156, 4158, 4160. *Sceloporus aeneus* ( $n = 7$ ): KU 62840–45, 62848. *Sceloporus arenicolus* ( $n = 11$ ): JJW 473; TNHC 32632, 32636–37, 32642–43, 32657–61. *Sceloporus asper* ( $n = 12$ ): FMNH 32043, 32876; MCZ 136523; UIMNH 20475–76; UMMZ 81959, 85399, 112573, 114889; USNM 111602, 111607; UTEP 10144. *Sceloporus bicanthalis* ( $n = 8$ ): AMNH 106372–73, 118148; MZFC 8034–35; KU 137728, 137736; UTA 4192. *Sceloporus bulleri* ( $n = 9$ ): AMNH 94810, 94814, 107307; KU 73687–88, 73691, 78626, 86605; LSUMZ 38303. *Sceloporus carinatus* ( $n = 16$ ): KU 46359, 116952–53; UIMNH 8679; UMMZ 126462 (6 specimens), 126463, 94740 (5 specimens). *Sceloporus cautus* ( $n = 10$ ): TNHC 30112, 30146, 30163, 30182, 30187, 30417–18, 33491, 33493, 33496. *Sceloporus chaneyi* ( $n = 6$ ): AMNH 139342–44; TCWC 69151, 70345–46. *Sceloporus chrysostictus* ( $n = 9$ ): KU 157365, 157367, 157369, 157371–72, 171514, 171516, 171518–19. *Sceloporus clarkii* ( $n = 13$ ): KU 48578, 48582–84, 48586, 77812, 77821; TNHC 16779; USNM 246170–71, 252906–08. *Sceloporus couchii* ( $n = 12$ ): KU 192577–79, 192581, 192583–84, 203247–49, 203252; MZFC 8030–31. *Sceloporus cozumelae* ( $n = 10$ ): KU 157416–19, 157421–26. *Sceloporus cryptus* ( $n = 13$ ): AMNH 65835, 98070–71, 100739; KU 70518–19, 70522–23, 70529, 137730–31; MCZ 134972–73. *Sceloporus cupreus* ( $n = 24$ ): AMNH 106881–83; FMNH 106501–06, 116158–61, 116291–97; UIMNH 60457–59, 87261. *Sceloporus cyanogenys* ( $n = 10$ ): TNHC 22552, 22557, 23086, 29979, 30307, 30311, 30318, 30328, 33488–89. *Sceloporus dugesii* ( $n = 11$ ): AMNH 62313, 136770; KU 67555, 67557–58; TCWC 12623–25, 54545; TNHC 27478–79. *Sceloporus dugesii intermedius* ( $n = 11$ ): AMNH 106411–12; FMNH 32536–37, 32548, 32553; TCWC 40763, 40766, 40771, 40781, 40783. *Sceloporus edwardtaylori* ( $n = 16$ ): AMNH 62318; UIMNH 10572–73, 10576, 28050, 40157–58; UMMZ 81827 (5 specimens), 81833, 81837, 81838 (2 specimens). *Sceloporus exsul* ( $n = 3$ ): TCWC 32376–77, 54821. *Sceloporus formosus formosus* ( $n = 6$ ): KU 70533–34, 101133–34; UTA 11642, 11659. *Sceloporus formosus scitulus* ( $n = 12$ ): MCZ 34228–31; UTA 4055–59, 4121, 4508, 4787. *Sceloporus gadoviae* ( $n = 9$ ): FMNH 115988, 115990, 115995, 115997; KU 68986–87; MZFC 8023–24; UCM 50028. *Sceloporus goldmani* ( $n = 4$ ): TCWC 51634; TNHC 33514; UMMZ 77266; USNM

46869. *Sceloporus graciosus* ( $n = 10$ ): KU 87530–33, 87535, 87551, 105964, 105966, 105972, 105980. *Sceloporus grammicus* ( $n = 10$ ): KU 59631, 70515, 87375, 200966; UTA 11695–98, 11701, 11707. *Sceloporus heterolepis* ( $n = 10$ ): UMMZ 19045, 112574 (2 specimens), 119045 (2 specimens), 121504–07; UTA 6053. *Sceloporus horridus albiventris* ( $n = 8$ ): AMNH 75777–78; 106436; MCZ 127003–04, 127134, 129895, 131788. *Sceloporus horridus horridus* ( $n = 13$ ): KU 29179, 29183, 29185, 67585, 67589, 67592, 67594; MCZ 136352–55, 136357–58. *Sceloporus hunsakeri* ( $n = 15$ ): AMNH 20505, 78841–42, 78844, 92926–27; KU 78680–81, 78685–86, 78689, 91499; UCM 51402, 51410, 51413. *Sceloporus insignis* ( $n = 14$ ): UMMZ 119099 (3 specimens), 119100 (2 specimens), 119101 (6 specimens); UTA 6054–56. *Sceloporus internasalis* ( $n = 15$ ): LSUMZ 33394; UIMNH 40170–71, 51010–11; UMMZ 126477 (6 specimens), 126498, 126529 (2 specimens), 126531. *Sceloporus jalapae* ( $n = 13$ ): KU 43719–23, 59693; MZFC 8029; UTA 4810–11, 8765, 8769, 11732, 11735. *Sceloporus jarrovii cyanostictus* ( $n = 3$ ): MCZ 4557; USNM 1677353, 192471. *Sceloporus jarrovii erythrocyaneus* ( $n = 5$ ): TCWC 35732, 40819, 40824, 40831, 40841. *Sceloporus jarrovii immucronatus* ( $n = 5$ ): TCWC 32476, 32493, 32508, 32546, 37681. *Sceloporus jarrovii jarrovii* ( $n = 8$ ): KU 51799–517802; TCWC 36860, 60360; USNM 246183–84. *Sceloporus jarrovii minor* ( $n = 7$ ): MCZ 20062–64, 20066–67, 20070, 20072. *Sceloporus jarrovii oberon* ( $n = 8$ ): AMNH 72734, 72738–40; TCWC 20789, 40869, 51690–91. *Sceloporus jarrovii sugillatus* ( $n = 5$ ): TCWC 3833–34, 3838, 3841; USNM 112100. *Sceloporus licki* ( $n = 9$ ): USNM 240129–30, 240132, 240134, 240646, 240648–50. *Sceloporus lineatulus* ( $n = 4$ ): AMNH 5477; MCZ 32429; SDSNH 50986; USNM 5478. *Sceloporus lineolateralis* ( $n = 16$ ): MCZ 135606, 135608, 135610; USNM 105382, 105384, 105389, 105398, 105401, 105409, 105450, 105456, 105463, 105470, 105481–82. *Sceloporus luhuae* ( $n = 15$ ): FMNH 68623–28, 68643–45, 68647, 68650–52; MCZ 49634–35. *Sceloporus lundelli* ( $n = 20$ ): FMNH 36471, 36473, 36475–80, 49225–27, 49229–33; KU 70537, 70543; MCZ 7119, 29236. *Sceloporus macdougalli* ( $n = 7$ ): AMNH 76119; MCZ 56014; UIMNH 37333–37. *Sceloporus maculosus* ( $n = 10$ ): UTEP 3721–22, 7185–88, 7200–01, 7203, 9513. *Sceloporus magister* ( $n = 9$ ): TNHC 12855, 12866, 12960, 12963, 12990, 14927, 14931, 14933, 48527. *Sceloporus malachiticus* ( $n = 10$ ): KU 62050, 62052–53, 62059, 67245–46, 67259–60, 67266, 184216. *Sceloporus megalepidurus halli* ( $n = 2$ ): KU 61698; UCM 41137. *Sceloporus megalepidurus megalepidurus* ( $n = 8$ ): MZFC 8026–27; UCM 29114, 29116–17, 29120, 29127, 29133. *Sceloporus melanorhinus melanorhinus* ( $n = 23$ ): AMNH 65043, 65047, 15648–49, 15652; FMNH 33339–41, 33344–45, 333448–49, 33351–52, 33354–57, 33359; UIMNH 37266, 56159, 76191, 76194. *Sceloporus melanorhinus stuarti* ( $n = 6$ ): TCWC 20993–94;

- UIMNH 8771, 37986, 87247–48. *Sceloporus merriami* ( $n = 14$ ): TNHC 32860, 32862, 32869–70, 32879, 32882–83, 32888, 32890, 32897–98, 49187, 49913, 49916. *Sceloporus mucronatus aureolus* ( $n = 4$ ): MCZ 129427, 136474–76. *Sceloporus mucronatus mucronatus* ( $n = 10$ ): AMNH 114569, 117858; TNHC 32828–30; USNM 112216, 112222–23, 112225, 112228. *Sceloporus mucronatus omiltemanus* ( $n = 6$ ): AMNH 98060, 106461, 106463–64, 102784, 102788. *Sceloporus nelsoni* ( $n = 7$ ): KU 47537–42, 91498. *Sceloporus occidentalis* ( $n = 9$ ): KU 192064–65; TNHC 19175–77, 32624–26, 33517. *Sceloporus ochoterenae* ( $n = 19$ ): FMNH 102111–13, 102115–18, 102120–23, 102126–33. *Sceloporus olivaceus* ( $n = 10$ ): TNHC 32434, 42261, 46354–55, 47241, 50038, 50043–44, 50434–35. *Sceloporus orcutti* ( $n = 15$ ): AMNH 20645, 60510, 60531, 64333, 65425, 75597; MCZ 44015–16; TNHC 33502, 35645–46, 35648; USNM 222653–55. *Sceloporus ornatus caeruleus* ( $n = 10$ ): USNM 105539–40, 105550, 105554, 105558, 105564, 105566–67, 105569, 105576. *Sceloporus ornatus ornatus* ( $n = 9$ ): MCZ 46933–34; TCWC 54295; TNHC 33497, 33500; USNM 105775, 105778, 105780, 105785. *Sceloporus palaciosi* ( $n = 6$ ): KU 197024–25; UMMZ 179341–42; USNM 245337–38. *Sceloporus parvus* ( $n = 15$ ): KU 33503, 33612–13, 33989–90, 39889–90; TNHC 30038–40, 30042, 30126–27, 30174, 33510. *Sceloporus pictus* ( $n = 6$ ): KU 59680–81, 59683, 59685–87. *Sceloporus poinsettii* ( $n = 10$ ): TNHC 32430–33, 32585, 49226, 49228, 49231–32, 49803. *Sceloporus prezygus* ( $n = 5$ ): TCWC 23774–75; UTA 6393, 8863, 11788. *Sceloporus pyrocephalus* ( $n = 7$ ): KU 62856–62. *Sceloporus salvini* ( $n = 8$ ): MCZ 136189, 136001; TCWC 21331, 26548; UTA 11783–85, 24008. *Sceloporus scalaris samcolemani* ( $n = 6$ ): AMNH 77245; TCWC 33513, 69140–41, 69144, 69147. *Sceloporus scalaris scalaris* ( $n = 10$ ): AMNH 15522, 15524–25, 18485; KU 47408–10, 51823, 63710–11. *Sceloporus scalaris slevini* ( $n = 6$ ): TCWC 63644–47; UCM 56074, 56114. *Sceloporus scalaris unicanthalis* ( $n = 3$ ): AMNH 17964, 82162; USNM 47884. *Sceloporus serifor* ( $n = 18$ ): FMNH 40692, 40695–96, 40698–40700, 40702–03; KU 61703, 157442, 157446, 171427; UMMZ 94654 (6 specimens). *Sceloporus shannorum* ( $n = 8$ ): UTEP 7030, 7179, 7361–63, 7365, 7415, 7453. *Sceloporus siniferus* ( $n = 11$ ): KU 43828–29, 43840–45, 43856–57; MZFC 8037. *Sceloporus smaragdinus* ( $n = 20$ ): KU 59634, 59643–44, 103177, 103185, 103188, 145793, 145795; UMMZ 100492, 100494 (4 specimens), 100495 (3 specimens); UTA 33560–61, 33569–70. *Sceloporus smithi* ( $n = 11$ ): AMNH 58044–45, 58048–49, 65852, 66900, 66902, 66941; MCZ 43108–09; MZFC 8036. *Sceloporus spinosus caeruleopunctatus* ( $n = 6$ ): AMNH 89719–20, 90911, 102763, 106519, 106523. *Sceloporus spinosus spinosus* ( $n = 10$ ): TNHC 30005, 30046, 30053, 30085, 30125, 30173, 30201, 30343–44, 30396. *Sceloporus squamosus* ( $n = 7$ ): KU 103245–50, 194329. *Sceloporus stejnegeri* ( $n = 8$ ): KU 182604; MCZ 56015; TCWC 7833; USNM 112634, 112636, 112641–42, 112644. *Sceloporus subniger* ( $n = 6$ ): AMNH 91576–79; USNM 111577, 111583. *Sceloporus subpictus* ( $n = 6$ ): AMNH 90913, 100738, 100749, 102765; MZFC 8028; UMMZ 130939. *Sceloporus taeniocnemis* ( $n = 17$ ): AMNH 90872–73, 90877–76, 98055–56, 99139, 102790, 113394, 114825; KU 59663, 59665, 59671, 59674–75, 187164, 187168. *Sceloporus tanneri* ( $n = 2$ ): UCM 49437, 52606. *Sceloporus teapensis* ( $n = 5$ ): KU 171483–84, 171486, 171501–02. *Sceloporus torquatus binocularis* ( $n = 6$ ): AMNH 129220–21; MZFC 8033; TCWC 49234, 51742, 51773. *Sceloporus torquatus melanogaster* ( $n = 10$ ): AMNH 88855, 109052, 118379–80; TCWC 27788, 29554; TNHC 30402, 30420, 30422, 30472. *Sceloporus torquatus torquatus* ( $n = 6$ ): USNM 111728–29, 111734–37. *Sceloporus undulatus consobrinus* ( $n = 11$ ): TCWC 64130, 64185, 64189, 64700, 65088; TNHC 21766–67, 28076, 32436, 33474, 42279. *Sceloporus undulatus elongatus* ( $n = 8$ ): UCM 6633, 7305, 21712, 52681, 52684–86, 52690. *Sceloporus undulatus erythrocheilus* ( $n = 8$ ): JJW 361–62, 364; UCM 7460, 11501–02, 43305, 50364. *Sceloporus undulatus garmani* ( $n = 6$ ): TCWC 57631, 57633, 57641, 63553, 63555; UCM 56591. *Sceloporus undulatus hyacinthinus* ( $n = 9$ ): AMNH 31930, 43275, 43281, 73536, 109237–38; USNM 325388, 325390, 325400. *Sceloporus undulatus tristichus* ( $n = 6$ ): UCM 16821, 43850, 43945–47, 43952. *Sceloporus undulatus undulatus* ( $n = 8$ ): AMNH 43070, 113405, 113407; MCZ 46367, 74239; USNM 223679, 223681, 223683. *Sceloporus utiformis* ( $n = 7$ ): KU 29623, 29629, 63403, 73733–36. *Sceloporus vandenburgianus* ( $n = 7$ ): TNHC 32655–56, 35652, 35657–59, 35661. *Sceloporus variabilis marmoratus* ( $n = 7$ ): TCWC 44167, 48761, 48882, 48888, 48893, 48900, 64709. *Sceloporus variabilis variabilis* ( $n = 12$ ): AMNH 107695–96, 107708; TCWC 59892, 59900, 59905, 59910, 59934, 59938; TNHC 32616, 32816, 32818. *Sceloporus virgatus* ( $n = 14$ ): KU 49531, 74453, 74455–56, 74458–60, 74462–63, 74468; TCWC 35355, 56299, 63642, 64632. *Sceloporus woodi* ( $n = 15$ ): FMNH 95004–05, 95008–13; UMMZ 54087, 100649, 109282, 109283 (3 specimens); UTA 10092. *Sceloporus zosteromus* ( $n = 19$ ): AMNH 77396, 136771, 136773–75; SDSNH 10304, 27692, 30185, 42624–25, 44657, 45674, 50988–89, 50991, 51048–49, 52956, 61311.
- Petrosaurus mearnsi* ( $n = 5$ ): CAS 90881–82; KU 31346, 91504, 176008. *Petrosaurus thalassinus* ( $n = 2$ ): CAS 3010, 91102. *Sator angustus* ( $n = 6$ ): JJW 474–475; LACM 134739, 134755, 135475, 135918. *Sator grandaeus* ( $n = 4$ ): LACM 9958, 9962, 9968–69. *Urosaurus bicarinatus* ( $n = 6$ ): KU 27185, 29249–53. *Urosaurus clarionensis* ( $n = 9$ ): LACM 19146, 19153, 19158, 19170; UMMZ 84224 (5 specimens). *Urosaurus gadovi* ( $n = 6$ ): KU 29237, 29239–40, 29242, 29244–45. *Urosaurus graciosus* ( $n = 6$ ): KU 72733, 72739, 72741; LACM 19038, 19076, 19083. *Urosaurus microscutatus* ( $n = 5$ ): LACM 128116, 128137, 128157, 128174; SDSNH 55384. *Urosaurus nigricaudus* ( $n = 6$ ): KU 78700, 78702, 78704, 78706–07, 78709. *Urosaurus ornatus* ( $n = 6$ ): JJW 97, 108–09; TNHC 31101, 31136–37. *Uta palmeri* ( $n = 5$ ): CAS 14122, 14128, 14130–31; KU 91523. *Uta stansburiana* ( $n = 6$ ): TNHC 33325, 33329–32, 48662.

## APPENDIX II

## Specimens Scored for Osteological Characters

Museum abbreviations are listed in Leviton et al. (1985), other abbreviations used are: MZFC (Museo de Zoología, Facultad de Ciencias, Universidad Nacional Autónoma de México), REE (Richard E. Etheridge, private collection), JJW (John J. Wiens field series). Abbreviations for skeletal preparations are as follow: DA (dry skull, cleared-and-stained hyoid and postcranial skeleton), AA (cleared and stained skeleton—scored for postcranial characters only), DS (dry skull only), SK (dry whole skeleton). *Sceloporus* and other genera are listed separately.

*Sceloporus acanthinus*: FMNH 20516 (DS); UMMZ 149146 (SK), 84067 (3 specimens, DA). *Sceloporus adleri*: KU 182555, 182561 (DA). *Sceloporus aeneus*: BYU 36137 (DS); FMNH 98398 (DS), 98401 (SK); REE 882 (SK). *Sceloporus arenicolus*: TNHC 32632, 32661 (DA). *Sceloporus asper*: FMNH 323041 (DS). *Sceloporus bicanthalis*: MZFC 8034–35 (DA). *Sceloporus bulleri*: KU 73687–88 (DA). *Sceloporus carinatus*: BYU 36424 (DS), UMMZ 94740 (3 specimens, DA), 149136 (SK). *Sceloporus caurus*: BYU 1628 (DS); TNHC 30013 (DA); REE 1627–1628 (SK). *Sceloporus chrysostictus*: KU 70453 (AA), 74948, 171516 (DA). *Sceloporus clarkii*: AMNH 73933 (SK); CM 48668 (SK); KU 13956, 16439 (SK); TNHC 16781 (AA). *Sceloporus couchii*: FMNH 98411 (SK); KU 192568, 192571, 192576 (DA), 192572 (AA); MZFC 8030–31 (DA); REE 998, 1590 (SK). *Sceloporus cozumelae*: KU 70455, 157411 (AA), 70477, 157420 (DA). *Sceloporus cryptus*: AMNH 65835 (DS); KU 137731, 137736 (DA). *Sceloporus cupreus*: BYU 36228 (DS); FMNH 106501, 116292 (DA). *Sceloporus cyanogenys*: AMNH 92179 (SK); KU 9124, 13971 (SK); TNHC 22559 (DA). *Sceloporus dugesii*: UTA 6037, 11556 (DA). *Sceloporus dugesii intermedius*: REE 859 (SK). *Sceloporus edwardtaylori*: UMMZ 81827 (3 specimens, DA). *Sceloporus formosus formosus*: AMNH 97573 (SK); KU 71764 (SK), 87477 (AA), 101134 (DA). *Sceloporus formosus scitulus*: UTA 4058, 4121 (DA). *Sceloporus gadoviae*: BYU 36148 (DS); KU 67574 (AA); MZFC 8023–24 (DA); REE 1688 (SK). *Sceloporus graciosus*: KU 87521–22 (AA); SDSNH 64450, 64520 (SK). *Sceloporus grammicus*: AMNH 90189 (SK); KU 182608–09 (DA), 182610 (AA). *Sceloporus heterolepis*: BYU 36420 (DS); UMMZ 112574, 119045, 121507 (DA). *Sceloporus horridus albiventris*: FMNH 98422 (SK). *Sceloporus horridus horridus*: BYU 36387 (DS); REE 20 (SK). *Sceloporus hunsakeri*: KU 78681, 91499 (DA). *Sceloporus insignis*: UMMZ 119101 (DA), 149135 (SK). *Sceloporus internasalis*: UMMZ 126477 (DA). *Sceloporus jalapae*: BYU 36423 (DS); MZFC 8029 (DA); UTA 4810 (DA). *Sceloporus jarrovii jarrovii*: AMNH 72630, 75604 (SK); CM 49007, 52797 (SK); KU 13961–62, 13965 (SK); TNHC 15332 (DA). *Sceloporus jarrovii immucronatus*: MVZ 78393 (SK). *Sceloporus jarrovii minor*: MZFC 8032 (DA). *Sceloporus laticaudatus*: USNM 240129, 240132 (DA). *Sceloporus lineatulus*: SDSNH

50986 (DA). *Sceloporus lineolateralis*: USNM 105381–82, 105393 (DA). *Sceloporus lunaei*: FMNH 64647 (DS), 68623, 68627 (DA). *Sceloporus lundelli*: FMNH 49225–26 (DA). *Sceloporus maculosus*: UTEP 7188, 7200, 7203 (DA). *Sceloporus magister*: FMNH 98423 (SK); SDSNH 57112 (SK); TNHC 12734 (DA). *Sceloporus malachiticus*: KU 68666–67 (SK); TNHC 32152 (DA). *Sceloporus megalepidurus megalepidurus*: BYU 36421 (DS); MZFC 8026–27 (DA). *Sceloporus melanorhinus melanorhinus*: BYU 14640 (DS); FMNH 33348 (DA); REE 860 (SK). *Sceloporus melanorhinus stuarti*: UMMZ 149237 (SK). *Sceloporus merriami*: KU 13967, 39947 (SK), 61655 (DA), 128835–36 (AA). *Sceloporus mucronatus mucronatus*: TNHC 32823 (DA). *Sceloporus mucronatus omiltemanus*: AMNH 92271 (SK); UTA 4042–43 (DA). *Sceloporus nelsoni*: BYU 14316 (DS); FMNH 98434 (SK); KU 44833 (AA). *Sceloporus occidentalis*: KU 1898 (SK), 68991 (AA); SDSNH 65175, 65395, 65838 (SK). *Sceloporus ochoterenae*: BYU 36004 (DS); FMNH 102112, 102118 (DA). *Sceloporus olivaceus*: AMNH 93183–85 (SK); CM 118964 (SK); KU 16418 (SK); TNHC 32435 (DA). *Sceloporus orcutti*: AMNH 75085 (SK); SDSNH 60416–19 (SK); TNHC 33501 (DA). *Sceloporus ornatus caeruleus*: USNM 105539–40, 105567 (DA). *Sceloporus ornatus ornatus*: TNHC 22575 (DA). *Sceloporus parvus*: BYU 36125 (DS); KU 33991 (AA), 39890 (DA). *Sceloporus pictus*: BYU 36419 (DS); KU 59679 (AA), MZFC 8025 (DA); REE 1687 (SK). *Sceloporus poinsettii*: AMNH 71302 (SK); CM 38707 (SK); KU 9123, 139868 (SK); TNHC 49930 (DA). *Sceloporus prezygus*: UMMZ 149261 (SK). *Sceloporus pyrocephalus*: BYU 36268 (DS); FMNH 98435 (SK); KU 62853 (AA), 62854 (DA); KU Anatomy (DA). *Sceloporus scalaris scalaris*: KU 102927 (AA), 102928 (DA). *Sceloporus scalaris slevini*: UCM 12088, 56067 (DA). *Sceloporus serrifer*: UMMZ 94654 (3 specimens, DA). *Sceloporus shannonorum*: UTEP 7453 (DA). *Sceloporus siniferus*: KU 43844, 43863 (DA), 43864 (AA); MZFC 8037 (DA). *Sceloporus smaragdinus*: KU 145795 (DA); UTA 33560–61 (DA). *Sceloporus smithi*: MZFC 8036 (DA). *Sceloporus spinosus caeruleopunctatus*: BYU 36213 (DS). *Sceloporus spinosus spinosus*: REE 1183, 1285, 1711–12 (SK); TNHC 30043 (DA). *Sceloporus squamosus*: KU 85857 (AA), 103249, 184227 (DA). *Sceloporus subniger*: AMNH 91576 (DA). *Sceloporus subpictus*: AMNH 100749 (DA); MZFC 8028 (DA). *Sceloporus taeniocnemis*: KU 59663 (DA); UMMZ 149153–54 (SK). *Sceloporus teapensis*: KU 55806 (DA), 59714 (AA). *Sceloporus torquatus binocularis*: CM 59722 (DA); MZFC 8033 (DA). *Sceloporus torquatus melanogaster*: CM 59726 (DA); TNHC 30386 (DA). *Sceloporus torquatus torquatus*: REE 881, 1713–1714, 1761 (SK). *Sceloporus undulatus consobrinus*: TNHC 28076, 42279 (DA). *Sceloporus undulatus elongatus*: UCM 52683, 52685 (DA). *Sceloporus undulatus erythrocheilus*: CM 48889–90 (SK);

JJW 361 (DA); UCM 7460, 43305 (DA). *Sceloporus undulatus garmani*: KU 20995 (SK); UCM 42503, 42505 (DA). *Sceloporus undulatus hyacinthinus*: CM 130102, 136658 (DA); KU 2206, 2210 (SK). *Sceloporus undulatus tristichus*: CM 53754–55 (SK), 75436, 75451 (DA); UCM 43952, 162821 (DA). *Sceloporus undulatus undulatus*: CM 28655 (SK), 1140, 8228 (DA). *Sceloporus uniformis*: BYU 36400 (DS); KU 73736 (DA), 73737 (AA). *Sceloporus vandenburgianus*: JJW 477 (SK); SDSNH 57111, 63250 (SK). *Sceloporus variabilis marmoratus*: CM 8294, 18393 (DA); JJW 372 (SK). *Sceloporus variabilis variabilis*: KU 67295 (AA), 187174 (DA). *Sceloporus virgatus*: KU 74454 (AA), 74466 (DA); SDSNH 63218, 63253, 64553–54 (SK). *Sceloporus woodi*: UMMZ 54087 (DA), 109283 (2 specimens, DA), 190166, 190168 (AA). *Sceloporus zosteromus*: SDSNH 10304, 42624, 51048 (DA).

*Petrosaurus mearnsi*: CAS 16544, 90879 (DA); KU 615600 (AA), 176009 (DS). *Petrosaurus thalassinus*: CAS 3009, 3012 (DA). *Sator angustus*: LACM 134742, 134749 (DA). *Sator grandaevis*: KU 91480 (SK), 91483 (DA); LACM 9936, 9961 (DA). *Urosaurus bicarinatus*: KU 29255–56 (DA); LACM 97732, 97736 (DA). *Urosaurus clarionensis*: LACM 19139, 19166 (DA). *Urosaurus gadovi*: KU 29236, 29238 (AA), 29239, 29671 (DA), KU Anatomy 83 (DA). *Urosaurus graciosus*: KU 72740, 72743 (DA); LACM 19040, 19066 (DA); SDSNH 63124 (SK). *Urosaurus microscutatus*: LACM 128138, 128172 (DA); SDSNH 49909, 49912 (AA). *Urosaurus nigricaudus*: KU 78732 (AA), 78745–46 (DA), 78754 (AA); SDSNH 65036 (SK). *Urosaurus ornatus*: KU 13936–38 (SK), 77867 (AA), 77868 (DA); SDSNH 63219, 63240, 63245, 66265 (SK). *Uta palmeri*: CAS 14123–24 (DA); KU 91525 (DA). *Uta stansburiana*: KU 7215, 73395–96 (SK), 194130, 194136–37 (AA).

### APPENDIX III

#### Voucher Specimens for Molecular Analysis

Standard museum abbreviations are listed in Leviton et al. (1985), nonstandard abbreviations used are: EDHEM (Escuela Nacional de Estudios Profesionales—Iztacala, Ecología de la Herpetofauna del Estado de México), MZFC (Museo de Zoología, Facultad de Ciencias, Universidad Nacional Autónoma de México), JAM (Jimmy A. McGuire field series), RWM (Robert W. Murphy, field series), TWR (Tod W. Reeder, field series), JJW (John J. Wiens field series).

*Sceloporus adleri*: MVZ 144176. *Sceloporus bicanthalis*: MZFC 8034. *Sceloporus cautus*: MZFC 7413. *Sceloporus chrysostictus*: BYU 38102. *Sceloporus clarkii*: LSUMZ 48830. *Sceloporus couchii*: MZFC 6676. *Sceloporus cozumelae*: BYU 38104. *Sceloporus cryptus*: MZFC 7438. *Sceloporus cyanogenys*: LSUMZ 48852. *Sceloporus dugesii dugesii*: UTA R-23955. *Sceloporus formosus formosus*: UTA R-23964. *Sceloporus gadoviae*: MZFC 7431. *Sceloporus graciosus*: ROM 26193. *Sceloporus grammicus*: UTA R-23970. *Sceloporus heterolepis*: MZFC 8017. *Sceloporus horridus horridus*: MZFC 7458. *Sceloporus hunsakeri*: LACM 128094. *Sceloporus jalapae*: MZFC 7427. *Sceloporus jarrovii cyanostictus*: MZFC 7411. *Sceloporus jarrovii jarrovii*: LSUMZ 48786. *Sceloporus jarrovii minor*: MZFC 8032. *Sceloporus licki*: LACM 128044. *Sceloporus lineolateralis*: MZFC 6650. *Sceloporus macdougalli*: MZFC 7017. *Sceloporus maculosus*: JAM 650. *Sceloporus magister*: LSUMZ 48819. *Sceloporus malachiticus*: MVZ 149857. *Sceloporus megalepidurus*: MZFC 8026. *Sceloporus melanorhinus melanorhinus*: MZFC 7454. *Sceloporus merriami*: LSUMZ 48844. *Sceloporus mucronatus omiltemanus*: UTA R-24004. *Sceloporus occidentalis*: MVZ 137487. *Sceloporus ochoterenae*: MZFC 7456. *Sceloporus olivaceus*: LSUMZ 48750. *Sceloporus orcutti*: LACM 128079. *Sceloporus ornatus caeruleus*: JAM 652. *Sceloporus parvus*: MZFC 6664. *Sceloporus pictus*: MZFC 7426. *Sceloporus poinsettii*: LSUMZ 48847. *Sceloporus scalaris slevini*: LSUMZ 48788. *Sceloporus siniferus*: MZFC 7437. *Sceloporus smaragdinus*: MVZ 143426. *Sceloporus smithi*: MZFC 7434. *Sceloporus spinosus caeruleopunctatus*: MZFC 7451. *Sceloporus spinosus spinosus*: EDHEM 2065. *Sceloporus stejnegeri*: MZFC 7452. *Sceloporus subpictus*: MZFC 8028. *Sceloporus tenuicnemis*: MVZ 4213. *Sceloporus torquatus binocularis*: MZFC 8033. *Sceloporus torquatus melanogaster*: UTA R-24016. *Sceloporus undulatus consobrinus*: LSUMZ 48817. *Sceloporus undulatus erythrocheilus*: JJW 363. *Sceloporus undulatus undulatus*: LSUMZ 48876. *Sceloporus uniformis*: MZFC 6091. *Sceloporus vandenburgianus*: TWR 430. *Sceloporus variabilis marmoratus*: LSUMZ 48723. *Sceloporus virgatus*: LSUMZ 48764. *Sceloporus woodi*: MVZ 150111. *Sceloporus zosteromus*: RWM 1215.

*Petrosaurus mearnsi*: ROM 13743. *Petrosaurus thalassinus*: RWM 2223. *Sator angustus*: ROM 26215. *Urosaurus graciosus*: LSUMZ 48825. *Urosaurus microscutatus*: ROM 26191. *Urosaurus nigricaudus*: ROM 26192. *Urosaurus ornatus*: LSUMZ 48828. *Uta palmeri* (no voucher). *Uta stansburiana*: LSUMZ 48840.

## APPENDIX IV

*Description of Morphological Characters*

Choice of traits as being "0" or "1" usually, but not always, indicates polarity. Trees were rooted by including species of *Petrosaurus*, *Urosaurus*, and *Uta* and constraining their relationships as outgroups. Many of the external characters were taken from Smith's (1939) prephylogenetic monograph, and most of the karyological characters were originally used by Hall (1973).

*Osteology*

1. Number of premaxillary teeth: (0) six; (1) five or fewer.
2. Number of premaxillary teeth: (0) six; (1) seven.
3. Base of nasal process of premaxilla: (0) entire; (1) with distinct notches or foramina laterally.
4. Median (anteriorly projecting) process on anterior margin of nasal: (0) absent (Fig. 12B); (1) present (Fig. 12A).
5. Nutritive foramina in maxilla: (0) small or absent; (1) large (diameter exceeds that of largest tooth).
6. Lacrimal: (0) present; (1) absent.
7. Frontal, anterolateral processes (Etheridge, 1964): (0) exposed (Fig. 12A); (1) completely covered by nasals and/or prefrontals (Fig. 12B).
8. Frontal-postorbital contact: (0) absent (Fig. 14B); (1) present (Fig. 14A).
9. Posterior parietal scale: (0) flat; (1) distinctly raised posteriorly, due to raised anterolateral process of parietal.
10. Raised anterolateral process of parietal: (0)

without posterior shelf at articulation with postorbital; (1) with posterior shelf at articulation with postorbital.

11. Posteroventral corner of squamosal (tip of dorsal process): (0) acuminate (Fig. 13A); (1) rounded (Fig. 13B).
12. Posterior articulation of squamosal: (0) articulates on or adjacent to dorsal crest of supratemporal process of parietal (Fig. 13A); (1) articulation more ventral, not reaching dorsal crest of supratemporal process (articulating on supratemporal; Fig. 13B).
13. Contact between anterolateral process of frontal and maxilla: (0) absent (Fig. 12B); (1) present (Fig. 12A). This character is not redundant with character 7 because the anterolateral processes are often exposed but only rarely contact the maxilla.
14. Median contact of right and left palatines at anterior end of pyriform recess: (0) present; (1) absent.
15. Posterior processes of basisphenoid: (0) not extending onto spheno-occipital tubercle; (1) elongate, extending onto spheno-occipital tubercle.
16. Separation of supraoccipital and posterior border of parietal roof: (0) small, slitlike fissure (Fig. 14A); (1) large, V-shaped gap in supraoccipital when viewed dorsally (Fig. 14B).
17. Process on crista interfenestralis of exoccipital: (0) rounded; (1) pointed.

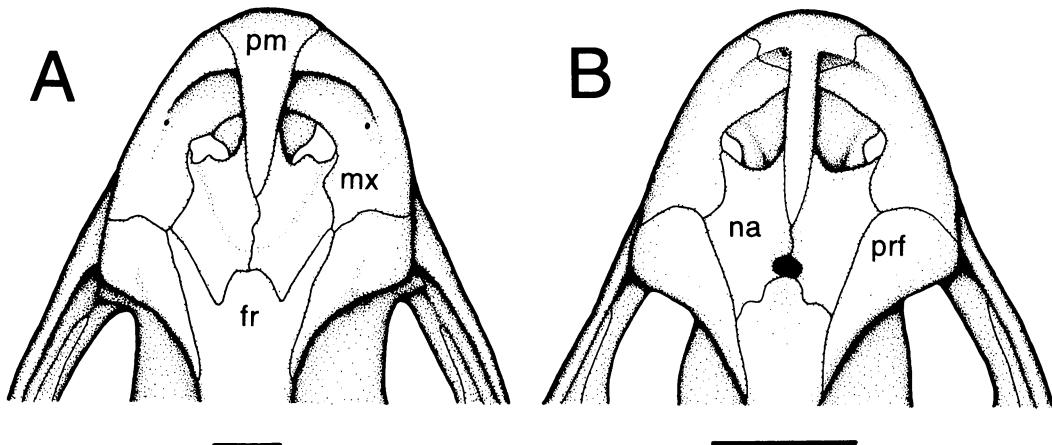


FIG. 12.—Dorsal view of the rostral region of the skull of two species of *Sceloporus*. (A) *S. torquatus binocularis*, MZFC 8033, showing median process on anterior margin of nasal (char 4.1), exposed anterolateral process of the frontal (char 7.0), and contact between anterolateral process of the frontal and the maxilla (13.1). (B) *S. couchii*, MZFC 8031, showing absence of median process on anterior margin of nasal (char 4.0), anterolateral process of frontal covered by nasal (char 7.1), and absence of contact between the frontal and maxilla (char 13.0). Abbreviations: fr, frontal; mx, maxilla; na, nasal; pm, premaxilla; prf, prefrontal. Scales = 2 mm.

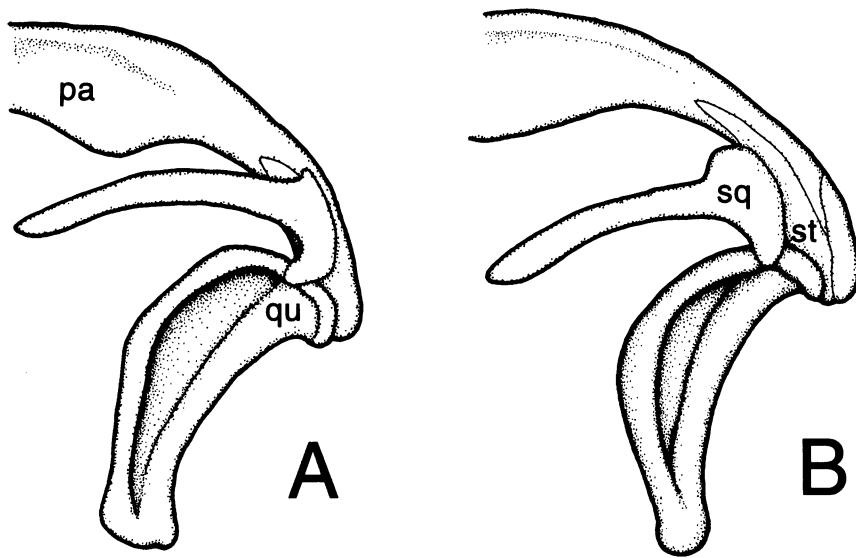


FIG. 13.—Lateral view of the outer posterior skull elements of two species of *Sceloporus*. (A) *S. subpictus*, MZFC 8028, showing acuminate posterodorsal corner of the squamosal (char 11.0) and articulation of squamosal near dorsal crest of supratemporal process of parietal (12.0). (B) *S. siniferus*, MZFC 8037, showing rounded posterodorsal corner of squamosal (char 11.1) and more ventral articulation of squamosal on the supratemporal (char 12.1). Abbreviations: pa, parietal; sq, squamosal; st, supratemporal. Scales = 1 mm.

- 18. Anterior inferior alveolar foramen, ventral margin: (0) in splenial (Fig. 15A); (1) in dentary (Fig. 15B).
- 19. Coronoid: (0) not extending to anterior inferior alveolar foramen of the splenial; (1) contacts anterior inferior alveolar foramen.
- 20. Meckel's groove: (0) open (Fig. 15A); (1) fused for some or all of its length (Fig. 15B).
- 21. Ventral margin of splenial: (0) not extending to ventral margin of lower jaw (Fig. 15A); (1) extending to ventral margin of lower jaw (Fig. 15B).

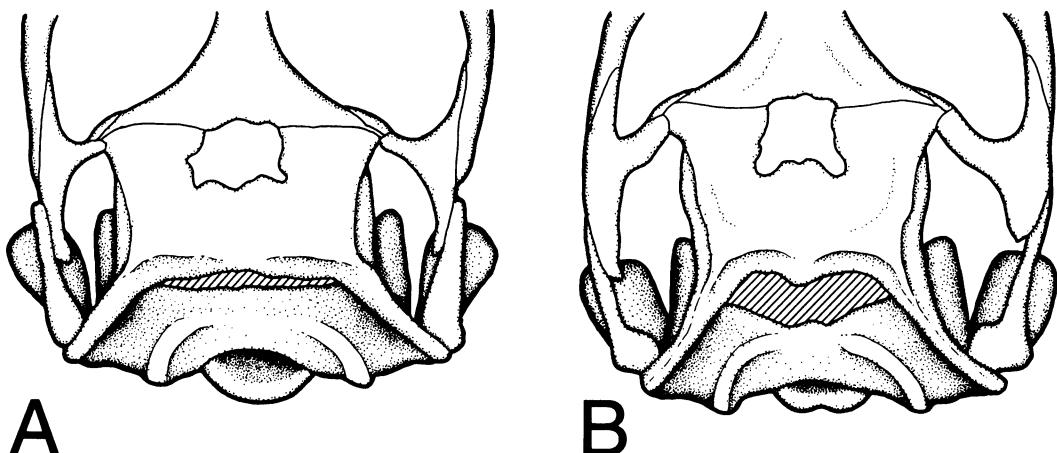


FIG. 14.—Dorsal view of the posterior region of the skull in two species of *Sceloporus*. (A) *S. couchii*, MZFC 8031, showing contact between the frontal and postorbital (pa) small fissure between the supraoccipital and posterior border of the parietal roof (diagonal lines; char 16.0). (B) *S. siniferus*, MZFC 8037, showing lack of contact between the frontal and postorbital (pa) and large, V-shaped gap in supraoccipital (char 16.1). Scales = 2 mm.

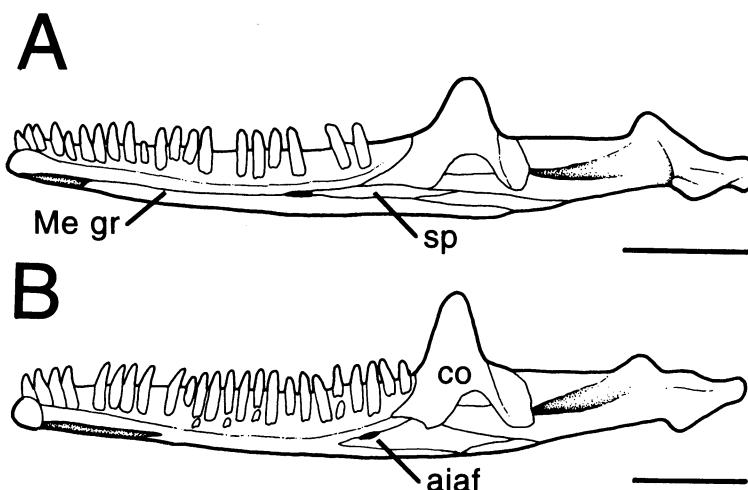


FIG. 15.—Lingual view of the right mandible of two species of *Sceloporus*. (A) *S. variabilis marmoratus*, JJW 372, showing anterior inferior alveolar foramen with ventral margin in dentary (char 18.1), open Meckel's groove (char 20.0), and ventral margin of splenial not extending to ventral margin of the mandible (char 21.0). (B) *S. gadoviae*, MZFC 8024, showing anterior inferior alveolar foramen with ventral margin in splenial (char 18.0), fused Meckel's groove (char 20.1), and ventral margin of splenial extending to ventral margin of the mandible (char 21.1). Abbreviations: aiaf, anterior inferior alveolar foramen; co, coronoid; Me gr, Meckel's groove; sp, splenial. Scales = 2 mm.

22. Angular process of mandible: (0) dorsoventrally flattened; (1) laterally compressed.
23. Cusps of posterior dentary teeth (Etheridge, 1964): (0) weak (Fig. 16A); (1) strongly expanded (Fig. 16B). Those species lacking cusps were treated as unknown for this character.
24. Cusps of posterior dentary teeth (Etheridge, 1964): (0) present (Fig. 16A, B); (1) absent (Fig. 16C).
25. Second ceratobranchials: (0) parallel through most of their lengths (Fig. 17A); (1) divergent through most of their lengths (Fig. 17B).
26. Second ceratobranchials: (0) close medially, in contact or almost in contact (Fig. 17A); (1) widely separated, nearly as distant as width of trachea (Fig. 17B). Character 26 is not redundant with character 25 in that the second ceratobranchials can be widely separated and yet remain parallel through most of their lengths.
27. Anteromedial process on ceratohyal: (0) lacking acuminate posterior process (Fig. 17B); (1) with acuminate posterior process (Fig. 17A).
28. Number of vertebrae (Etheridge, 1964): (0) 23; (1) 22.
29. Number of vertebrae (Etheridge, 1964): (0) 23; (1) 24.
30. First pair of cervical ribs on vertebra (Etheridge, 1964): (0) four; (1) three.
31. Posterior process on terminal cartilage of rib of vertebra 6: (0) present (Fig. 18A); (1) absent (Fig. 18B).
32. Posterior flange on second sacral diapophyses: (0) present; (1) absent.
33. Tail shape in males (Smith, 1939): (0) cylindrical or depressed; (1) laterally compressed. Assessed externally.
34. Fused hemal arches begin between caudal vertebrae: (0) three and four; (1) four and five.
35. Processes on terminal cartilage of 20th presacral vertebra: (0) absent; (1) present.
36. Postxiphisternal ribs: (0) posteriomost seven or eight distinctly shorter than xiphisternal ribs; (1) posteriomost six distinctly shorter.
37. Postxiphisternal ribs: (0) posteriomost six or seven distinctly shorter than xiphisternal ribs; (2) posteriomost eight distinctly shorter.
38. Scapular fenestra (Etheridge, 1964): (0) present (Fig. 19A); (1) absent (Fig. 19B).
39. Scapular fenestra: (0) bordered by at least some cartilage anteriorly; (1) surrounded completely by bone. Species lacking a scapular fenestra were scored as unknown for this character.
40. Secondary (or posterior) coracoid fenestra (Etheridge, 1964): (0) absent (Fig. 19B); (1) present (Fig. 19A).
41. Primary (or anterior) coracoid fenestra: (0) formed mostly in bone (Fig. 19A); (1) formed nearly 50% in cartilage anteriorly (Fig. 19B).
42. Xiphisternal ribs (Etheridge, 1964): (0) two or one (Fig. 20A); (1) three (Fig. 20B).
43. Free posterior extensions of xiphisternal rods (Etheridge, 1964): (0) absent (Fig. 20A); (1) present (Fig. 20B).
44. Xiphisternal ribs (Etheridge, 1964): (0) closely spaced (distance between them at sternum equal to or less than the diameter of two xiphisternal ribs; Fig. 20B); (1) widely separated

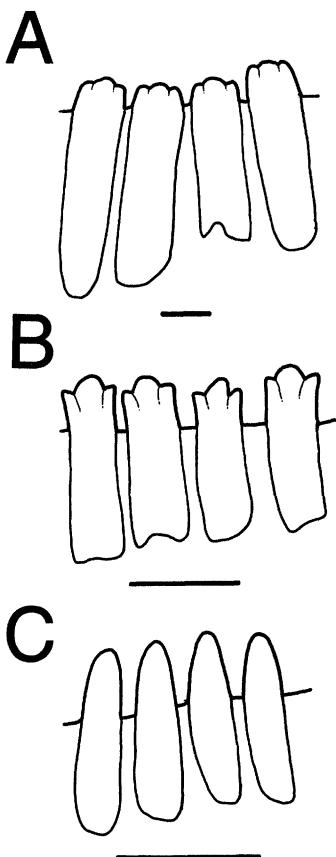


FIG. 16.—Lingual view of the posterior (second to fifth most posterior) dentary teeth in three species of *Sceloporus*. (A) *S. poinsettii*, CM 38707, showing weakly expanded cusps (char 23.0, 24.0). (B) *S. siniferus*, MZFC 8037, showing strongly expanded cusps (char 23.1, 24.0). (C) *S. jalapae*, MZFC 8029, showing lack of cusps (24.1). Scales = 0.5 mm.

- (distance between them at sternum greater than diameter of two xiphisternal ribs; Fig. 20A).
45. Suprascapular fenestrations: (0) absent; (1) present.
  46. Median notch in anterior border of sternal fontanelle (Etheridge, 1964): (0) absent (Fig. 20B); (1) present (Fig. 20A).
  47. Foramen anterior to sternal fontanelle (Etheridge, 1964): (0) absent; (1) present (Fig. 20B). Because this foramen may represent a modification of the median notch (char. 47), specimens with a median notch were scored as unknown for this character.
  48. Hypoischiac foramen: (0) present (Fig. 21A); (1) absent (Fig. 21B).
  49. Epipubic cartilage: (0) not extending past pubic symphysis (Fig. 21B); (1) extends well past pubic symphysis (Fig. 21A).
  50. Posterolateral processes or expansions on hy-

poischaic cartilage: (0) present (Fig. 21A); (1) absent (Fig. 21B).

#### *Squamation*

51. Cephalic scales (Smith, 1939): (0) smooth (Fig. 22B, C, E, F); (1) keeled, surface of some or all scales raised into small (usually longitudinal) ridges (Fig. 22A, D).
52. Scattered black keratinizations on dorsal cephalic scales: (0) keratinizations absent; (1) present.
53. Subnasal-postrostral contact: (0) absent (Fig. 22D); (1) present (Fig. 22E, right side). Scored as unknown in specimens lacking postrostrals.
54. Rostral-nasal contact (Smith, 1939): (0) absent (prevented by postrostrals; Fig. 22C-F); (1) present (postrostrals separated or absent; Fig. 22B).
55. Number of postrostrals (Smith, 1939): (0) six; (1) four (Fig. 22D); (2) two (Fig. 22A). Unordered and coded with the majority method.
56. Postrostrals (Smith, 1939): (0) present (Fig. 22A, D); (1) absent (Fig. 22B).
57. Median postrostrals (Smith, 1939): (0) in contact (Fig. 22A, D); (1) separated, rostral contacts internasal.
58. Posterior postrostrals: (0) absent (Fig. 22D); (1) present (Fig. 22E, right side). A row of scales just posterior to those postrostrals in contact with the rostral.
59. Supranasals: (0) separated medially (Fig. 22C-F); (1) contacting medially, excluding internasals (Fig. 22A, B).
60. Supranasal: (0) lateral to nasal (Fig. 22A, D); (1) extends anteromedial to nasal (Fig. 22E).
61. Internasals: (0) present (Fig. 22C); (1) absent.
62. Internasals (Smith, 1939): (0) single pair (Fig. 22C); (1) divided into four or more smaller scales. Scored as unknown in specimens lacking internasals.
63. Anterior frontonasals: (0) present (Fig. 22E, F); (1) absent (Fig. 22C). Figured but not discussed by Smith (1939), a row of scales between the enlarged anterior internasals (situated between the nasals) and the frontonasals is present in most *Sceloporus* species. We refer to these as the anterior frontonasals.
64. Anterior frontonasals: (0) two or four (Fig. 22E); (1) three or one (Fig. 22F). Scored as unknown in specimens lacking anterior frontonasals.
65. Median and lateral frontonasals (Smith, 1939): (0) in contact (Fig. 22A-C, E, F); (1) separated (Fig. 22D).
66. Frontal (Smith, 1939): (0) paired (Fig. 22); (1) fused, single scale.
67. Frontal (Smith, 1939): (0) not divided sagittally (Fig. 22B, C, E, F); (1) one or both scales divided sagittally (Fig. 22A, D).
68. Frontal (Smith, 1939): (0) divided into two or three scales (Fig. 22B-F); (1) divided into four asymmetric scales (Fig. 22A).
69. Frontal-interparietal contact (Smith, 1939): (0)

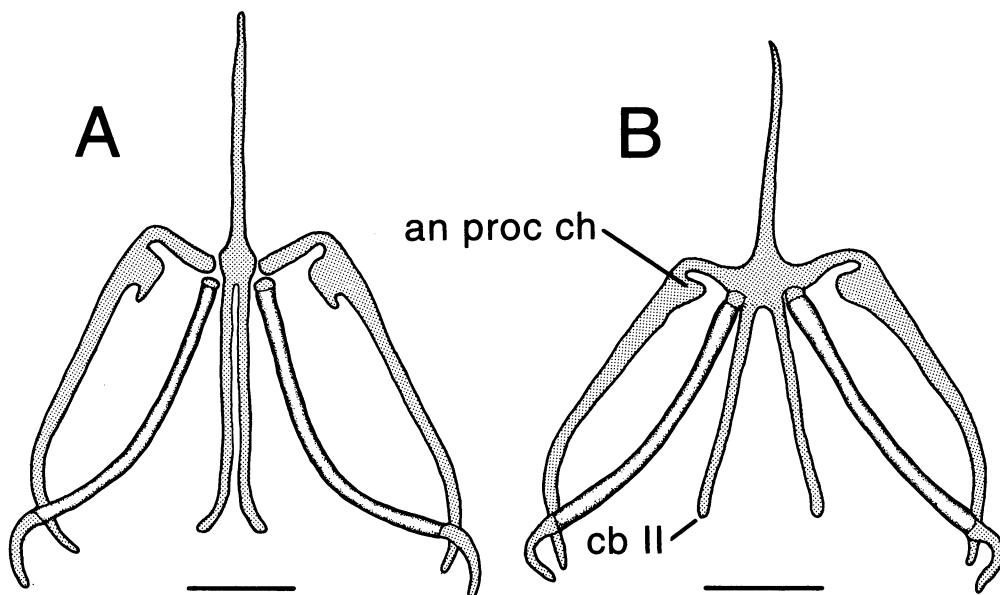


FIG. 17.—Ventral view of hyoid in two species of *Sceloporus*. (A) *S. gadoviae*, MZFC 8024, showing second ceratobranchials parallel (char 25.0) and close set medially (char 26.0) and an acuminate posterior process on anteromedial process of the ceratohyal (or epihyal; char 27.1). (B) *S. bicanthalis*, MZFC 8035, showing second ceratobranchials divergent (char 25.0) and widely separated (char 26.0) and lack of acuminate posterior process on the anterior margin of the ceratohyal (char 27.0). Abbreviations: an proc ch, anteromedial process of ceratohyal; cb II, ceratobranchial II. Scales = 2 mm.

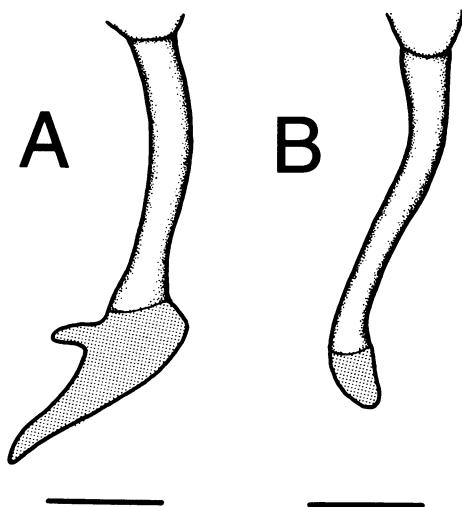


FIG. 18.—Dorsolateral view of the right rib of vertebra 6 in two species of *Sceloporus*. (A) *S. gadoviae*, MZFC 8024, showing posterior process on the terminal cartilage (char 31.0). (B) *S. siniferus*, MZFC 8037, showing lack of posterior process (char 31.1). Scales = 1 mm.

- absent (Fig. 22A, B, D, E); (1) present (Fig. 22C, F).
- 70. Frontal–median frontonasal contact (Smith, 1939): (0) absent (Fig. 22A–E); (1) present (Fig. 22F).
- 71. Median prefrontal (Smith, 1939): (0) absent (Fig. 22C, E, F); (1) present (Fig. 22A, B, D).
- 72. Median parietal (Smith, 1939): (0) absent (Fig. 22A–D, F); (1) present (between frontal and interparietal; Fig. 22E).
- 73. Frontoparietals (number on each side; Smith, 1939): (0) three or more (Fig. 22B, D); (1) two (Fig. 22A, C, E, F).
- 74. Posterior parietals: (0) not distinctly imbricate; (1) distinctly imbricate.
- 75. Interparietal: (0) not divided posteriorly (Fig. 22C–F); (1) with distinct “fissure” posteriorly, partially divided (Fig. 22A, B).
- 76. Posterior circumorbital scales: (0) present (Fig. 22E); (1) absent (Fig. 22F). Considered absent if none are present posterior to the anterior margin of the penultimate (next to most anterior) supraocular.
- 77. Posterior circumorbital rows: (0) two; (1) one (Fig. 22A, B, D, E).
- 78. Supraocular–parietal contact (Smith, 1939): (0) absent (prevented by circumorbitals; Fig. 22A,

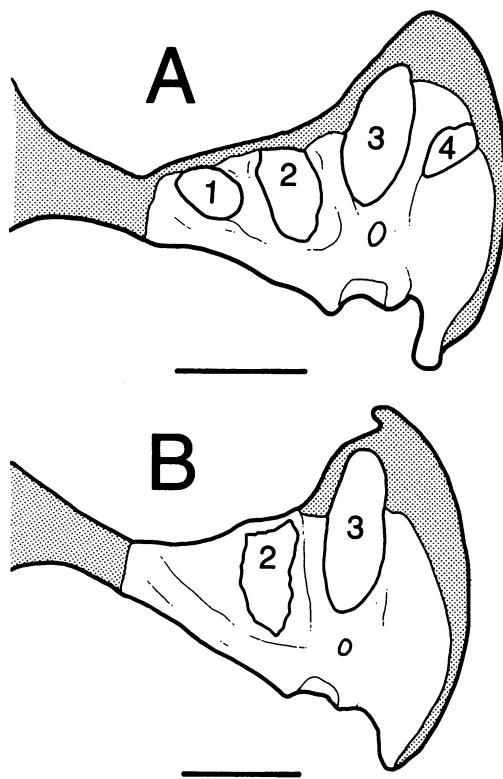


FIG. 19.—Ventral view of the right scapulocoracoid of two species of *Sceloporus*. (A) *S. gadoviae*, MZFC 8024, showing presence of the scapular fenestra (char 38.0) and secondary coracoid fenestra (char 40.0) and primary coracoid fenestra formed mostly in bone (char 41.0). (B) *S. siniferus*, MZFC 8037, showing absence of scapular fenestra (char 38.1) and secondary coracoid fenestra (char 40.0) and primary coracoid fenestra formed nearly 50% in cartilage (char 41.1). Symbols: 1, scapular fenestra; 2, scapulocoracoid fenestra; 3, primary coracoid fenestra; 4, secondary coracoid fenestra. Scales = 2 mm.

- B, D, E); (1) present (Fig. 22C, F). This character is not redundant with character 76 because it is possible to have contact between the supraocular and parietal scales while still retaining the posterior circumorbitals.
79. Supraoculars (maximum number of rows of scales between circumorbitals and superciliaries; the maximum row length must be present for a length of at least two contiguous scales; modified from Smith, 1939): (0) three or more (Fig. 22B–E); (1) two (Fig. 22F).
  80. Supraoculars (modified from Smith, 1939): (0) three or fewer (Fig. 22D); (2) four (Fig. 22E).
  81. Contact between superciliary and enlarged, median supraocular (Smith, 1939): (0) absent (Fig. 22C); (1) present (Fig. 22F). In most *Sceloporus*, the contact is prevented by a row of small, lateral supraocular scales.

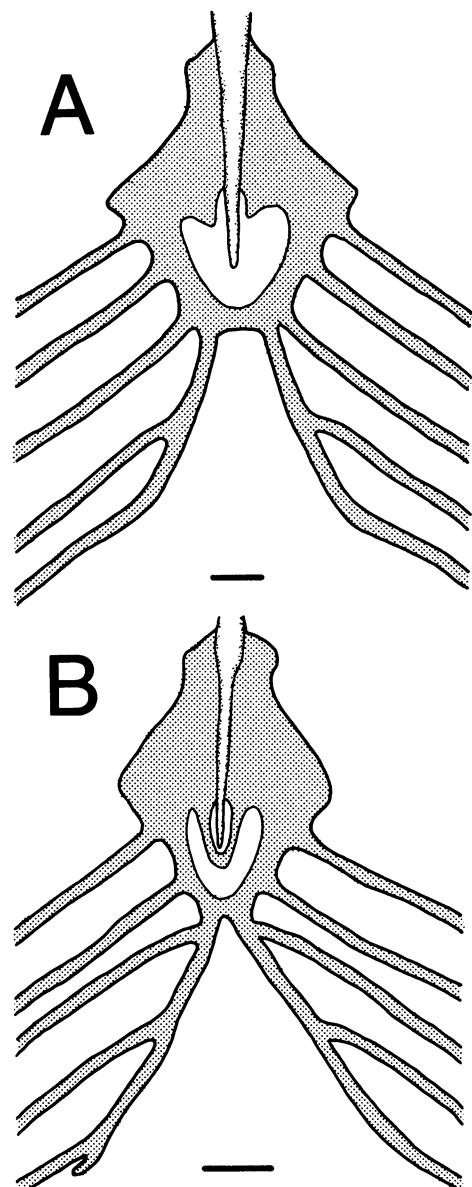


FIG. 20.—Ventral view of sternum in two species of *Sceloporus*. (A) *S. jarrovii minor*, MZFC 8032, showing two xiphisternal rib connections (char 42.0), no free xiphisternal rib endings (char 43.0), widely separated xiphisternal ribs (char 44.1), and median notch in anterior border of sternal fontanelle (46.1). (B) *S. gadoviae*, MZFC 8024, showing three xiphisternal rib connections (char 42.1), one free xiphisternal rib ending (right side, char 43.1), absence of median notch in anterior border of sternal fontanelle (46.1), and presence of a foramen anterior to sternal fontanelle (47.1). Scales = 2 mm.

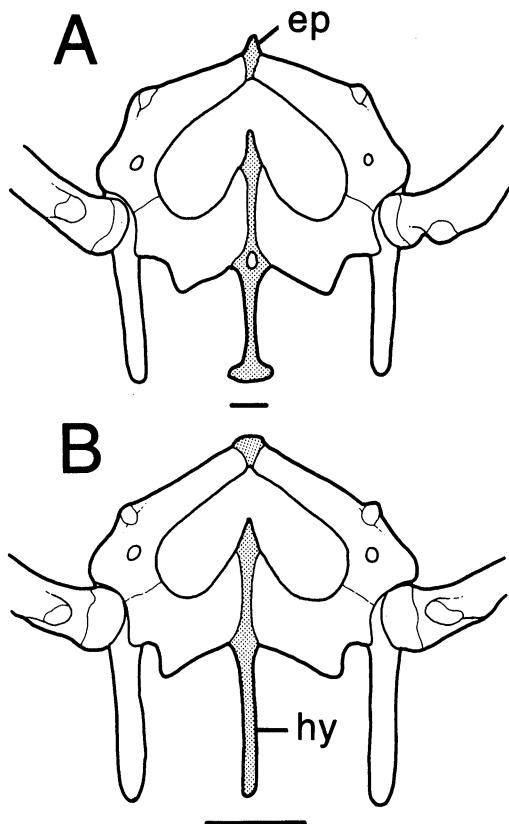


FIG. 21.—Ventral view of pelvic girdle in two species of *Sceloporus*. (A) *S. torquatus binocularis*, MZFC 8033, showing elongate epipubic cartilage (char 49.1), presence of foramen in hypoischiac cartilage (char 48.0), and posterolateral processes on hypoischiac cartilage (char 50.0). (B) *S. bicanthalis*, MZFC 8034, showing short epipubic cartilage (char 49.0), and absence of hypoischiac foramen (char 48.1) and posterolateral processes (char 50.1). Scales = 2 mm.

82. Contact between superciliaries and median supraoculars (Smith, 1939): (0) small, involving only a single supraocular; (1) extensive, involving more than one supraocular. Specimens lacking any contact between superciliaries and supraoculars were scored as having condition "0."
83. Superciliaries (Smith, 1939): (0) six (or five); (1) seven (or eight).
84. First canthal-lorilabial contact (Smith, 1939): (0) absent (Fig. 23A, D); (1) present (Fig. 23B, C).
85. Canthal-subnasal fusion (Smith, 1939): (0) absent (Fig. 23A, C, D); (1) present (Fig. 23B).
86. Canthals (Smith, 1939): (0) two (Fig. 23B, C); (1) one (Fig. 23A, D).
87. Preocular (Smith, 1939): (0) entire (or with small scale present at preocular–subocular con-

- tact; Fig. 23D); (1) divided longitudinally (Fig. 23A, B, C).
88. Loreals (Smith, 1939): (0) one (Fig. 23A–C); (1) two or more (Fig. 23D).
89. Minimum height of lorilabial series (modified from Smith, 1939): (0) one row high (Fig. 23A–C); (1) two rows high (Fig. 23D).
90. Maximum height lorilabial series (modified from Smith, 1939): (0) two scales high (Fig. 23B–D); (1) single row high (Fig. 23A).
91. Subocular (Smith, 1939): (0) not reduced (Fig. 23A, B, D); (1) reduced (Fig. 23C). The subocular was considered reduced if it was not expanded anterior to midorbit, as seen in most species.
92. Subocular–supralabial contact (Smith, 1939): (0) absent; (1) present.
93. Supralabials (Smith, 1939): (0) five or six (Fig. 23); (1) four. The number on the margin of the lip only are counted.
94. Penultimate and ultimate (usually fourth and fifth) supralabials: (0) not broadly overlapping (not diagonal; Fig. 23B–D); (1) broadly overlapping (diagonal; Fig. 23A).
95. Penultimate and ultimate (usually fourth and fifth) supralabials: (0) in broad contact, similar to contact between third and fourth (Fig. 23A, C); (1) contact greatly reduced or absent (Fig. 23B, D). Character 95 is not redundant with character 94 in that the fourth and fifth supralabials can be in broad contact and be either broadly or not overlapping.
96. Rostral–supralabial suture: (0) straight (vertical; Fig. 23B–D); (1) distinctly overlapping (Fig. 23A).
97. Sublabials (Smith, 1939): (0) first (anteriomost) contacts first infralabial (Fig. 24A, B, D); (1) first sublabial contacts second infralabial (Fig. 24C).
98. Mental–sublabial contact (Smith, 1939): (0) absent (Fig. 24A–C); (1) present (Fig. 24D).
99. Mental: (0) not deeply indented by infralabials (Fig. 24A, C, D); (1) deeply indented by infralabials (Fig. 24B).
100. Mental: (0) wider anteriorly than posteriorly or similar widths anteriorly and posteriorly (Fig. 24A–C); (1) distinctly wider posteriorly than anteriorly (Fig. 24D).
101. Second infralabial contacts: (0) one or two sublabials (Fig. 24B–D); (1) three sublabials (Fig. 24A).
102. Second pair of postmentals (Smith, 1939): (0) separated by gular(s); (1) in contact.
103. Anteriomost gulars (between anterior chinshields): (0) paired (Fig. 24A, C, D); (1) single (Fig. 24B).
104. Gulars: (0) granular or not strongly imbricate (Fig. 24C); (1) strongly imbricate (Fig. 24A, B, D).
105. Posterior gulars (Smith, 1939): (0) all entire; (1) some or all notched.
106. Gular fold (Smith, 1939): (0) present, complete; (1) interrupted medially, remnant laterally; (2)

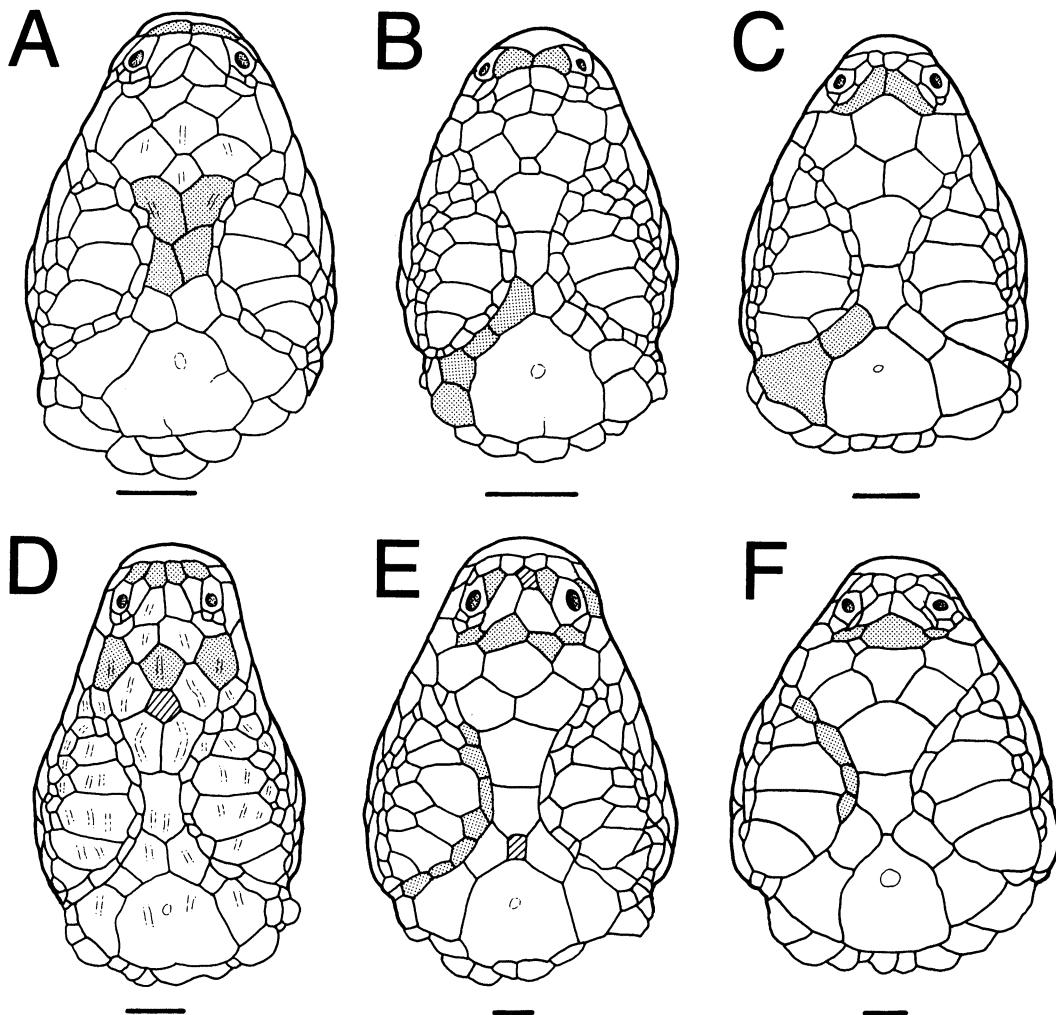


FIG. 22.—Dorsal view of head scales in six species of *Sceloporus*. (A) *S. squamosus*, CM 64860, showing two postrostral scales (stippled; char 55.2) and frontal divided into four asymmetric scales (stippled, 68.1). (B) *S. jalapae*, CM 36477, showing rostral-nasal contact (char 54.1), absence of postrostrals (char 56.1), median contact of supranasals (stippled, char 59.1), two frontals (chars 66.0, 67.0, 68.0), four frontoparietals (stippled, char 73.0), lack of contact between frontal and interparietal (char 69.0), and interparietal with "crack" posteriorly (char 75.1). (C) *S. laticaudatus*, CM 38329, showing presence of internasals (stippled, char 61.0), absence of anterior frontonasals (char 63.1), contact between frontal and interparietal (char 69.1), and two frontoparietals (stippled, char 73.1). (D) *S. chrysostictus*, CM 40135, showing rugose cephalic scales (char 51.1), four postrostrals (stippled, char 55.1), median and lateral frontonasals separated (stippled, char 65.1), and presence of median prefrontal (diagonal lines, char 71.1). (E) *S. cyanogenys*, CM 64780, showing smooth cephalic scales (char 51.0), contact between subnasal (stippled) and postrostral on right side (char 53.1), posterior postrostral (diagonal line, char 58.1), supranasal (stippled) extending anteromedial to nasal (char 60.1), four anterior frontonasals (stippled, char 64.0), median parietal (diagonal lines, char 72.1), posterior circumorbitals (stippled, char 76.0), absence of supraocular-parietal contact (char 78.0), and four supraoculars (chars 79.0, 80.1). (F) *S. lundelli*, CM 49909, showing three anterior frontonasals (stippled, char 64.1), frontal-median frontonasal contact (char 70.1), absence of posterior circumorbital scales (circumorbitals stippled, char 76.1), presence of supraocular-parietal contact (char 78.1), two rows of supraoculars on right side (chars 79.1, 80.0), and contact between supraciliary and median supraocular (char 81.1). Scales = 2 mm.

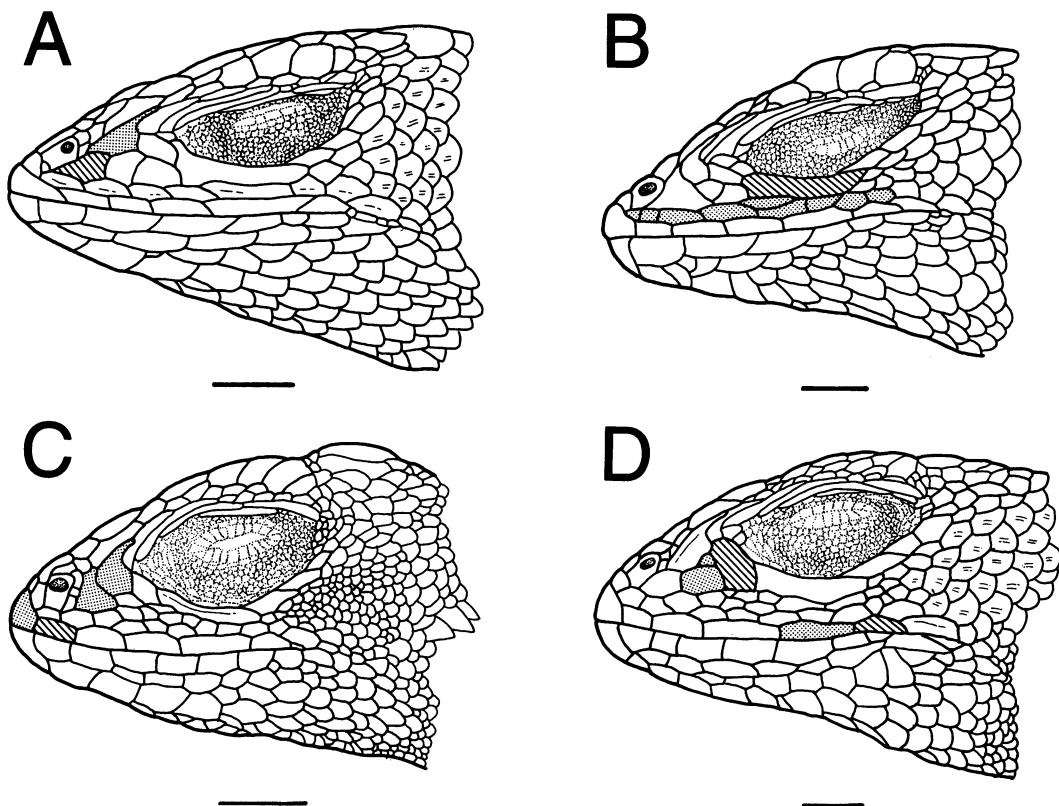


FIG. 23.—Lateral view of the head scales in four species of *Sceloporus*. (A) *S. squamosus*, CM 64860, showing absence of contact between the canthal (stippled) and lorilabial scales (char 84.1), absence of fusion between the subnasal (diagonal lines) and canthal (char 85.0), one canthal (char 86.1), preocular divided (87.1), single loreal (88.0), lorilabial scales one row high (minimum and maximum, char 89.0, 90.1), fourth and fifth supralabials broadly overlapping (char 94.1) and in broad contact (char 95.1), and rostral-supralabial suture distinctly overlapping (char 96.1). (B) *S. nelsoni*, CM 38225, showing fusion between the canthal and subnasal (char 85.1), lorilabials (stippled) minimum of one row high (char 89.0) and maximum of two rows high (char 90.1), subocular not reduced (diagonal lines, char 91.0), and temporals enlarged (char 109.1). (C) *S. merriami*, CM 59656, showing contact between the first canthal and lorilabials (char 84.1), two canthals (char 86.0), reduced subocular (char 91.1), fourth and fifth supralabial not broadly overlapping (char 94.0) but in broad contact (char 95.0), suture between rostral (stippled) and first supralabial (diagonal lines) straight, not overlapping (char 96.0), temporals small and granular (char 109.0). (D) *S. smaragdinus*, CM 41918 (374), preocular (diagonal lines) entire (char 87.0), two loreals (stippled, char 88.1), lorilabial series minimum of two rows high (char 89.1), fourth (stippled) and fifth (diagonal lines) supralabials not broadly overlapping (char 94.0) and with reduced contact (char 95.1). Scales = 2 mm.

- completely absent. Unordered and coded with the majority method.
107. Preauricular fringe (Smith, 1939): (0) not reduced dorsally (Fig. 25A, C); (1) reduced to few small scales at median part of opening (Fig. 25B).
  108. Preauricular scales: (0) not covering upper part of opening (Fig. 25A, B); (1) covering upper part of opening (Fig. 25C).
  109. Temporals (between postoculars and ear opening; Smith, 1939): (0) small, heterogeneous, some granular (Fig. 23C); (1) enlarged, homogeneous (Fig. 23A, B, D).
  110. Dorsal nuchals (Smith, 1939): (0) homogeneous

in size; (1) median scales distinctly reduced in size.

111. Lateral nuchals (Smith, 1939): (0) not enlarged, laying flat; (1) enlarged and projecting laterally.
112. Lateral nuchals (Smith, 1939): (0) distinctly smaller than dorsal nuchals; (1) about same size as dorsal nuchals.
113. Lateral mite pocket (Smith, 1939): (0) distinct pocket; (1) no distinct pocket, region of smaller scales only.
114. Antehumeral fold: (0) present; (1) absent. Terminology from Frost (1992).
115. Dorsals: (0) rounded, nonoverlapping; (1) pointed, overlapping.

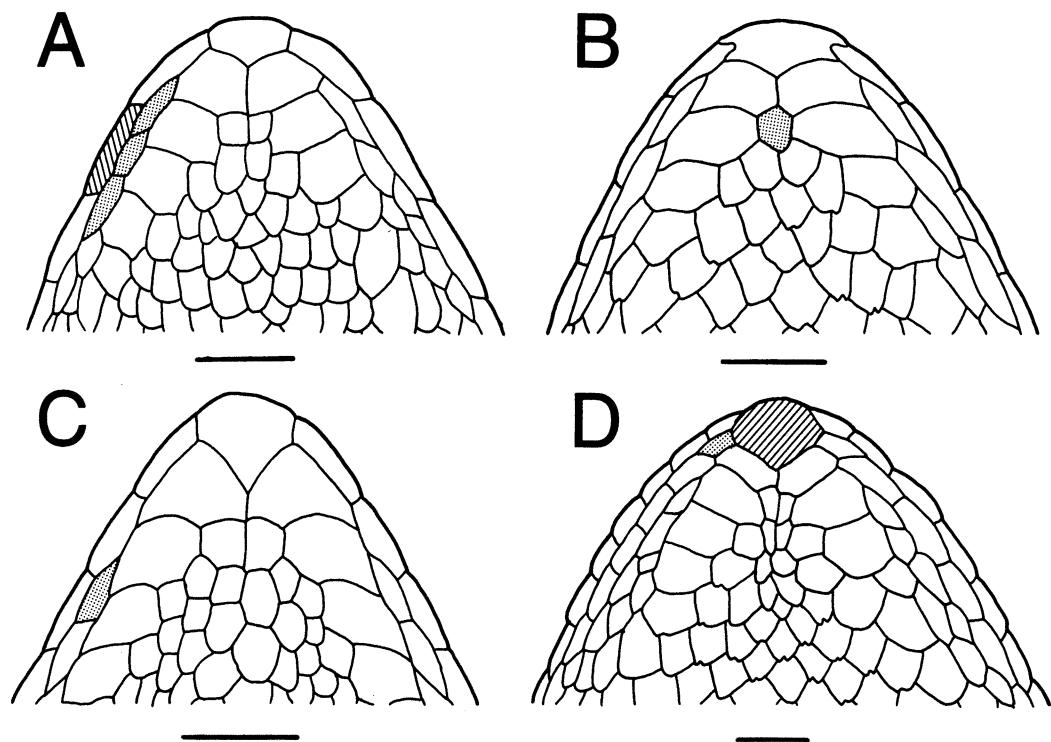


FIG. 24.—Ventral view of the chin scales in four species of *Sceloporus*. (A) *S. chrysostictus*, CM 40134, showing second infralabial (diagonal lines) contacting three sublabials (stippled, char 101.1), first sublabial contacting first infralabial (97.0), and mental–sublabial contact absent (98.0). (B) *S. bicentauris*, CM 36470, showing mental scale deeply indented by infralabials (99.1) and anteriormost gular (stippled) single (char 103.1). (C) *S. merriami*, CM 43014, showing first sublabial (stippled) contacting only second infralabial (char 97.1) and granular gular scales (104.0). (D) *S. magister*, CM 71516, showing contact between the mental (diagonal lines) and first sublabial (stippled, char 98.1), and gular scales imbricate (char 104.1) and notched (char 105.1). Scales = 2 mm.

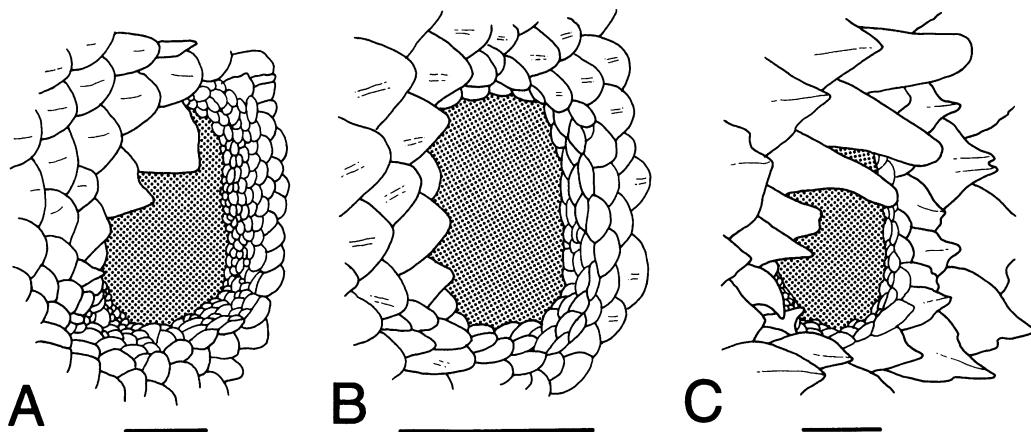


FIG. 25.—Lateral view of left ear opening (stippled) in three species of *Sceloporus*. (A) *S. jarrovii jarrovii*, CM 53696 (CJM 8877), showing preauricular fringe not reduced dorsally (char 107.0) and not covering upper part of ear opening (char 108.0). (B) *S. squamosus*, CM 64860, showing preauricular fringe reduced dorsally (char 107.1). (C) *S. magister*, CM 71690, showing preauricular scales elongate and covering upper part of ear opening (char 108.1). Scales = 2 mm.

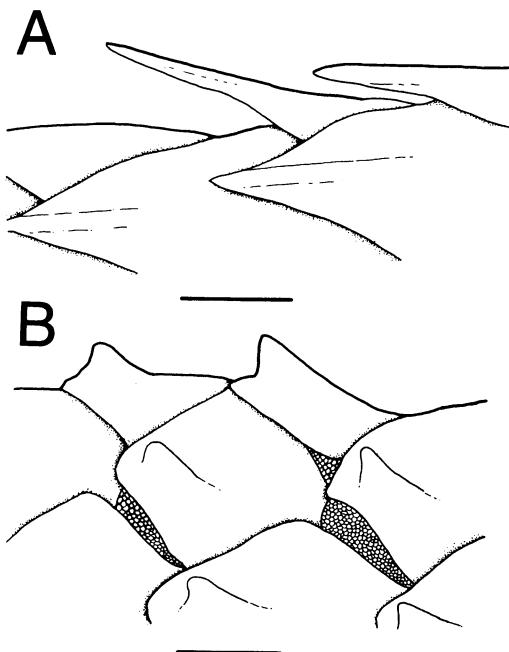


FIG. 26.—Dorsal view of left midbody lateral scales in two species of *Sceloporus*. (A) *S. magister*, CM 71707, showing absence of lip below tip of scales (char 121.0). (B) *S. cyanogenys*, CM 64782, showing lip below tip of scales (char 121.1) and granular skin between scales (123.1). Scales = 1 mm.

- 116. Dorsals: (0) all distinctly keeled; (1) some dorsals smooth.
- 117. Median dorsals (Smith, 1939): (0) dorsals more-or-less homogeneous in size; (1) dorsals reduced in size medially.
- 118. Posterior lateral dorsals: (0) grade evenly in size into laterals; (1) lateralmost row of dorsals distinct, strongly keeled, forming angle between dorsum and flanks.
- 119. Posterior laterals (Smith, 1939): (0) granular; (1) imbricate. Individuals with any lateral scales truly granular are coded as being granular.
- 120. Orientation of midbody lateral scales (Smith, 1939): (0) oblique to dorsal scales; (1) parallel to dorsal scales.
- 121. Distinct lip below tip of midbody lateral scales: (0) absent (Fig. 26A); (1) present (Fig. 26B). Many species in the *formosus* group (sensu Hall) are intermediate for this character.
- 122. Margins of lateral and dorsal scales (Smith, 1939): (0) not denticulate; (1) denticulate, with two or more points on each side of the median mucron. Scales in the process of being shed are not scored.
- 123. Skin between dorsal and lateral scales: (0) smooth or creased, not distinctly granular; (1) distinctly granular (Fig. 26B).
- 124. Posterior thigh scales (Smith, 1939): (0) smooth; (1) most keeled.

- 125. Keels on ultimate subdigital lamellae of fourth finger of forelimb: (0) three; (1) one.
- 126. Postanals (Smith, 1939): (0) enlarged in males; (1) absent or about same size as surrounding scales.
- 127. Interpostanals (scales in row between enlarged postanal scales): (0) two or more; (1) one or none.
- 128. Interpostanals: (0) two or fewer; (1) three or more.
- 129. Preanal scales in females (Smith, 1939): (0) all smooth; (1) some or all keeled.
- 130. Femoral pore number (one side; Smith, 1939): (0) greater than or equal to 10; (1) nine or fewer. In most species of *Sceloporus*, the number of femoral pores (per side) is in the teens. Characters 130 and 131 represent extreme conditions seen in only a small number of taxa; relatively few taxa are intermediate.
- 131. Femoral pore number (one side; Smith 1939): (0) less than or equal to twenty; (1) twenty-one or more.
- 132. Femoral pore scales (Smith, 1939): (0) separated medially by one or more interfemoral scales; (1) in contact medially, no interfemoral scales.
- 133. Interfemoral scales (median scales between femoral pore rows; Smith, 1939): (0) greater than 4; (1) less than or equal to 4. The derived state of character 132 represents a subset of the derived state of character 133. They are treated as separate characters to facilitate the coding of intraspecific variation.
- 134. Male preanal scales: (0) lacking distinct pores; (1) with distinct pores.
- 135. Male preanal scales: (0) without glandular appearance; (1) with distinct glandular appearance.
- 136. Male ventral thigh scales: (0) without glandular appearance; (1) with distinct glandular appearance.
- 137. Basal subcaudals (females; Smith, 1939): (0) keeled; (1) smooth.
- 138. Deep postfemoral dermal pocket (Smith, 1939): (0) absent; (1) present.

#### Coloration

- 139. "Scalaris" pattern on head: (0) no distinct pattern on head; (1) characteristic *Sceloporus scalaris* color pattern consisting of dark inverted "V" anterior to pineal foramen and dark transverse bar over each eye.
- 140. "Melanorhinus" pattern (Smith, 1939): (0) absent (snout not dark, no dark nuchal blotch); (1) present, snout black, large dark blotch on dorsal nuchal region.
- 141. Black interparietal spot (Smith, 1939): (0) absent; (1) present.
- 142. Dark bars on upper lip (Smith, 1939): (0) absent; (1) present.
- 143. Distinct white spots on nape and/or head (males; Smith, 1939): (0) absent; (1) present.
- 144. Dark nuchal collar in males (Smith, 1939): (0) present; (1) absent.

145. Dark nuchal collar in females (Smith, 1939): (0) present; (1) absent.
146. Dark nuchal collar (males; modified from Smith, 1939): (0) dark wedge anterior to insertion of forelimbs; (1) black bands thin, elongate, convergent posteriorly but not contacting; (2) dark spot dorsal to forelimb; (3) wide, black collar, complete dorsally. Unordered and coded with the majority method.
147. Dark nuchal collar (males; Smith, 1939): (0) high, extends well dorsal to level of forelimb insertion; (1) low; does not extend well dorsal to level of forelimb insertion.
148. Dark nuchal collar (males; Smith, 1939): (0) lacking distinct light border; (1) with distinct light border.
149. Distinct blue spot within or anterior to nuchal collar (males; Smith, 1939): (0) absent; (1) present.
150. Dark nuchal collar (males; Smith, 1939): (0) single blotch or band; (1) series of elongate blotches.
151. Light dorsolateral stripe (males; Smith, 1939): (0) absent; (1) present.
152. Light dorsolateral stripe (females; Smith, 1939): (0) absent; (1) present.
153. Dorsum of female dark brown-black with large white/light blue spots (Smith and Bumzahem, 1953): (0) absent; (1) present.
154. Continuous, dark middorsal stripe on tail (Smith, 1939): (0) absent; (1) present.
155. Distinct black and white banding on tail (Smith, 1939): (0) absent; (1) present.
156. Ventral surface of tail lavender (Smith, 1939): (0) absent; (1) present.
157. Male dorsal coloration (in life; Smith, 1939): (0) not bright blue or green (dull brown to gray); (1) bright blue or green ground color.
158. Black-bordered light stripe anterior to hindlimb insertion: (0) absent; (1) present.
159. Large black spot anterior to hindlimb insertion: (0) absent; (1) present.
160. Posterior surface of thigh (males; modified from Smith, 1939): (0) white spots (with or without black border); (1) continuous light stripe; (2) no distinct pattern, but with black bar on postero-medial surface of thigh; (3) no distinct pattern. Unordered and coded with the majority method.
161. Dark midventral stripe (discontinuous or continuous): (0) absent; (1) present.
162. Male gular coloration (modified from Smith, 1939): (0) absent; (1) reticulate pattern (netlike, spots, or bars; Fig. 27A, B, F); (2) paired lateral blotches (Fig. 27D); (3) single blotch or wash (Fig. 27C, E, G, H). Unordered and coded with the majority method.
163. Dark male gular coloration (modified from Smith, 1939): (0) blue; (1) black (Fig. 27A); (2) brown; (3) flesh-colored with blue spots; (4) pink, yellow, or red. Unordered and coded with the majority method.
164. Male gular coloration (Smith, 1939): (0) not extending onto chest (Fig. 27A, B, D-G); (1) ex-
- tending onto chest (Fig. 27H). In some species of *Sceloporus* (such as *S. lundelli*), the male gular patch extends onto the chest yet is clearly distinct from the belly patches. Taxa in which the gular and belly patches are seemingly fused (character 181.1) are coded as unknown for this character.
165. Continuous black ventral collar (males; Smith, 1939): (0) absent (Fig. 27A-D, F, H); (1) present (Fig. 27E, G).
166. Male gular coloration, median light stripe (Smith, 1939): (0) absent; (1) present.
167. Male blue gular blotch (single; Smith, 1939): (0) covers posterior section of gular area (Fig. 27E, G, H); (1) completely covers gular area (Fig. 27C). Only the single blotch pattern is coded for this character; all other conditions are coded as missing.
168. Male blue gular blotch (single; Smith, 1939): (0) without dark longitudinal bars; (1) with dark longitudinal bars.
169. Male blue gular blotch(es) (Smith, 1939): (0) not bordered by black pigment anteriorly (Fig. 27B-F, H); (1) bordered by black pigment anteriorly (Fig. 27G).
170. White, dark-bordered mental spot (males; Smith, 1939): (0) absent (Fig. 27B-F, H); (1) present (Fig. 27G).
171. Male gular pattern (reticulate only): (0) not distinctly darker posteriorly; (1) distinctly darker posteriorly.
172. Female gular coloration (Smith, 1939): (0) absent; (1) reticulate pattern; (2) paired lateral blotches; (3) single blotch. Unordered and coded with the majority method.
173. Female gular pattern single black blotch: (0) absent; (1) present.
174. Female gular coloration with median light stripe (Smith, 1939): (0) absent; (1) present.
175. Female gular coloration arranged as dark longitudinal bars (Smith, 1939): (0) absent; (1) present.
176. Male belly patches (Smith, 1939): (0) absent (Fig. 27F); (1) present (Fig. 27A-E, G, H).
177. Male belly patches: (0) solid blotch (Fig. 27); (1) arranged as series of bars or blotches.
178. Male belly patches (Smith, 1939): (0) separate (Fig. 27A, B, D, E, G, H); (1) fused medially for some or all of their lengths (Fig. 27C).
179. Male belly patch (in preservative; Smith, 1939): (0) blue (or very similar color); (1) lavender (or very similar color).
180. Male belly patch (Smith, 1939): (0) not extending onto chest (between forelimbs); (1) extends onto chest. Taxa in which the gular and belly patches are seemingly fused (character 181.1) are coded as unknown for this character.
181. Male belly patch (Smith, 1939): (0) separate from gular blotch (Fig. 27A, B, D, E, G, H); (1) continuous with gular blotch (Fig. 27C).
182. Male belly patch (exclusive of dark margin): (0) not extending onto hindlimbs (Fig. 27A, B, D, E, G, H); (1) extends onto hindlimbs (Fig. 27C).
183. Male belly patch (Smith, 1939): (0) without

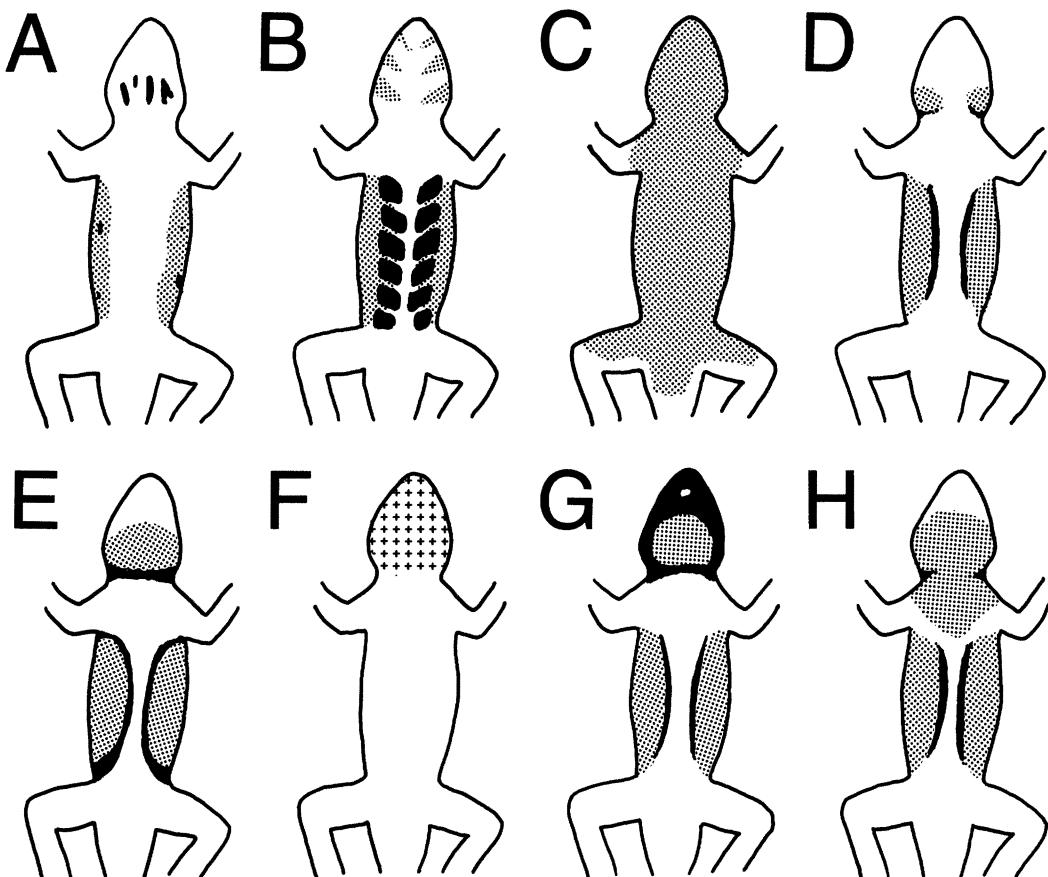


FIG. 27.—Diagrammatic illustration of male ventral color patterns in eight species of *Sceloporus*. (A) *S. scalaris*, showing black, reticulate gular pattern (chars 162.1, 163.1) and belly patch with black spots (char 183.1). (B) *S. pyrocephalus*, showing reticulate gular pattern (char 162.1) and belly patch with dark margins (char 184.1) arranged as series of blotches (char 188.1). (C) *S. ornatus*, showing gular blotch completely covering gular area (char 167.1), belly patches fused medially (char 178.1), continuous with gular blotch (char 181.1), and extending onto hindlimbs (char 182.1). (D) *S. caurus*, showing paired gular blotches (char 162.2) and belly patch with dark margin (char 184.1) incomplete posteriorly (char 186.0), and continuous (char 188.0). (E) *S. malachiticus*, showing single gular blotch (char 162.3), continuous black ventral collar (char 165.1), gular blotch covering only posterior region of gular area (char 167.0), and belly patch dark margin complete posteriorly (char 186.1). (F) *S. chrysostictus*, showing reticulate gular pattern (char 162.1) and absence of belly patches (char 176.1). (G) *S. melanorhinus*, showing single gular blotch (char 162.3), continuous black ventral collar (char 165.1), gular blotch bordered by black pigment anteriorly (char 169.1), and white, dark-bordered mental spot (char 170.1). (H) *S. lundelli*, showing gular blotch extending onto chest (char 164.1).

- black spots (Fig. 27B–E, G, H); (1) with black spots (Fig. 27A). Refers to black spots within the patch and not to the margin of the patch.
184. Male belly patches (Smith, 1939): (0) no distinct dark margins (Fig. 27A, C); (1) dark margin on each belly patch (Fig. 27B, D, E, G, H).
185. Male belly patch: (0) dark margin not reduced (Fig. 27); (1) dark margin reduced, absent near limbs and present medially only where blotches approach each other.
186. Male belly patch, dark margin: (0) incomplete

posteriorly (Fig. 27D, G, H); (1) complete posteriorly (Fig. 27E).

187. Male belly patch, dark margin: (0) not extending to posterior to forelimb insertion; (1) extends anterodorsally to posterior to forelimb insertion. In most species of *Sceloporus*, the dark margins of the belly patches are not extensive and terminate on the venter (Fig. 27D, G, H). In species with highly developed dark margins, the black coloration extends anterodorsally to terminate just posterior to the insertion of the forelimb.

188. Male belly patch, dark margin (Smith, 1939): (0) continuous (Fig. 27D, E, G, H); (1) discontinuous, arranged as series of dark blotches (Fig. 27B).
189. Female belly patches (Smith, 1939): (0) absent; (1) present.
190. Female belly patch (Smith, 1939): (0) faint; (1) distinct (as distinct as in males of the species).
191. Female belly patches: (0) no distinct dark margins; (1) dark margin on each belly patch.
192. Female belly patches (Smith, 1939): (0) solid blotch; (1) transverse bars.
193. Extensive dark pigment on underside of fore-limb (males; Smith, 1939): (0) absent; (1) present.
194. Extensive dark pigment on underside of hind-limb (males; Smith, 1939): (0) absent; (1) present.
195. Extensive dark pigment on underside of fore-limb (females; Smith, 1939): (0) absent; (1) present.
196. Extensive dark pigment on underside of hind-limb (females; Smith, 1939): (0) absent; (1) present.

#### *Life History*

197. Reproductive mode (Smith, 1939): (0) oviparous; (1) viviparous. Data from Guillette et al. (1980) and Guillette and Smith (1985).

#### *Karyology*

198. Number of microchromosomes (Hall, 1973): (0) twenty; (1) eighteen; (2) sixteen; (3) fourteen; (4) twelve; (5) ten. Ordered. Data from Sites et al. (1992) and Goyenechea Mayer-Goyenechea and Mendoza Quijano (1993).
199. Macrochromosome pair 1 (Hall, 1973): (0) metacentric or submetacentric; (1) acrocentric, presumably via centric fission; (2) acrocentric via pericentric inversion. Unordered. Data from Sites et al. (1992) and Goyenechea Mayer-Goyenechea and Mendoza Quijano (1993).
200. Macrochromosome pair 2 (Hall, 1973): (0) metacentric or submetacentric; (1) acrocentric,

- presumably via centric fission. Data from Sites et al. (1992) and Goyenechea Mayer-Goyenechea and Mendoza Quijano (1993).
201. Macrochromosome pair 3 (Hall, 1973): (0) metacentric or submetacentric; (1) acrocentric, presumably via centric fission. Data from Sites et al. (1992) and Goyenechea Mayer-Goyenechea and Mendoza Quijano (1993).
  202. Macrochromosome pair 4 (Hall, 1973): (0) metacentric or submetacentric; (1) acrocentric, presumably via centric fission. Data from Sites et al. (1992) and Goyenechea Mayer-Goyenechea and Mendoza Quijano (1993).
  203. Macrochromosome pair 5 (Hall, 1973): (0) metacentric or submetacentric; (1) acrocentric, presumably via centric fission. Data from Sites et al. (1992) and Goyenechea Mayer-Goyenechea and Mendoza Quijano (1993).
  204. Macrochromosome pair 6 (Hall, 1973): (0) metacentric or submetacentric; (1) acrocentric, presumably via centric fission. Data from Sites et al. (1992) and Goyenechea Mayer-Goyenechea and Mendoza Quijano (1993).
  205. Sex chromosome system (Hall, 1973): (0) Y chromosome minute, (1) Y chromosome enlarged. Data from Sites et al. (1992).
  206. Sex chromosome system (Hall, 1973): (0) no Y-autosomal fusion; (1) Y-autosomal fusion, fusion to metacentric autosome; (2) Y-autosomal fusion, fusion to acrocentric autosome. Data from Sites et al. (1992).
  207. Sex chromosomes (Hall, 1973): (0) heteromorphic, differing in size and/or shape; (1) X and Y indistinct.
  208. Em9 mutation (Hall, 1973): (0) absent; (1) present. Data from Sites et al. (1992).
  209. Secondary constriction near centromere on large microchromosome (Cole, 1978): (0) absent; (1) present. Data from Sites et al. (1992) and Porter et al. (1994). We assume that this character corresponds to the differences in ribosomal gene location described by Porter et al. (1994), with the ribosomal gene either on a single pair of microchromosomes (state 0) or on the long arm of chromosome pair 2 (state 1).

## APPENDIX V

*Complete Data Matrix Used in Phylogenetic Analyses*

The format of the matrix is exactly as used in the combined, all-taxon analyses, except that in the PAUP matrix the character states of polymorphic taxa are within parentheses and on the same line, and the order of taxa in the matrix is not alphabetized. The “\*” above the DNA data denote the stem regions that were constrained in the multiple sequence alignments. Stem number designations follow Van de Peer et al. (1994) for the 12S rDNA and our Figure 1 for the 16S rDNA. Abbreviations are as follows: PEMEA = *Petrosaurus mearnsi*; PETHA = *Petrosaurus thalassinus*; URBIC = *Urosaurus bicarinatus*; URCLA = *Urosaurus clarionensis*; URGAD = *Urosaurus gadovi*; URGRA = *Urosaurus graciosus*; URMIC = *Urosaurus microscutatus*; URNIG = *Urosaurus microscutatus*; URORN = *Urosaurus ornatus*; UTPAL = *Uta palmeri*; UTSTA = *Uta stansburiana*; SAANG = *Sator angustus*; SAGRA = *Sator grandaevis*; SCACA = *Sceloporus acanthinus*; SCADL = *Sceloporus adleri*; SCAEN = *Sceloporus aeneus*; SCARE = *Sceloporus arenicolus*; SCASP = *Sceloporus asper*; SCBIC = *Sceloporus bicanthalis*; SCBUL = *Sceloporus bulleri*; SCCAR = *Sceloporus carinatus*; SCCAU = *Sceloporus cautus*; SCCHA = *Sceloporus chaneyi*; SCCHR = *Sceloporus chrysostictus*; SCCLA = *Sceloporus clarkii*; SCCOU = *Sceloporus couchii*; SCCOZ = *Sceloporus cozumelae*; SCCRY = *Sceloporus cryptus*; SCSCU = *Sceloporus (siniferus) cuypreus*; SCCYA = *Sceloporus cyanogenys*; SCDUG = *Sceloporus dugesii dugesii*; SCDIN = *Sceloporus dugesii intermedius*; SCEDW = *Sceloporus edwardtaylori*; SCEXS = *Sceloporus exsul*; SCFOR = *Sceloporus formosus formosus*; SCFSC = *Sceloporus formosus scitulus*; SCGAD = *Sceloporus gadoviae*; SCGOL = *Sceloporus goldmani*; SCGRC = *Sceloporus graciosus*; SCGRM = *Sceloporus grammicus*; SCHET = *Sceloporus heterolepis*; SCHAL = *Sceloporus horridus albiventris*; SCHOR = *Sceloporus horridus horridus*; SCHUN = *Sceloporus hunsakeri*; SCINS = *Sceloporus insignis*; SCINT = *Sceloporus internasalis*; SCJAL = *Sceloporus jalapae*; SCCYS = *Sceloporus jarrovii cyanostictus*; SCJER = *Sceloporus jarrovii erythrocyaneus*; SCJIM = *Sceloporus jarrovii immucronatus*; SCJAR = *Sceloporus jarrovii jarrovii*; SCMIN = *Sceloporus jarrovii minor*; SCJOB = *Sceloporus jarrovii oberon*; SCJSU = *Sceloporus jarrovii sugillatus*; SCLIC = *Sceloporus licki*; SCMLI = *Sceloporus (magister) lineatulus*; SCLIN

= *Sceloporus lineolateralis*; SCLUA = *Sceloporus luhuae*; SCLUD = *Sceloporus lundelli*; SCMAG = *Sceloporus maculosus*; SCMCD = *Sceloporus macdougalii*; SCMAG = *Sceloporus magister*; SCMAL = *Sceloporus malachiticus*; SCMEG = *Sceloporus megalepidurus megalepidurus*; SCMHA = *Sceloporus (megalepidurus) halli*; SCMEL = *Sceloporus melanorhinus melanorhinus*; SCMST = *Sceloporus melanorhinus stuarti*; SCMER = *Sceloporus merriami*; SCMAU = *Sceloporus mucronatus aureolus*; SCMUC = *Sceloporus mucronatus mucronatus*; SCMOM = *Sceloporus mucronatus omiltemanus*; SCNEL = *Sceloporus nelsoni*; SCOCH = *Sceloporus ochoterenae*; SCOCC = *Sceloporus occidentalis*; SCOLI = *Sceloporus olivaceus*; SCORC = *Sceloporus orcutti*; SCÓCA = *Sceloporus ornatus caeruleus*; SCORN = *Sceloporus ornatus ornatus*; SCPAL = *Sceloporus palaciosi*; SCPAR = *Sceloporus parvus*; SCPIC = *Sceloporus pictus*; SCPOI = *Sceloporus poinsetti*; SCPRE = *Sceloporus prezygus*; SCPYR = *Sceloporus pyrocephalus*; SCSAL = *Sceloporus salvini*; SCSSA = *Sceloporus scalaris samcolemani*; SCSCA = *Sceloporus scalaris scalaris*; SCSSL = *Sceloporus scalaris slevini*; SCSUN = *Sceloporus scalaris unicentralis*; SCSER = *Sceloporus serrifer*; SCSHA = *Sceloporus shannonorum*; SCSIN = *Sceloporus siniferus*; SCSMA = *Sceloporus smaragdinus*; SCSMI = *Sceloporus smithi*; SCCAE = *Sceloporus spinosus caerulopunctatus*; SCSPI = *Sceloporus spinosus spinosus*; SCSQU = *Sceloporus squamosus*; SCSTE = *Sceloporus stejnegeri*; SCSBN = *Sceloporus subniger*; SCSBP = *Sceloporus subpictus*; SCTAE = *Sceloporus taeniocnemis*; SCTAN = *Sceloporus tanneri*; SCTEA = *Sceloporus teapensis*; SCBIN = *Sceloporus torquatus binocularis*; SCTME = *Sceloporus torquatus melanogaster*; SCTOR = *Sceloporus torquatus torquatus*; SCON = *Sceloporus undulatus consobrinus*; SCELO = *Sceloporus undulatus elongatus*; SCERY = *Sceloporus undulatus erythrocheilus*; SCGAR = *Sceloporus undulatus garmani*; SCHYA = *Sceloporus undulatus hyacinthinus*; SCTRI = *Sceloporus undulatus tristichus*; SCUND = *Sceloporus undulatus undulatus*; SCUTI = *Sceloporus uniformis*; SCVAN = *Sceloporus vandenburgianus*; SCVMA = *Sceloporus variabilis marmoratus*; SCVAR = *Sceloporus variabilis variabilis*; SCVIR = *Sceloporus virgatus*; SCWOO = *Sceloporus woodi*; SCZOS = *Sceloporus zosteromus*.



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externally
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SCMLI	agyy2aayyaaipyfyaaayaaayaaayaaayaaayaaaaaaaaa0aaaaaa	SCHYA	aify2aeyaaayayyaayacaayayaaayaaayaaayaaayaaayaaam0aaaaaa
SCLIN	acyy2aayyaaayyyfaayayrsryaafaaadaayaaahaa3ay?aaa	SCTR I	aeyy2asyaayayyaayaaayaaayaaayaaayaaayaa0ggayaa
SCLUA	adyx2acyrayayxxayaaayacyayaaayaaayaaap0maccas	SCUND	aayy2aayaaayayaaayaaayaaayaaayaaayaaayaaayaaayaa
SCLUD	adyy2aixyraayyyayaaayaaayaaayaaayaaayaaayaaayaa	SCUTI	aayy2aayaaayayaaayaaayaaayaaayaaayaaayaaayaaatf?2?saam
SCMCD	aaya2aayyaaayyyayaaayaaayaaayaaayaaayaaayaaabaa	SCVAN	davy2aayaaayayaaayaaayaaayaaayaaayaaayaaayaa0aEafy
SCMAC	aayy2aayyaaayyyayaaayaaayaaayaaayaaayaaayaaayaa	SCVMA	arys1ayayaaayayaaayaaayaaayaaayaaayaaayaaayaaaym
SCMAG	aify2aayyaaipyfyayaaayaaayaaayaaayaaayaaayaaayaa	SCVIR	acyk1xayaaaydyayaaayaaayaaayaaayaaayaaayaaayaa
SCMAL	aayy2aayyaaayyyayaaayaaayaaayaaayaaayaaayaaayaa	SCWOO	aayy2aayyaaayayaaayaaayaaayaaayaaayaaayaaayaaay
SCMHA	aayy2aayyaaayyyayaaayaaayaaayaaayaaayaaayaaayaa	SCZOS	aayy2aeyaaayayyyayaaayaaayaaayaaayaaayaaayaaayaa
SCMEG	aify2aayyaaayyyayaaayaaayaaayaaayaaayaaayaaayaa	PETHA	aryy2zayyaayayyyayaaaycamawqhaaaaaacvhyaaaaa0arcas
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SCMER	agyy2agyyayyyayaaayaaayaaayaaayaaayaaayaaayaaayaa	URGAD	[ 5 0 5 0 5 0 5 5 ]
SCMUC	aayy2bgyraayayyyoayayyyayaaayaaayaaayaaayaaayaa	PEMEA	[External 153-196, life history 197]
SCMOM	aayy2akyrayayyyayaaayayyyayaaayaaayaaayaaayaaayaa	aamaaa0a1?maa?aaa1laayayaaaaaaa??a??aaaaa	aamaaa0a1?maa?aaa1laayayaaaaaaa??a??aaaaa
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SCOLI	acyw2awyrayayayaaayaaayaaayaaayaaayaaayaaayaaayaa	URCLA	?aa!rga0a???????????????????????aa?aa?aa?
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SCORN	aayy2aayyayayayaaayaaayaaayaaayaaayaaayaaayaaayaa	URGRA	aaaaaaa0a0?aa?aaa0aaayayaaaaaaa??aa?aa?aa?
SCPAL	aayy2aayyayayayaaayaaayaaayaaayaaayaaayaaayaaayaa	URMIC	aaaaaaa30aaaiaaa?0?7?yegaaaaaa?????aa?aa?aa?
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SCPIC	adyy2aayyayayayaaayaaayaaayaaayaaayaaayaaayaaayaa	URORN	aaaaaaag0a30aaaiaaa?0?aaayaaaaaaa?????aa?aa?aa?
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SCPYR	afyy2aayyaa	SAANG	aaaaaaa0a010aa?aaa1laayayaaaa?aa?aa?aa?aa?
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SCSSL	afyy2rayaa	SCAEN	aaaaaaa3a11yaaya?aa1aaayayaaaaaaa?????aa?aa?aa?
SCSUN	afyy2rayaa	SCARE	aaaaaaa3a10aa?aaa0?7?yaaaaaaayqaaa??aaaaaa
SCSER	afyy2aayyaa	SCASP	aaaaaaa3a12aayayaaa?0?ayawaca??adryaaaa??aaaaay
SCSHA	ahyp2aayyaa	SCBIC	aoaaaaa11lyaa?i?aa1aaami?aaaaayaaaa?aa?aa?aa?
SCSIN	afya2ayaa	SCBUL	aaaaaaa3a30?13amaya1ayyaayysaayyaaaa?aa?aa?aa?
SCCAE	afyy2axayaa	SCCAR	aaaaaaa0a12?ya?aa?aa0?7?aa?1amayaamaaaaayaaaa?aa?
SCSMI	afyy1mayaa	SCCHR	aaaaaaa3a30?13amaya1ayyaayysaayyaaaa?aa?aa?aa?
SCSP1	amyy2axayayayayayayayayayayayayayayayayayayayaa	SCCAU	aaaaaaa0a10aa?aaa1laaa?aaa0?7?aa?1amayaamaaaaayaaaa?aa?
SCSQU	irya2ayaa	SCCHA	aaaaaaa0a12?ya?aa?aa0?7?aa?1amayaamaaaaayaaaa?aa?
SCSTE	amys2aayayayayayayayayayayayayayayayayayayayaa	SCCBP	aaaaaaa3a30?13amaya1ayyaayysaayyaaaa?aa?aa?aa?
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SCERY	aiyu2adcyayayayayayayayayayayayayayayayaa	SCCTE	aaaaaaa3a30?13amaya1ayyaayysaayyaaaa?aa?aa?aa?
SCGAR	aiyu2aayayayayayayayayayayayayayayayayaa	SCCTE	aaaaaaa3a30?13amaya1ayyaayysaayyaaaa?aa?aa?aa?



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			SCSVC	1000000?1001	SCSSIN	200000011001
0	5		SCSYA	200000011001	SCSMA	5000000?7???
			SCDUG	20000011001	SCSMC	000000000000
			SCDIN	20000011001	SCCAE	500000010101
			SCEDW	500000110101	SCSPI	500000010101
			SCEXS	500000101011	SCSQU	???????????
			SCFOR	500000101011	SCSTE	500000101011
			SCFSC	500000101011	SCSBN	???????????
			SCGAD	000000000001	SCSBP	5000000010101
			SCGOL	400000101011	SCTAE	500000010101
			SCGRIC	100000101011	SCNOM	200000011001
			SCGRM	200000011001	SCNEL	000000000001
			SCHET	200000011001	SCCOH	0000000?0?01
			SCHAL	500000101011	SCOCC	500000010101
			SCHOR	500000010101	SCOLI	500000010101
			SCHUN	000000000001	SCORC	000000000001
			SCINA	?7?7?7?7?7?	SCOCA	200000011001
			SCINT	?7?7?7?7?7?	SCORN	200000011001
			SCJAL	0000000?201	SCPAL	200000011001
			SCSYS	200000011001	SCPAP	000000000000
			SCJER	200000011001	SCPIC	200000011001
			SCJIM	200000011001	SCP01	200000011001
			SCBUL	200000011001	SCPRE	???????????
			SCMIN	200000011001	SCPYR	020000000001
			SCJOB	200000011001	SCSAL	???????????
			SCARE	200000011011	SCSSA	400000010101
			SCASP	200000011011	SCSCA	400000010101
			CBIC	4000000?2?0?	SCMLI	?7?7?7?7?7?
			CCAR	??7?7?7?7?7?	SCUTI	000000000001
			CCAU	500000010101	SCVAN	100000010101
			CCCHA	?7?7?7?7?7?	SCVAR	000000000000
			CCCHR	000000000000	SCVIR	500000010101
			CCCLA	11011010011	SCWOO	500000010101
			CCCOLA	000000000000	SCCSIN	4000000110101
			CCCOZ	000000000000	SCCTIN	22222222222222













SCINS	TTTTAAGATGAAACACA--CGGCATGGTACTATGAAAC--TTCTCACCTAA	SCTAE	TTTTAAGATAAAACACA--GGGCATGGTACTATGAAAC--TTTACCTAA
SCIINT	TTTTAATATAAACACA--ACGGATGAATCATGAAAT--TTTCCTCTGA	SCTAN	TTTTAAGATAAAACACA--GGGCATGGTACTATGAAAC--TTTACCTAA
SCJAL	TTTTGAGATAAAACACA--CGGCATGGTACTATGAAAC--TTCTCACCTAA	SCTEA	TTTTAAGATAAAACACA--GGGCATGGTACTATGAAAC--TTTACCTAA
SCJAR	TTTTGAGATAAAACACA--CGGCATGGTACTATGAAAC--TTCTCACCTAA	SCTR	TTTTAAGATAAAACACA--GGGCATGGTACTATGAAAC--TTTACCTAA
SCJER	TTTTAAGATAAAACACA--GGGCATGGTACTATGAAAC--TTCTCACCTAA	SCTOR	TTTTAAGATAAAACACA--GGGCATGGTACTATGAAAC--TTTACCTAA
SCJIM	TTTTAAGATAAAACACA--GGGCATGGTACTATGAAAC--TTCTCACCTAA	SCTRI	TTTTAAGATAAAACACA--GGGCATGGTACTATGAAAC--TTTACCTAA
SCJOB	TTTTAAGATAAAACACA--GGGCATGGTACTATGAAAC--TTCTCACCTAA	SCUND	TTTTAAGATAAAACACA--GGGCATGGTACTATGAAAC--TTTACCTAA
SCJSU	TTTTAAGATAAAACACA--GGGCATGGTACTATGAAAC--TTCTCACCTAA	SCUTI	TTTTAAGATAAAACACA--GGGCATGGTACTATGAAAC--TTTACCTAA
SCCLIC	TTTTAAGATAAAACACA--GGGCATGGTACTATGAAAT--TTTACCTGA	SCVAN	TTTTAAGATAAAATATA--ACGGCACGGTACAATGAAAC--TTCTACCCAA
SCLIN	TTTTAAGATAAAACACA--GGGCATGGTACTATGAAAC--TTTACCTAA	SCVAR	TTTTAAGATAAAACATA--ACGGCATGGTACTATGAAAC--TTCTACCTAA
SCLUA	TTTTAAGATAAAACACA--GGGCATGGTACTATGAAAC--TTTACCTAA	SCVIR	TTTTAAGATAAAACATA--ACGGCATGGTACTATGAAAC--TTCTACCTAA
SCCLUD	TTTTAAGATAAAACACA--GGGCATGGTACTATGAAAC--TTTACCTAA	SCVMO	TTTTAAGATAAAACATA--ACGGCACGGTACTATGAAAC--TTCTACCTAA
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SCMAG	TTTTAAGATAAAACATA--ACGGCAAGGTACATGAAAT--TTCTACCCAA	SCZOS	TTTTAAGATAAAACATA--ACGGCACGGTACTATGAAAT--TTTACCTAA
SCMAL	TTTTAAGATAAAACACA--GGGCATGGTACTATGAAAC--TTCTACCCAA	[ ]	[ ]
SCMAD	TTTTAAGATAAAACACA--GGGCATGGTACTATGAAAC--TTCTACCCAA	[ ]	[ ]
SCMBG	TTTTAAGATAAAAGCACA--CGGCATGGCATTATGAAAC--TCCCTGCCTGA	[ ]	[ ]
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SCMST	TTTTAAGATAAAACATA--GGGCATGGTACTATGAAAC--TTTATACCAA	[ ]	[ ]
SCMUC	TTTTAAGATAAAACACA--GGGCATGGTACTATGAAAC--TTTATACCAA	[ ]	[ ]
SCNEL	TTTTAAGATAAAACACA--GGGCAGGGTACTATGAAAC--TCTTACCGA	[ ]	[ ]
SCOCA	TTTTAAGATAAAACACA--GGGCAGGGTACTATGAAAC--TCTTACCAA	[ ]	[ ]
SCOCH	TTTTAAGATAAAACACA--GGGCATGGTACTATGAAAC--TCTTACCGA	[ ]	[ ]
SCOLI	TTTTAAGATAAAACATA--GGGCATGGTACTATGAAAC--TCTTACCAA	[ ]	[ ]
SCORC	TTTTAAGATAAAACATA--GGGCAGGGTACTATGAAAC--TCTTACCGA	[ ]	[ ]
SCORN	TTTTAAGATAAAACATA--GGGCAGGGTACTATGAAAT--ATCTRCCTGA	[ ]	[ ]
SCPAL	TTTTAAGATAAAACATA--GGGCAGGTACTATGAAAC--TATGCCCCA	[ ]	[ ]
SCPAB	TTTTAAGATAAAACACA--CGACATGGCATTATGAAAC--TCCCTGCCTGA	[ ]	[ ]
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SCPBI	TTTTAAGATAAAACATA--CGACATGGCATTATGAAAC--TCTTACCAA	[ ]	[ ]
SCPCE	TTTTAAGATAAAACATA--CGACATGGCATTATGAAAC--TCTTACCAA	[ ]	[ ]
SCPFR	TTTTAAGATAAAACAAA--ACGACATGGTACTATGAAAC--TATTACCTGA	[ ]	[ ]
SCSAL	TTTTAAGATAAAACATA--CGACATGGCATTATGAAAC--TCTTACCAA	[ ]	[ ]
SCSBP	TTTTAAGATAAAACACA--GGGCATGGTACTATGAAAC--TTCTACCAA	[ ]	[ ]
SCSCA	TTTTAAGATAAAACATA--GGGCATGGTACTATGAAAC--TTCTACCAA	[ ]	[ ]
SCSBU	TTTTAAGATAAAACATA--GGGCATGGTACTATGAAAC--TTCTACCAA	[ ]	[ ]
SCSBR	TTTTAAGATAAAACATA--GGGCATGGTACTATGAAAC--TTCTACCAA	[ ]	[ ]
SCSHA	TTTTAAGATAAAACCA--GGGCATGGTACTATGAAAC--TGGGGGCCGA	[ ]	[ ]
SCSIN	TTTTAAGATAAAACCA--GGGCATGGTACTATGAAAC--TGGGGGCCGA	[ ]	[ ]
SCSBN	TTTTAAGATAAAACACA--GGGCATGGTACTATGAAAC--TGGGGGCCGA	[ ]	[ ]
SCSBP	TTTTAAGATAAAACACA--GGGCATGGTACTATGAAAC--TGGGGGCCGA	[ ]	[ ]
SCSCA	TTTTAAGATAAAACACA--GGGCATGGTACTATGAAAC--TGGGGGCCGA	[ ]	[ ]
SCSBU	TTTTAAGATAAAACACA--GGGCATGGTACTATGAAAC--TGGGGGCCGA	[ ]	[ ]
SCSBR	TTTTAAGATAAAACACA--GGGCATGGTACTATGAAAC--TGGGGGCCGA	[ ]	[ ]
SCSFA	TTTTAAGATAAAACCA--GGGCATGGTACTATGAAAC--TGGGGGCCGA	[ ]	[ ]
SCSMA	TTTTAAGATAAAACACA--GGGCATGGTACTATGAAAC--TGGGGGCCGA	[ ]	[ ]
SCSMI	TTTTAAGATAAAACATA--GGGCACACCCGGAAAT--GGGGGCCGA	[ ]	[ ]
SCSP1	TTTTAAGATAAAACACA--GGGCACACCCGGAAAT--GGGGGCCGA	[ ]	[ ]
SCSQU	TTTTAAGATAAAACACA--GGGCACGGTACTATGAAAC--TTCTACCAA	[ ]	[ ]
SCSSA	TTTTAAGATAAAACATA--ACGGCATGGTATATGAAACCTTCTACCTAA	[ ]	[ ]
SCSSL	TTTTAAGATAAAACATA--ACGGCATGGTACTATGAAAC--TTCTACCTAA	[ ]	[ ]
SCSTE	TTTTAAGATAAAACATA--ACGGCATGGTACTATGAAAC--TTCTACCTAA	[ ]	[ ]
SCSUN	TTTTAAGATAAAACATA--ACGGCATGGTACTATGAAAC--TTCTACCTAA	[ ]	[ ]











	760	770	780	790	800	800	1
SCMIN	.	.	30-2*	30-1'	31	.	{31'}/{32}
SCMLI	A-----	ACACAGCACACCA-TGGCCAA--AATTTAACTTAAATT?TAACCCA--GCACCAA					
SCMOM	A-----	AGACGAGAGACCCCTGTGAGCTTTAAATT?TAACCCA--ACAACTTA					
SCMST	.....	AGACGAGAGACCCCTGTGAGCTTTAAATT?TAACCCA--ACAACTTA					
SCMUC	.....	AGACGAGAGACCCCTGTGAGCTTTAAATT?TAACCCA--ACAACTTA					
SCNEL	.....	AGACGAGAGACCCCTGTGAGCTTTAAATT?TAACCCA--GCACCAA					
SCOCA	.....	AGACGAGAGACCCCTGTGAGCTTTAAATT?TAACCCA--GCACCAA					
SCOCC	.....	AGACGAGAGACCCCTGTGAGCTTTAAATT?TAACCAA-TAGCAACGCC					
SCOCH	.....	AGACGAGAGACCCCTGTGAGCTTTAAATT?TAACCAA-GCACCAA					
SCORC	.....	AGACGAGAGACCCCTGTGAGCTTTAAATT?TAACCAA-GCACCAA					
SCORN	.....	AGACGAGAGACCCCTGTGAGCTTTAAATT?TAACCAA-GCACCAA					
SCPAL	.....	AGACGAGAGACCCCTGTGAGCTTTAAATT?TAACCAA-GCACCAA					
SCPAR	.....	AGACGAGAGACCCCTGTGAGCTTTAAATT?TAACCAA-GCACCAA					
SCPIC	.....	AGACGAGAGACCCCTGTGAGCTTTAAATT?TAACCAA-GCACCAA					
SCPOI	.....	AGACGAGAGACCCCTGTGAGCTTTAAATT?TAACCAA-GCACCAA					
SCPRE	.....	AGACGAGAGACCCCTGTGAGCTTTAAATT?TAACCAA-GAACACC					
SCPYR	.....	AGACGAGAGACCCCTGTGAGCTTTAAATT?TAACCAA-GAACACC					
SCSBN	.....	AGACGAGAGACCCCTGTGAGCTTTAAATT?TAACCAA-GAACACC					
SCSBP	.....	AGACGAGAGACCCCTGTGAGCTTTAAATT?TAAGCCA--GCAGCAA					
SCSCU	.....	AGACGAGAGACCCCTGTGAGCTTTAAATT?TAAGCCA--GCAGCAA					
SCSER	.....	AGACGAGAGACCCCTGTGAGCTTTAAATT?TAAGCCA--GCAGCAA					
SCSINA	.....	AGACGAGAGACCCCTGTGAGCTTTAAATT?TAAGCCA--GCAGCAA					
SCSIN	.....	AGACGAGAGACCCCTGTGAGCTTTAAATT?TAAGCCA--GCAGCAA					
SCSMA	.....	AGACGAGAGACCCCTGTGAGCTTTAAATT?TAAGCCA--GCAGCAA					
SCSMI	.....	AGACGAGAGACCCCTGTGAGCTTTAAATT?TAAGCCA--GCAGCAA					
SCSPJ	.....	AGACGAGAGACCCCTGTGAGCTTTAAATT?TAAGCCA--GCAGCAA					
SCSQJ	.....	AGACGAGAGACCCCTGTGAGCTTTAAATT?TAAGCCA--GCAGCAA					
SCSSA	.....	AGACGAGAGACCCCTGTGAGCTTTAAATT?TAAGCCA--GCAGCAA					
SCSSL	.....	AGACGAGAGACCCCTGTGAGCTTTAAATT?TAAGCCA--GCAGCAA					
SCSTE	.....	AGACGAGAGACCCCTGTGAGCTTTAAATT?TAAGCCA--GCAGCAA					
SCSUN	.....	AGACGAGAGACCCCTGTGAGCTTTAAATT?TAAGCCA--GCAGCAA					
SCTAE	.....	AGACGAGAGACCCCTGTGAGCTTTAAATT?TAAGCCA--GCAGCAA					
SCSTAN	.....	AGACGAGAGACCCCTGTGAGCTTTAAATT?TAAGCCA--GCAGCAA					
SCTEA	.....	AGACGAGAGACCCCTGTGAGCTTTAAATT?TAAGCCA--GCAGCAA					
SCTEW	.....	AGACGAGAGACCCCTGTGAGCTTTAAATT?TAAGCCA--GCAGCAA					
SCTOR	.....	AGACGAGAGACCCCTGTGAGCTTTAAATT?TAAGCCA--GCAGCAA					
SCTRJ	.....	AGACGAGAGACCCCTGTGAGCTTTAAATT?TAACCA--GTAACCA					
SCUND	.....	AGACGAGAGACCCCTGTGAGCTTTAAATT?TAACCA--AAACCA					
SCUTI	.....	AGACGAGAGACCCCTGTGAGCTTTAAATT?TAAGCCA--CCACCAA					
SCVAN	.....	AGACGAGAGACCCCTGTGAGCTTTAAATT?TAAGCCA--CCACCAA					
SCVAR	.....	AGACGAGAGACCCCTGTGAGCTTTAAATT?TAACCA--GCAACTAA					
SCVIR	.....	AGACGAGAGACCCCTGTGAGCTTTAAATT?TAACCA--GCAACTAA					
SCVMA	.....	AGACGAGAGACCCCTGTGAGCTTTAAACCCCTAGGCCAA--GTATACTAT					
SCWOO	.....	AGACGAGAGACCCCTGTGAGCTTTAAATT?TAACCA--GCAACTAA					
SCZOS	.....	AGACGAGAGACCCCTGTGAGCTTTAAATT?TAACCA--ACAACTGA					
PMEA	A-----	ACACAGCACACCA-TGGCCAA--AATTTAACTTAAATT?TAAGTGGGGACTT					
PETHA	A-----	ACACAGCACACCA-TGGCCAA--AATTTAACTTAAATT?TAAGTGGGGACTT					
URBLA	.....	.....					
URGAD	.....	.....					
URGIA	.....	.....					
URMIC	C-----	CACTAGACACTGTGGTAAAA-AGTTTAAGTGGGGCGACTT					
URNIG	C-----	CACTAGACACTGTGGTAAAA-AGTTTAAGTGGGGCGACTT					
URORN	AT-----	CAACATAACACCDATGGCCAA-AGTTTAAGTGGGGCGACTT					
UTPAL	.....	CAATGAGACACTATGGCAAAA-AGTTTAAGTGGGGCGACTT					
UTSTA	.....	AAATTACATATACACT-A-TGGCCAA-AATTTAACTTAAATT?TAAGTGGGGCGACTT					
SAANG	A-----	CAACAAACACCAAC-TGATCTAAACATTAAATT?TAAGTGGGGCGACTT					
SCACA	.....	.....					
SCAEN	T-----	CAC-AACTAGACCA-TGGCAA-AATTTAACTTAAATT?TAAGTGGGGCGACTT					
SCARE	.....	.....					
SCASP	.....	.....					
SCBIC	AC-----	AC-AATC-AAGCAA-TGACTAA-AATTTAACTTAAATT?TAAGTGGGGCGACTT					
SCBIN	AC-----	AC-AAAC-TAGCTAA-TGGCTAA-AATTTAACTTAAATT?TAAGTGGGGCAAATT					
SCBUL	.....	.....					
SCCAE	CAT-----	AACTTAAAC-TGGCTAA-AATTTAACTTAAATT?TAAGTGGGGCGACTT					
SCCAR	.....	.....					
SCCHA	G-----	C-AAGCTAGACCA-TGGCTAA-AATTTAACTTAAATT?TAAGTGGGGCGACTT					
SCCHR	A-----	CAACACAGGTAT-TGGCTAA-AATTTAACTTAAATT?TAAGTGGGGCGACTT					
SCCLA	A-----	CAAAACTAGACCAA-TGACTAA-AATTTAACTTAAATT?TAAGTGGGGCGACTT					
SCCON	G-----	C-AAGCTAGACCAA-TGGCTAA-AATTTAACTTAAATT?TAAGTGGGGCGACTT					
SCCOU	T-----	AAATA-ATTACCTA-TGGCTAA-AATTTAACTTAAATT?TAAGTGGGGCGACTT					
SCCOZ	A-----	ACATA---CGCTT-TGGTAGAA-AATTTAACTTAAATT?TAAGTGGGGCGACTT					
SCCRY	CA-----	AG-TAC---AGCCCAA-TGGCTAA-AATTTAACTTAAATT?TAAGTGGGGCGACTT					
SCCYA	C-----	ACAAT---TGCTCTCA-TGGCTAA-AATTTAACTTAAATT?TAAGTGGGGCGACTT					
SCCYC	C-----	AC-AAAATTGCCCCCTA-TGGCTAA-AATTTAACTTAAATT?TAAGTGGGGCGACTT					
SCDIN	.....	.....					
SCDUG	A-----	CAAAATTGACACA-TGGCTAA-AATTTAACTTAAATT?TAAGTGGGGCGACTT					
SCEDW	.....	.....					
SCELD	.....	.....					
SCERY	G-----	CAATCCAGACCAA-TGGCTAA-AATTTAACTTAAATT?TAAGTGGGGCGACTT					
SCEXS	.....	.....					
SCFOR	A-----	CAATA-CAGCTAA-TGGCTAA-AATTTAACTTAAATT?TAAGTGGGGCGACTT					
SCFSC	.....	.....					
SCGAD	.....	.....					
SCGOL	.....	.....					
SCGRC	T-----	CAGAAC-TGACTAA-TGGCAA-AATTTAACTTAAATT?TAAGTGGGGCGACTT					
SCGRM	A-----	CAGAAC-TCTACA-TGGTAATA-AATTTAACTTAAATT?TAAGTGGGGCGACTT					
SCHAL	AT-----	AC-AAGT-TAGTTA-TGGCTAA-AATTTAACTTAAATT?TAAGTGGGGCGACTT					
SCHET	CAT-----	AA-CACC-TAGCTAA-TGGCTAA-AATTTAACTTAAATT?TAAGTGGGGCGACTT					
SCHOR	CAT-----	AA-CAGCA-TAGCTAA-TGGCTAA-AATTTAACTTAAATT?TAAGTGGGGCGACTT					
SCHUN	A-----	CAAAACA-CAGCTAA-TGGCTAA-AATTTAACTTAAATT?TAAGTGGGGCGACTT					
SCHYA	.....	.....					

SCINS	AC--AC-AAAC-TAGCTAA-TGGCTAA-AATTAAAGTTGGGCAAATT	A---ACAAGGGCAGCTAA-TGGCTAA-AATTAAAGTTGGGCGACTT
SCIINT	AC---AC-ATCTATGA-TGGTGTGA-AATCTTAAGTTGGCGAACATT	SCTAN
SCCTL	AC---ACTAAT-T-AGCCGA-TGGTNAAA-AATTAAAGTTGGCAACTT	SCTEA
SCCUR	.	SCTR
SCJTR	.	SCTR1
SCJTM	.	SCOND
SCJUB	.	SCUT1
SCJUS	.	SCVAN
SCLIC	A---TAATA-CTAGTCCA-TGGCTAA-AATTAAAGTTGGCGAACATT	SCVAR
SCLIN	AC---AC-TAATTAGCCC-A-TGGTAA-AATTAAAGTTGGCGAACATT	SCVIR
SCLUJ	.	SCVMA
SCLOUD	.	SCWOO
SCMAC	C---CATGCCCTGCTAA-TGGCTAA-AACTTAAAGTTGGCGAACATT	A---C-AAGCTACGCC-A-TGGCTAA-AATTAAAGTTGGCGAACATT
SCMAG	CAC-AATTACCAAGCTCTA-TGGCTAA-AATTAAAGTTGGCGAACATT	CAC-AA-ACACAGTCC-A-TGGCTAA-AATTAAAGTTGGCGAACATT
SCMAL	A---CAAGCG--CAGCTAA-TGGCTAA-AATTAAAGTTGGCGAACATT	SCZOS
SCMAU	.	
SCMD	C---AA-AATTAGTAT-A-TGGTAA-AATTAAAGTTGGCGAACATT	[ 810 . 820 . 830 . 840 . 850 ]
SCMBG	AC---AC-AACATAGCA-A-TGGTCAA-AATTAAAGTTGGCGAACATT	[ 32 . 32 ; 33 ]
SCMEL	ACC-AC-ATAATGACG-A-TGGTAA-AATTAAAGTTGGCGAACATT	[ * * * * * . * * * * * ]
SCMHA	---CACTAAAACACATA-TGGCTAA-AATTAAAGTTGGCGAACATT	[ PEMA ]
SCMIN	C---AC-AATTTCGCTTA-TGGCTAA-AATTAAAGTTGGCGAACATT	[ PETMA ]
SCMLI	CAC-AA-ACACTAGTC-A-TGGCTAA-AATTAAAGTTGGCGAACATT	[ URBIC ]
SCMOM	C---A-AAA-TTGTCTACA-TGGCTAA-AATTAAAGTTGGCGAACATT	[ URCLA ]
SCMSF	.	[ URGAD ]
SCMUC	.	[ URGRA ]
SCNEL	C---AC-AATTTCGCTCA-TGGCTAA-AATTAAAGTTGGCGAACATT	[ URMIC ]
SCOCA	A---CAAAACTAGCTAA-TGGCTAA-AATTAAAGTTGGCGAACATT	[ URNING ]
SCOCH	A---ACCAACTAGCTAA-TGGCTAA-AATTAAAGTTGGCGAACATT	[ URONR ]
SCOLI	G---CACAG-TTGCGCAA-TGGCTAA-AATTAAAGTTGGCGAACATT	[ UTPAL ]
SCORN	A---CAAAAC-CTAGTCCA-TGGCTAA-AATTAAAGTTGGCGAACATT	[ UTSTA ]
SCPAL	.	[ SANG ]
SCPAP	A---AGTA---TTGCTAA-GATTAAAGTTGGCGAACATT	[ SAGRA ]
SCPIC	AC---AT-AACACTAGCTA-A-TGGCTAA-AATTAAAGTTGGCGAACATT	[ SCADA ]
SCPPOI	C---ACAAAC-TTGCACAA-TGGCTAA-AATTAAAGTTGGCGAACATT	[ SCAREN ]
SCPRE	.	[ SCARE ]
SCPYR	AAACA---CAAACACACTAA-TGGCTAA-AATTAAAGTTGGCGAACATT	[ SCASP ]
SCSAL	.	[ SCBIC ]
SCSBN	CA---AG-TAC---AGCCAA-TGGCTAA-AATTAAAGTTGGCGAACATT	[ SCBIN ]
SCSCA	.	[ SCCAE ]
SCCSR	.	[ SCCAU ]
SCSHA	.	[ SCCHA ]
SCSIN	C---CACATAGCTAA-TGGCTAA-AATTAAAGTTGGCGAACATT	[ CGGAACAAACACTTCGAGCTAA-GACTAT-GTCTT-GCCAGA ]
SCSMA	A---CAAAAC-TGGCTAA-TGCACTAA-AATTAAAGTTGGCGAACATT	[ SCCLIA ]
SCSMI	A---ACATTTATCACCTT-TGCACTAA-AATTAAAGTTGGCGAACATT	[ SCCON ]
SCSP1	A---TAAAT---AGCCAA-TGGCTAA-AATTAAAGTTGGCGAACATT	[ SCCOU ]
SCSSQ	.	[ CGGAACAAACACTTCGAGCTAA-GACTAT-GTCTT-GCCAGA ]
SCSSL	A---CACTAC-T-AGCCAA-TGGCTAA-AATTAAAGTTGGCGAACATT	[ SCCR ]
SCSTE	ACC-AA-AAAC-AGCTT-A-TGGCTAA-AATTAAAGTTGGCGAACATT	[ SCCYS ]
SCSUN	.	[ SC DIN ]

CGGAAAAAAACTTCCGAGCATATA-GACTAC--GTCTAT-ATCAAGA	CGGAAACAAACTTCCGAGCATATA-GACTAT-GTCTCTT-ACCAAGA
SCDUG	SCAL
SCEDW	SCBN
SCFLO	SCBP
SCERY	SCCA
SCDXS	SCCU
SCFOR	SCBR
SCFSC	SCHA
SCCAD	SCSN
SCCAR	CGGAACAAACAAACTTCCGAGCATATA-GACAAAC-ACTTC-CCTAAAGA
SCCOL	CGGAACAAACAAACTTCCGAGCATATA-GACAAAC-ACTTC-CCTAAAGA
SCGRC	CGGAACAAACAAACTTCCGAGCATATA-GACAAAC-ACTTC-CCTAAAGA
SCCRM	CGGAACAAACAAACTTCCGAGCATATA-GACAAAC-ACTTC-CCTAAAGA
SCHAL	CGGAACAAACAAACTTCCGAGCATATA-GACAAAC-ACTTC-CCTAAAGA
SCHET	CGGAACAAACAAACTTCCGAGCATATA-GACAAAC-ACTTC-CCTAAAGA
SCHOR	CGGAACAAACAAACTTCCGAGCATATA-GACAAAC-ACTTC-CCTAAAGA
SCHUN	CGGAACAAACAAACTTCCGAGCATATA-GACAAAC-ACTTC-CCTAAAGA
SCHYA	CGGAACAAACAAACTTCCGAGCATATA-GACAAAC-ACTTC-CCTAAAGA
SCINS	CGGAACAAACAAACTTCCGAGCATATA-GACAAAC-ACTTC-CCTAAAGA
SCINT	CGGAACAAACAAACTTCCGAGCATATA-GACAAAC-ACTTC-CCTAAAGA
SCJAL	CGGAACAAACAAACTTCCGAGCATATA-GACAAAC-ACTTC-CCTAAAGA
SCJAR	CGGAACAAACAAACTTCCGAGCATATA-GACAAAC-ACTTC-CCTAAAGA
SCJEM	CGGAACAAACAAACTTCCGAGCATATA-GACAAAC-ACTTC-CCTAAAGA
SCJOB	CGGAACAAACAAACTTCCGAGCATATA-GACAAAC-ACTTC-CCTAAAGA
SCJU	CGGAACAAACAAACTTCCGAGCATATA-GACAAAC-ACTTC-CCTAAAGA
SCJUC	CGGAACAAACAAACTTCCGAGCATATA-GACAAAC-ACTTC-CCTAAAGA
SCJUN	CGGAACAAACAAACTTCCGAGCATATA-GACAAAC-ACTTC-CCTAAAGA
SCJUD	CGGAACAAACAAACTTCCGAGCATATA-GACAAAC-ACTTC-CCTAAAGA
SCMAC	CGGAACAAACAAACTTCCGAGCATATA-GACAAAC-ACTTC-CCTAAAGA
SCMAG	CGGAACAAACAAACTTCCGAGCATATA-GACAAAC-ACTTC-CCTAAAGA
SCMAM	CGGAACAAACAAACTTCCGAGCATATA-GACAAAC-ACTTC-CCTAAAGA
SCMCD	CGGAACAAACAAACTTCCGAGCATATA-GACAAAC-ACTTC-CCTAAAGA
SCMEG	CGGAACAAACAAACTTCCGAGCATATA-GACAAAC-ACTTC-CCTAAAGA
SCMEL	CGGAACAAACAAACTTCCGAGCATATA-GACAAAC-ACTTC-CCTAAAGA
SCMER	CGGAACAAACAAACTTCCGAGCATATA-GACAAAC-ACTTC-CCTAAAGA
SCMHA	CGGAACAAACAAACTTCCGAGCATATA-GACAAAC-ACTTC-CCTAAAGA
SCMIN	CGGAACAAACAAACTTCCGAGCATATA-GACAAAC-ACTTC-CCTAAAGA
SCMLI	CGGAACAAACAAACTTCCGAGCATATA-GACAAAC-ACTTC-CCTAAAGA
SCNOM	CGGAACAAACAAACTTCCGAGCATATA-GACAAAC-ACTTC-CCTAAAGA
SCMSL	CGGAACAAACAAACTTCCGAGCATATA-GACAAAC-ACTTC-CCTAAAGA
SCNUC	CGGAACAAACAAACTTCCGAGCATATA-GACAAAC-ACTTC-CCTAAAGA
SCNEL	CGGAACAAACAAACTTCCGAGCATATA-GACAAAC-ACTTC-CCTAAAGA
SCOCA	CGGAACAAACAAACTTCCGAGCATATA-GACAAAC-ACTTC-CCTAAAGA
SCOCC	CGGAACAAACAAACTTCCGAGCATATA-GACAAAC-ACTTC-CCTAAAGA
SCOCH	CGGAACAAACAAACTTCCGAGCATATA-GACAAAC-ACTTC-CCTAAAGA
SCOLI	CGGAACAAACAAACTTCCGAGCATATA-GACAAAC-ACTTC-CCTAAAGA
SCORN	CGGAACAAACAAACTTCCGAGCATATA-GACAAAC-ACTTC-CCTAAAGA
SCPAL	CGGAACAAACAAACTTCCGAGCATATA-GACAAAC-ACTTC-CCTAAAGA
SCPARI	CGGAACAAACAAACTTCCGAGCATATA-GACAAAC-ACTTC-CCTAAAGA
SCPBI	CGGAACAAACAAACTTCCGAGCATATA-GACAAAC-ACTTC-CCTAAAGA
SCPRE	CGGAACAAACAAACTTCCGAGCATATA-GACAAAC-ACTTC-CCTAAAGA

SCASP	CCCAAGTCAAAGCCAAA?TTGACCCAGTATT?ACTGATAACCGAACCC		
SCRIC	CCTAAAGTCAAAGGAAAC?ACTGACAAACCGAACCC		
SCBIN	CCTAAAGTCAAAGCTAAAA?TTGACCCAGTACA?ACTGACAAACCGAACCC		
SCBUL	CCAACAAGTCAAAGCTAAAA?TTGACCCAGTACA?ACTGATCAACCGAACCC		
SCCAR	CCTAAAGTCAAAGCTAAAA?TTGACCCAGTACA?ACTGATCAACCGAACCC		
SCCAU	CCTAAAGTCAAAGCTAAAA?TTGACCCAGTACA?ACTGACAAACCGAACCC		
SCCHA	CCAAGAAGTCAAAGCTAAAC?TTGATCAGTATTACTGATCATCGAACCC		
SCCHR	CCTPAAAGTCAAAGCCAAA?CTGACCCAGTAC?ACTGACAAACCGAACCC		
SCCLLA	CCTAAAGTCAAAGCTAAAA?TTGACCCAGTACA?ACTGACAAACCGAACCC		
SCCON	CITAAGAAGTCAAAGCTAAAC?TTGACCCAGTACA?ACTGACAAACCGAACCC		
SCCOU	CTTCCAAAGTCAAAGCTAAAC?TTGACCCAGTACA?ACTGACAAACCGAACCC		
SCCOZ	CCAAAGTCAAAGCTAAAC?TTGACCCAGTACA?ACTGACAAACCGAACCC		
SCCRY	CCTAAAGTCAAAGCTAAAC?TTGACCCAGTACA?ACTGACAAACCGAACCC		
SCCYS	CCTAAAGTCAAAGCTAAAC?TTGACCCAGTACA?ACTGACAAACCGAACCC		
SCDIN	CATAAGTCAAAGCTAAAC?TTGACCCAGTACA?ACTGACAAACCGAACCC		
SCEDW	SCELO	CCTAAAGTCAAAGCTAAAA?TTGACCCAGTACA?ACTGACAAACCGAACCC	
SCERY	SCEXS	CCAACAAGTCAAAGCTAAAC?TTGACCCAGTACA?ACTGATAACCGAACCC	
SCFOR	SCFSC	CCAACAAGTCAAAGCTAAAC?TTGACCCAGTACA?ACTGATAACCGAACCC	
SCGAD	SCGAD	CCAACAAGTCAAAGCTAAAC?TTGACCCAGTACA?ACTGATCAACCGAACCC	
SCGOL	SCGOL	CCAAGAAGTCAAAGCCAAA?TTGATCAGTATA?ACTGACAAACCGAACCC	
SCGRC	SCGRC	CACAGAAGTCAAAGCTAAAA?TTGACCCAGTACA?ACTGATAACCGAACCC	
SCGRM	SCHAL	SCHAL	CATAAGTCAAAGCTAAAC?TTGACCCAGTATA?ACTGACAAACCGAACCC
SCHEI	SCHEI	SCHET	CCAAGAAGTCAAAGCTAAAA?TTGACCCAGTATA?ACTGATCAACCGAACCC
SCHOR	SCHUN	SCHUN	CATAAGTCAAAGCTAAAC?TTGACCCAGTACA?ACTGATPAACCGAACCC
SCHYA	SCINS	SCINS	CCTAAAGTCAAAGCTAAAA?TTGACCCAGTACA?ACTGACAAATCGAACCC
SCINT	SCUAL	SCUAL	CCAACAAGTCAAAGCTAAAC?TTGACCCAGTACA?ACTGATCATCGAACCC
SCJER	SCJER	CCTAAAGTCAAAGCTAAAT?TTGACCCAGTACA?ACTGATAATCGAACCC	
SCJIM	SCJIM	SCJIM	CCAACAAGTCAAAGCTAAAC?TTGACCCAGTACA?ACTGACAAATCGAACCC
SCJOB	SCJOB	SCJOB	CCAACAAGTCAAAGCTAAAC?TTGACCCAGTACA?ACTGACAAATCGAACCC
SCJUC	SCJUC	SCJUC	CCAACAAGTCAAAGCTAAAC?TTGACCCAGTACA?ACTGACAAATCGAACCC
SCJUN	SCJUN	SCJUN	CCAACAAGTCAAAGCTAAAC?TTGACCCAGTACA?ACTGACAAATCGAACCC
SCJUA	SCJUD	SCJUD	CCAACAAGTCAAAGCTAAAC?TTGRCCCAGTAA?ACTGATCACCGAACCC
SCMAC	SCMAC	SCMAC	CCAACAAGTCAAAGCTAAAC?TTGACCCAGTACA?ACTGATCAACCGAACCC
SCMAG	SCMAG	SCMAG	CCTAAAGTCAAAGCTAAAC?TTGACCCAGTACA?ACTGATCAACCGAACCC
SCNAL	SCNAU	SCNAU	CCTAAAGTCAAAGCTAAAC?TTGACCCAGTACA?ACTGATAAACCGAACCC
SCNUD	SCMEG	SCMEG	CCTAAAGTCAAAGCTAAAC?TTGACCCAGTACA?ACTGACACTCGAACCC

[	910	920	930	940	950	]
.	.	29	.	*	35	]
*****	*****	*****	*****	*****	35'	*****
PEMEA	PEMEA	AAGTACCCAGGGATAAACAGCGGAATCTCTTCAGAGTCCCATATCGAC	AAGTACCCAGGGATAAACAGCGGAATCTCTTCAGAGTCCCATATCGAC	AAGTACCCAGGGATAAACAGCGGAATCTCTTCAGAGTCCCATATCGAC	AAGTACCCAGGGATAAACAGCGGAATCTCTTCAGAGTCCCATATCGAC	AAGTACCCAGGGATAAACAGCGGAATCTCTTCAGAGTCCCATATCGAC
RETHA	RETHA	AAGTACCCAGGGATAAACAGCGGAATCTCTTCAGAGTCCCATATCGAC	AAGTACCCAGGGATAAACAGCGGAATCTCTTCAGAGTCCCATATCGAC	AAGTACCCAGGGATAAACAGCGGAATCTCTTCAGAGTCCCATATCGAC	AAGTACCCAGGGATAAACAGCGGAATCTCTTCAGAGTCCCATATCGAC	AAGTACCCAGGGATAAACAGCGGAATCTCTTCAGAGTCCCATATCGAC
JRBIC	JRBIC	.....	.....	.....	.....	.....
JURCL	JURCL	.....	.....	.....	.....	.....
URGAD	URGAD	.....	.....	.....	.....	.....
URMIC	URMIC	.....	.....	.....	.....	.....
URORN	URORN	.....	.....	.....	.....	.....
UPITAL	UPITAL	.....	.....	.....	.....	.....
UTISTIA	UTISTIA	.....	.....	.....	.....	.....
SAANG	SAANG	.....	.....	.....	.....	.....
SAGRA	SAGRA	.....	.....	.....	.....	.....
SCADM	SCADM	.....	.....	.....	.....	.....
SCAEIN	SCAEIN	.....	.....	.....	.....	.....
SCARF	SCARF	.....	.....	.....	.....	.....
SCASP	SCASP	.....	.....	.....	.....	.....
SCBLIC	SCBLIC	.....	.....	.....	.....	.....
SCBUL	SCBUL	.....	.....	.....	.....	.....
SCCAE	SCCAE	.....	.....	.....	.....	.....
SCCAU	SCCAU	.....	.....	.....	.....	.....
SCCHA	SCCHA	.....	.....	.....	.....	.....
SCCLIA	SCCLIA	.....	.....	.....	.....	.....
SCCON	SCCON	.....	.....	.....	.....	.....
SCCOU	SCCOU	.....	.....	.....	.....	.....
SCCOZ	SCCOZ	.....	.....	.....	.....	.....
SCCRY	SCCRY	.....	.....	.....	.....	.....
SCDUN	SCDUN	.....	.....	.....	.....	.....
SCEDW	SCEDW	.....	.....	.....	.....	.....
SCELIO	SCELIO	.....	.....	.....	.....	.....
SCERY	SCERY	.....	.....	.....	.....	.....
SCEXS	SCEXS	.....	.....	.....	.....	.....
SCFOR	SCFOR	.....	.....	.....	.....	.....
SCFSC	SCFSC	.....	.....	.....	.....	.....
SCGAD	SCGAD	.....	.....	.....	.....	.....
SCGAR	SCGAR	.....	.....	.....	.....	.....
SCGOL	SCGOL	.....	.....	.....	.....	.....
SCGRIC	SCGRIC	.....	.....	.....	.....	.....
SCGRM	SCGRM	.....	.....	.....	.....	.....
SCHAL	SCHAL	.....	.....	.....	.....	.....
SCHEIT	SCHEIT	.....	.....	.....	.....	.....
SCHORI	SCHORI	.....	.....	.....	.....	.....
SCSCH	SCSCH	.....	.....	.....	.....	.....
SCSSL	SCSSL	.....	.....	.....	.....	.....
SCSUN	SCSUN	.....	.....	.....	.....	.....



SCPYR	AAGAAGGTTTACGACCTCGATGTTGCATCAGGACACCCAAATGGTGAGC	CGCTATTAAAGGTTTC.
SCSBN	.....	SCASP
SCSBP	.....	SCBIC
SCSCU	.....	SCBIN
SCSER	.....	SCBUL
SCSIN	.....	SCCAE
SCSNA	.....	SCCAR
SCSMN	.....	SCCAU
SCSP1	.....	SCCHA
SCSOU	.....	SCCHR
SCSSA	.....	SCCIA
SCSPB	.....	SCCOH
SCSUN	.....	SCCON
SCTPAN	.....	SCCOU
SCTPA	.....	SCCROZ
SCTOR	.....	SCCYA
SCPRI	.....	SCCTS
SCUND	.....	SCDIN
SCUTI	.....	SCDUG
SCVAN	.....	SCEDW
SCVAR	.....	SCELD
SCVIR	.....	SCERY
SCVNA	.....	SCEXS
SCWOO	.....	SCFSC
SCZOS	.....	SCGAD
	1010 1020 1030 1040 1050	SCGAR
	16S rDNA pt. 2->16S rDNA pt. 1	SCGOL
	{38 (in pt.)	SCGRC
PEMBA	*****	SCGRM
PETHA	CGCTATTAAAGGTTTC.	SCHAL
URBIC	CGCTATTAAAGGTTTC.	SCHET
URGAD	CGCTATTAAAGGTTTC.	SCHOR
URGRA	CGCTATTAAAGGTTTC.	SCHUN
URMITC	CGCTATTAAAGGTTTC.	SCHYA
URNIG	CGCTATTAAAGGTTTC.	SCINS
URORN	CGCTATTAAAGGTTTC.	SCINT
UTPAL	CGCTATTAAAGGTTTC.	SCJAL
UTSTA	CGCTATTAAAGGTTTC.	CGCTRTTAAAGGTTTC.
SAANG	CGCTATTAAAGGTTTC.	ACAGCACACACATACA-AA
SAGRA	.....	CGCTATTAAAGGTTTC.
SCACA	.....	CGCTATTAAAGGTTTC.
SCADL	CGCTATTAAAGGTTTC.	CGCTATTAAAGGTTTC.
SCAEN	.....	CGCTATTAAAGGTTTC.

SCMIN	CGCTTAAAGGTIC.	1060	1070	1080	1090	1100
SCMLI	CGCTTAAAGGTIC.	PEMEA	CAAACCTTGCCAAACAATCAGGCCCACTCTATAAAAATATAGAGCACT			
SCMOM	CGCTTAAAGGTIC.	PETHA	PETHA			
SCMNST	CGCTTAAAGGTIC.	URBIC	URBIC			
SCMUC	CGCTTAAAGGTIC.	URGAD	URGAD			
SCNBL	CGCTTAAAGGTIC.	URGRA	URGRA			
SCOCA	CGCTTAAAGGTIC.	URMIC	URMIC			
SCOCC	CGCTTAAAGGTIC.	URNIG	URNIG			
SCOCH	CGCTTAAAGGTIC.	UTPAL	UTPAL			
SCOLI	CGCTTAAAGGTICATAGAC-ACACAAAAAAATACACCACATAA-AA	CAACTCTGCCAAACAACCCAGG-CCTCTCTATTANAAATATAGAGCACT				
SCORC	CGCTTAAAGGTICATAGAC-ACACAAAAAAATACACCACATAA-AA	CAACTCTGCCAAACAACCCAGG-CCTCTCTATTANAAATATAGAGCACT				
SCORN	CGCTTAAAGGTICATAGAT-ACAGAT-ACACAAAAAAATACACCACATAA-AA	CAACTCTGCCAAACAACCCAGG-CCTCTCTATTANAAATATAGAGCACT				
SCPAL	CGCTTAAAGGTIC.	USTSTA	USTSTA			
SCPAP	CGCTTAAAGGTIC.	SAGRAS	SAGRAS			
SCPIC	CGCTTAAAGGTICACAGAC-ACACCAAAATACACACATAA-AA	SCACAS	SCACAS			
SCPPI	CGCTTAAAGGTICACAGAC-ACACCAAAATACACACATAA-AA	SCADL	CAACTCTTACAGCAATACTAGTCGCAATCTATATATAGAGAGCT			
SCPRA	CGCTTAAAGGTIC.	SCAEN	SCAEN			
SCPRE	CGCTTAAAGGTIC.	SCARE	SCARE			
SCPYR	CGCTTAAAGGTIC.	SCASP	SCASP			
SCSAL	CGCTTAAAGGTIC.	SCBIC	SCBIC			
SCSAN	CGCTTAAAGGTIC.	SCBTIN	SCBTIN			
SCSPB	CGCTTAAAGGTIC.	SCBUL	SCBUL			
SCSCA	CGCTTAAAGGTIC.	SCCAE	SCCAE			
SCSCU	CGCTTAAAGGTIC.	SCCAR	SCCAR			
SCSER	CGCTTAAAGGTIC.	SCCAU	SCCAU			
SCSHA	CGCTTAAAGGTIC.	SCCHA	SCCHA			
SCSIN	CGCTTAAAGGTIC.	SCCHR	CAACTCTGCCAAACAATCAGIGCTTATTCCTATAGACATATAGAGCACT			
SCSMW	CGCTTAAAGGTIC.	SCCLIA	CAACTCTGCCAAACAATCAGIGCTTATTCCTATAGACATATAGAGCACT			
SCSMI	CGCTTAAAGGTIC.	SCCON	CAACTCTGCCAAACAATCAGIGCTTATTCCTATAGACATATAGAGCACT			
SCSPI	CGCTTAAAGGTICACAGCT-ACCATATAAAAATACACACATAA-AG	SCCOU				
SCSSU	CGCTTAAAGGTICACAGCT-ACCATATAAAAATACACACATAA-AG	SCCOZ				
SCSSA	CGCTTAAAGGTIC.	SCCRV	CAGCCTCTTACAATNTCTCAGGCCCAATCTATATAAAAATATAGAGCACT			
SCSSE	CGCTTAAAGGTIC.	SCCVYA				
SCSUN	CGCTTAAAGGTICACAGAC-ACACCAAAATGTCAACACATAA-AA	SCCYIS				
SCTAE	CGCTTAAAGGTICACAGAC-ACACCAAAATGTCAACACATAA-AA	SCDIN				
SCTAN	CGCTTAAAGGTICACAGAC-ACACCAAAATGTCAACACATAA-AA	SCDUG				
SCTEA	CGCTTAAAGGTIC.	SCEDW				
SCTME	CGCTTAAAGGTIC.	SCELD				
SCTOR	CGCTTAAAGGTICACAGAC-ACACCAAAATTTACACACATAA-AA	SCERY				
SCPRI	CGCTTAAAGGTICACAGAC-ACACCAAAATTTACACACATAA-AA	SCEXS				
SCUND	CGCTTAAAGGTICACAGAC-ACACCAAAATTTACACACATAA-AA	SCFOR	CAACTCTTACAACAACTCTCAGGCCCAATCTATATAAAAATATAGAGCACT			
SCUTI	CGCTTAAAGGTIC.	SCFSC				
SCVAN	CGCTTAAAGGTIC.	SCGAD				
SCVAR	CGCTTAAAGGTICACAGAC-ACACCAAAATTCCTACACACATAA-AA	SCGAR				
SCVTR	CGCTTAAAGGTICACAGAC-ACACCAAAATTCCTACACACATAA-AA	SCGOL				
SCVMO	CGCTTAAAGGTICACAGAC-CTAACACTAAAAATCTCACATTAA-AA	SCGRM				
SCZOS	CGCTTAAAGGTIC.	SCHAL				
		SCHET				
		SCHOR				
		SCHUN	CAACNTCTTACAACAACTATCAGGCCCAATCTATATAAAAATATAGAGCACT			
		SCHYA				
		SCINS				
		SCINT				





SCCAR	.
SCCAU	.
SCCHA	CCTCAGC?AATGAAAAACCTACT-GAAAATTAAACAG
SCCHR	.
SCCLLA	ATCA.
SCCON	.
SCCOU	.
SCCOZ	.
SCCRY	ACCAGT?CANNAGNNACTACT-GNANNNTANCAA
SCCYA	.
SCCYS	.
SCDIN	GCCAGC?TAGAGAAAACCTACT-GAAAATTAAACAA
SCDUG	.
SCEDW	.
SCEL0	.
SCERY	.
SCEXS	.
SCFOR	ATCAGT?CTC2GAAAACCTACT-GAAAATTAAACAG
SCFSC	.
SCGAD	.
SCGAR	.
SCGOL	.
SCGRC	ATCAGC?AACGAAAGTCTACT-GAAAATTAAACA.
SCGRM	ATCAGT?CACGGAATACTACT-GAAAATTAAACAG
SCHAL	.
SCHET	.
SCHOR	.
SCHUN	ATNACTTCACGAAAATCTACT-GAAAATTAAACAA
SCHYA	.
SCINS	.
SCINT	.
SCJAL	ATCAGT?CACGAAAATCTACTTGAAAATTAAACAG
SCJAR	.
SCJER	.
SCJIM	.
SCJOB	.
SCJSU	GTCACTCCACGAAAATCTACT-GACAATTAAACAG
SCLIC	.
SCLIN	.
SCLUD	.
SCMAC	.
SCMAG	.
SCMAL	ATCAGT?TACAGAAGGCCCTACT-GAAAATTAAACAG
SCMAU	.
SCMCD	.
SCMEG	.
SCMEL	ATCAGT?AACGAAAACCTACT-GAAAATTAAACAG
SCMER	.
SCMIN	.
SCMLI	.
SCMOM	ACCAGT?CACAGAAAACCTACT-GAAAATTAAACAG
SCNST	.
SCMUC	.
SCNEL	.
SCOCA	ATCAGC?CATAGAAAACCTACT-GAAAATTAAACAG
SCOCH	.
SCOLI	ATCAGT?CACAGAAAACCTACT-GAAAATTAAACAG
SCORC	GTCAGT?CACAGAAAACCTACT-GATAATTAAACAG
SCORN	.
SCPAL	.
SCPIC	.
SCPPI	ACCAGT?CACAGAAAACCTACT-GAAAATTAAACAA
SCPPE	.
SCPRR	.
SCSAL	.
SCSBN	.
SCSBP	.
SCSCA	.
SCSCU	.
SCSPR	.
SCSHA	.
SCSIN	.
SCSNA	ATCAGT?CACAGAAGGCCCTACT-GAAAATTAAACAG
SCSMI	.
SCSPI	ACCAGT?CACAGAAGGCCCTACT-GAAAATTAAACAG
SCSOU	.
SCSSA	.
SCSSE	ATCAGT?ATAGAAAACCTACT-GAAAATTAAACAA
SCSVE	.
SCSUN	.
SCTAE	ATCAGT?CACAGAAAACCTACT-GAAAATTAAACAG
SCTAN	.
SCTEA	.
SCTME	ATCAGT?CACAGAAAACCTACTTGAAAATTAAACAG
SCTOR	.
SCTRI	.
SCUND	ATCAGC?CATAGAAAACCTACT-GAAAATTAAACAG
SCUTI	.
SCVAN	.
SCVIR	AACAGC?CACAGAAAACCTACT-GGAAATT.
SCVMA	CTCAGT?ATAGAAAAGACTACT-GAAAATTAAACAA
SCWOO	.
SCZOS	.

[Gap characters and their nucleotide position. ]  
 [Deletions = "0", Insertions = "1"]

SCCHR	11.011010	SCCLIA	1000100?	SCCLIN	1000101?
		SCCLA	1000100?	SCCSNA	1000100?
		SCCON	11.010101?	SCCLIN	1000100?
		SCCOU	11.010101?	SCLUVA	.....
		SCCOZ	11.01101?	SCCLUD	.....
		SCCRY	1000110?	SCMAD	1000100?
		SCCYA	10001000	SCMAG	1000110?
		SCCYS	1000100?	SCMAL	10001100
		SCDIN	10001100	SCMAU	.....
		SCDUG	10001000	SCMD	1000100?
		SCCEDW	.....	SCMEG	1000100?
		SCELC	.....	SCMEL	1000100?
		SCERO	1000100?	SCMER	11001000
		SCEXS	.....	SCMHA	.....
		SCFOR	10001100	SCMIN	1000100?
		SCFSC	.....	SCMLI	1000010?
		SCGAD	1001100?	SCMOM	10001000
		SCGAR	.....	SCMRST	.....
		SCGOL	.....	SCMDC	.....
		SCGRCL	10001000	SCNIEL	.....
		SCGRM	10001000	SCOCA	1000100?
		SCHAL	.....	SCOCC	10001000
		SCHEIT	1000100?	SCOCH	1000100?
		SCHOR	10001000	SCCOLI	10001000
		SCIAEN	.....	SCORC	10001101
		SCARE	11.00110?	SCORN	.....
		SCASP	1000100?	SCPAR	1101101?
		SCBIC	1000100?	SCPIC	10001000?
		SCBIN	1000100?	SCPPI	10001000
		SCCBUL	1000100?	SCPRE	.....
		SCCBAE	10001000	SCCPYR	1000100?
		SCCAR	.....	SCCBAU	1000100?
		SCCAU	1000100?	SCCBAU	1000100?

## APPENDIX VI

*Character Changes Supporting Internal Splits of Combined-All Taxa Tree*

Numbered stems correspond to the tree based on the combined data and including all taxa (Figs. 9, 10). The derived character state of each character is placed after the decimal point. Numbers in parentheses indicate the relative weight of the change for frequency-coded morphological characters, from 1 to 24. For DNA characters and non-frequency-coded morphological characters, each change has a relative weight of 24.

**Stem 1.**—ACCTRAN: 11.e (4), 38.a (24), 40.e (4), 67.c (2), 71.u (8), 77.y (24), 78.d (3), 80.h (8), 84.x (15), 88.q (1), 104.y (24), 105.w (22), 106.l, 109.y (24), 112.a (4), 115.y (24), 123.a (24), 125.a (24), 136.m (12), 142.y (8), 148.u (4), 167.m (4), 179.y (24), 184.y (24), 224.C, 269.C, 390.T, 504.G, 530.C, 533.A, 542.T, 614.A, 661.T, 704.A, 744.A. DELTRAN: 71.i (2), 77.k (10), 78.d (3), 80.i (8), 84.q (10), 104.y (24), 112.a (4), 123.a (24), 142.r (7), 146.0, 148.s (2), 269.C, 333.A, 334.A, 390.T, 504.G, 530.C, 533.A, 661.T, 704.A, 1053.T, 1165.T.

**Stem 2.**—ACCTRAN: 8.a (12), 14.a (10), 88.f (11), 90.a (2), 106.2, 138.a (4), 209.1, 310.C, 356.A, 367.T, 374.A, 607.T, 639.A, 703.A, 1045.A, 1054.A, 1082.T, 1087.A, 1138.A. DELTRAN: 42.e (4), 50.m (6), 73.n (3), 88.g (17), 106.2, 138.a (4), 209.1, 310.C, 367.T, 374.A, 607.T, 703.A, 1054.A, 1087.A.

**Stem 3.**—ACCTRAN: 18.y (12), 31.i (8), 37.q (10), 38.y (24), 40.a (4), 41.i (8), 42.m (8), 55.0, 58.m (12), 69.a (2), 73.t (6), 80.i (1), 94.y (21), 105.a (22), 120.d (3), 126.f (5), 142.r (7), 145.g (6), 152.g (6), 177.y (24), 179.a (24), 184.a (24), 192.y (24), 303.A, 336.A, 475.C, 486.A, 553.T, 557.T, 658.G, 744.G, 785.T, 786.T, 789.C, 952.C, 1033.C, 1035.T, 1046.A, 1048.G, 1053.C, 1146.C, 1185.C, 1193.C. DELTRAN: 37.m (6), 42.i (4), 58.c (2), 73.q (3), 94.y (21), 125.a (24), 137.a (12), 152.d (3), 177.y (24), 224.C, 336.A, 486.A, 639.A, 785.T, 789.C.

**Stem 4.**—ACCTRAN: 11.a (4), 14.i (8), 34.a (6), 47.i (8), 54.c (2), 64.a (3), 66.y (24), 67.a (2), 71.g (14), 73.w (3), 77.i (16), 84.y (1), 87.g (4), 109.a (24), 115.a (24), 148.y (4), 189.m (12), 222.G, 334.C, 378.G, 393.T, 431.C, 484.C, 489.C, 500.A, 507.C, 513.T, 655.C, 687.T, 688.A, 745.T, 782.A, 783.T, 788.A, 851.A, 881.C, 882.A, 892.C, 1006.T. DELTRAN: 14.i (8), 18.y (12), 27.g (2), 34.a (6), 37.q (4), 43.m (4), 47.i (8), 54.c (2), 58.m (10), 64.a (2), 66.y (24), 71.g (2), 73.w (6), 77.i (2), 84.y (8), 87.g (4), 148.y (6).

**Stem 5.**—ACCTRAN: 11.y (20), 12.y (24), 16.y (24), 27.a (6), 31.m (4), 34.m (6), 41.m (4), 43.g (6), 51.w (22), 67.v (19), 68.k (10), 71.y (4), 84.a (23), 87.y (14), 107.y (24), 114.d (3), 118.y (24), 129.y (24), 144.e (4), 146.2, 269.T, 397.C, 740.C, 862.T, 901.A. DELTRAN: 11.y (24), 12.y (24), 16.y (24), 31.m (12), 41.m (12), 42.m (4), 43.g (2), 51.w (22), 67.v (21), 68.k (10), 71.y (16), 77.y (14), 84.a (16), 87.y (14), 107.y (24), 109.y (24), 114.d (3), 115.y (24), 118.y (24), 126.f (5), 129.y (24), 146.2, 269.T, 397.C, 557.T, 862.T.

**Stem 6.**—ACCTRAN: 2.i (8), 4.m (12), 6.q (16), 8.q (16), 19.e (4), 20.y (24), 23.y (24), 37.y (8), 41.y (12), 55.2, 58.c (10), 59.j (9), 61.e (4), 65.d (3), 67.y (3), 68.n (3), 72.a (5), 80.c (6), 81.c (2), 88.g (1), 90.t (19), 96.v (21), 98.b (1), 99.e (4), 103.f (5), 111.d (8), 114.j (6), 119.y (24), 124.j (9), 126.l (6), 130.l (11), 135.k (5), 136.a (12), 142.y (7), 151.m (12), 152.d (3), 164.e (4), 176.a (24), 267.T, 271.T, 325.A, 326.C, 356.G, 431.T, 465.T, 467.C, 473.C, 474.C, 475.A, 476., 487.T, 488.C, 490.C, 501.G, 503.G, 508.G, 512.A, 531.C, 533.G, 620.C, 644.C, 658.A, 682.T, 738.A, 739.C, 743.C, 744.A, 786.A, 790.G, 851.C, 853.C, 855.T, 943.T, 952.A. DELTRAN: 2.f (5), 4.i (8), 6.q (16), 8.q (16), 18.y (12), 20.y (24), 23.y (24), 37.y (12), 41.y (12), 55.2, 59.j (9), 61.e (4), 65.c (2), 67.y (3), 68.n (3), 72.a (5), 73.t (3), 80.c (6), 83.b (1), 90.t (19), 96.v (21), 99.c (2), 103.f (5), 111.d (3), 114.j (6), 119.y (24), 124.j (9), 126.l (6), 130.l (11), 135.k (5), 142.y (7), 148.u (2), 151.m (12), 164.e (4), 176.a (22).

**Stem 7.**—ACCTRAN: 6.w (6), 8.y (8), 14.m (12), 31.y (12), 34.a (12), 59.k (1), 64.a (3), 68.t (6), 79.k (10), 80.a (2), 86.y (24), 93.b (1), 96.y (3), 111.a (3), 114.y (15), 120.a (3), 124.y (15), 126.p (4), 130.y (13), 135.a (10), 145.a (6), 148.y (4), 152.a (3), 163.2, 164.m (8). DELTRAN: 8.y (8), 14.m (12), 27.a (4), 31.u (8), 64.a (2), 68.s (5), 79.d (3), 80.a (2), 111.a (3), 114.y (15), 126.p (4), 135.g (4), 144.d (3), 148.y (4), 164.m (8).

**Stem 8.**—ACCTRAN: 2.f (3), 4.i (4), 14.y (12), 45.j (9), 50.a (12), 51.r (5), 65.c (1), 71.w (2), 73.v (2), 78.a (3), 81.d (1), 83.b (1), 88.a (6), 98.a (1), 99.c (2), 126.w (7), 164.u (8). DELTRAN: 14.y (12), 19.e (4), 45.j (9), 50.a (12), 51.r (5), 71.w (2), 73.v (2), 78.a (3), 81.d (3), 88.a (6), 126.w (7), 164.u (8).

**Stem 9.**—ACCTRAN: 3.e (4), 4.g (6), 5.m (12), 7.m (12), 18.i (4), 21.i (8), 24.y (24), 37.a (6), 94.a (3), 100.c (2), 125.y (24), 131.v (21), 133.w (22), 135.s (3), 148.s (2), 224.T, 304.C, 362.C, 369.G, 390.C, 438.A, 473.C, 487.T, 502.A, 504.A, 522.T, 642.T, 660.T, 815.A, 900.C, 1034.C, 1036.C, 1038.A, 1051.A, 1058.T, 1071.A, 1082.C, 1109.C, 1169.C, 1194.G, 1198.0. DELTRAN: 4.g (6), 5.m (12), 18.i (4), 24.q (16), 37.a (6), 38.a (24), 40.d (3), 55.1, 69.c (2), 80.h (1), 83.b (1), 94.a (3), 100.c (2), 105.w (22), 133.p (15), 135.s (3), 142.y (7), 176.y (2), 179.y (24), 184.y (24), 304.C, 390.C, 438.A, 473.C, 502.A, 504.A, 542.T, 642.T, 660.T, 815.A, 1034.C, 1036.C, 1038.A, 1071.A, 1082.C, 1169.C, 1198.0.

**Stem 10.**—ACCTRAN: 11.a (4), 18.a (8), 27.e (2), 34.i (2), 64.j (6), 67.a (2), 69.i (6), 71.i (12), 75.h (1), 80.e (3), 84.q (7), 95.y (24), 105.y (2), 111.a (11), 112.y (24), 119.y (24), 135.y (6), 137.m (12), 147.i (8), 211.A, 273.G, 332.C, 356.G, 377.T, 381.T, 397.C, 639.G, 643.A, 704.T, 784.T, 1055.C, 1069.A, 1076.C, 1077.C, 1137.T, 1146.A, 1176.A. DELTRAN: 77.y (14), 95.c (2), 105.y (2), 111.a (6), 115.y (24), 119.w (22), 135.t (1), 211.A, 273.G, 332.C.

**Stem 11.**—ACCTRAN: 27.a (4), 34.q (8), 42.a (4),

65.b (1), 72.d (2), 131.a (21), 136.a (12), 151.q (16), 152.d (3), 167.y (12), 475.T, 478.A, 501.T, 502.T, 508.G, 620.A, 641.G, 704.C, 952.C. DELTRAN: 18.a (8), 27.a (4), 43.m (4), 64.i (6), 83.a (1), 95.x (21), 109.y (24), 112.y (24), 119.y (2), 151.m (12), 502.T, 704.C, 952.C.

*Stem 12*.—ACCTRAN: 3.a (4), 7.a (12), 24.a (24), 58.e (4), 64.p (6), 69.u (12), 73.u (7), 89.i (8), 100.a (2), 114.y (24), 133.a (22), 147.a (8), 160.1, 189.m (12), 357.T, 369.A, 489.C, 541.G, 703.C, 740.C, 744.G, 862.T, 892.T. DELTRAN: 24.a (16), 58.d (3), 69.p (13), 73.t (6), 89.i (8), 95.y (1), 114.y (24), 133.a (15), 478.A, 487.T, 489.C, 541.G, 703.C, 862.T, 900.C.

*Stem 13*.—ACCTRAN: 4.i (2), 5.u (8), 21.m (4), 45.g (6), 46.q (16), 71.j (1), 78.a (3), 80.i (4), 84.f (11), 87.e (6), 89.m (4), 103.c (2), 137.y (12), 142.o (10), 152.y (21), 179.a (24), 198.1, 205.1, 207.1, 332.A, 377.A, 466.G, 502.C, 508.A, 641.A, 660.C, 661.A, 787.-, 821.C, 875.C, 879.A, 892.C. DELTRAN: 4.i (2), 5.u (8), 21.m (12), 42.a (4), 46.m (12), 65.b (1), 78.a (3), 84.i (8), 137.y (12), 142.o (10), 152.i (8), 167.y (24), 179.a (24), 198.1, 205.1, 207.1, 501.T, 502.C, 620.A, 643.A, 660.C, 661.A, 821.C, 875.C, 892.C, 1055.C, 1069.A, 1076.C, 1085.T, 1146.A.

*Stem 14*.—ACCTRAN: 15.q (16), 21.y (12), 27.g (6), 45.m (6), 64.d (12), 84.a (5), 99.c (2), 135.a (24), 142.i (6), 189.a (12), 198.4, 224.C, 335.C, 397.T, 475.C, 606.C, 614.G, 744.A, 880.C, 893.C, 901.A, 1049.C, 1051.C, 1058.A, 1073.C, 1082.T, 1109.T. DELTRAN: 21.q (4), 45.m (12), 64.e (4), 69.q (1), 72.e (1), 84.a (8), 135.a (19), 142.i (6), 198.2, 224.C, 357.T, 475.C, 606.C, 614.G, 744.A, 784.T, 879.A, 893.C, 901.A, 1049.C, 1073.C, 1082.T.

*Stem 15*.—ACCTRAN: 17.e (4), 27.m (6), 34.a (16), 40.a (4), 50.a (12), 53.e (4), 60.g (6), 73.x (3), 75.f (2), 88.b (4), 124.y (24), 152.i (16), 160.0, 186.i (16), 381.C, 557.T, 787.A, 875.T, 1133.C, 1167.C. DELTRAN: 40.a (3), 46.p (3), 50.a (12), 53.d (3), 60.e (4), 69.u (4), 73.u (1), 87.g (4), 88.c (4), 124.y (24), 186.s (6), 332.A, 557.T, 875.T, 1046.C, 1133.C, 1167.C, 1194.G.

*Stem 16*.—ACCTRAN: 2.i (8), 3.m (12), 15.y (8), 25.g (6), 43.j (3), 58.c (2), 65.c (1), 73.y (1), 75.c (3), 80.b (7), 83.b (1), 100.e (4), 108.e (4), 134.f (5), 145.u (20), 148.a (18), 160.2, 161.d (3), 162.2, 167.a (24), 186.g (2), 189.d (3), 198.5, 1076.T. DELTRAN: 2.e (4), 15.y (24), 65.c (1), 75.d (3), 80.c (5), 87.e (2), 108.e (4), 145.m (12), 148.k (8), 160.2, 162.2, 167.e (20), 186.m (6), 198.5, 1076.T.

*Stem 17*.—ACCTRAN: 5.p (5), 9.o (14), 22.i (8), 46.p (1), 47.m (12), 53.o (10), 60.m (6), 64.g (3), 79.i (8), 84.b (1), 87.c (2), 98.c (2), 108.w (18), 122.e (4), 134.y (19), 149.b (1), 175.h (7), 184.q (8), 186.a (6), 484.A, 744.G, 862.A, 1085.C, 1134.T. DELTRAN: 2.f (1), 5.s (2), 9.o (14), 34.a (6), 73.y (4), 79.i (8), 80.b (1), 84.b (1), 87.d (1), 103.c (2), 108.w (18), 122.e (4), 134.y (24), 148.a (10), 175.h (7), 862.A, 1085.C, 1134.T.

*Stem 18*.—ACCTRAN: 4.a (8), 9.u (6), 14.i (8), 17.a (4), 25.a (6), 27.s (6), 42.e (4), 43.m (3), 46.i (7), 58.d (1), 69.w (2), 70.i (8), 71.e (5), 72.c (1), 75.d (1), 78.g (6), 79.w (14), 80.a (1), 83.a (1), 89.x (11), 99.a (2), 103.g (4), 122.r (13), 145.m (8), 151.a (16), 152.a

(8), 161.a (3), 162.3, 165.f (5), 175.i (1), 179.c (2), 357.C, 478.-, 484.C, 620.C, 893.A, 900.T, 1037.A, 1077.A, 1176.C, 1200.1. DELTRAN: 21.y (8), 27.s (18), 70.d (3), 72.c (2), 78.d (3), 79.u (12), 89.w (14), 103.e (2), 122.q (12), 151.f (7), 152.a (8), 162.3, 357.C, 466.G, 620.C, 900.T, 1176.C.

*Stem 19*.—ACCTRAN: 3.a (12), 5.s (3), 27.y (6), 45.a (12), 47.a (12), 53.c (12), 64.a (6), 65.b (1), 75.f (2), 76.s (18), 78.y (18), 79.y (2), 81.f (5), 87.a (2), 98.a (2), 113.g (6), 122.s (1), 127.g (6), 149.a (1), 160.3, 178.p (15), 186.s (18), 269.T, 332.C, 507.C, 508.G, 744.A, 1073.A, 1202.1. DELTRAN: 22.i (8), 27.y (6), 45.g (6), 46.i (7), 53.c (1), 64.a (4), 65.b (1), 71.e (4), 76.s (18), 78.y (21), 80.a (1), 81.b (1), 87.a (3), 100.e (2), 103.f (1), 122.s (2), 151.a (5), 175.i (1).

*Stem 20*.—ACCTRAN: 2.a (8), 22.q (8), 46.g (2), 53.a (2), 58.c (1), 65.a (1), 70.d (5), 71.a (4), 76.w (4), 89.w (1), 108.s (4), 142.a (8), 145.a (12), 165.i (3), 175.m (4), 189.m (9), 198.1, 207.0. DELTRAN: 2.a (5), 46.g (2), 58.c (1), 65.a (1), 71.d (1), 145.c (10), 160.3, 178.k (10), 189.c (2), 198.1, 484.C, 1073.A.

*Stem 21*.—ACCTRAN: 4.y (24), 9.y (4), 14.a (8), 42.m (8), 58.a (2), 60.x (11), 69.r (5), 72.d (1), 75.a (5), 86.d (3), 99.b (1), 105.w (2), 127.a (6), 128.i (8), 134.a (24), 143.c (2), 165.m (4), 169.u (20), 175.y (12), 199.1, 201.1, 202.1, 203.1, 208.1, 478.A, 513.T, 538.T, 539.T, 541.A, 862.T, 875.C, 893.T, 952.A, 1034.T, 1037.C, 1039.T, 1051.T, 1076.C, 1085.T, 1137.A, 1200.0. DELTRAN: 4.y (16), 9.y (10), 42.m (12), 53.a (2), 60.u (16), 69.r (3), 72.d (1), 75.b (2), 86.b (1), 105.w (2), 134.c (22), 142.b (7), 165.m (12), 169.u (20), 175.y (16), 179.c (2), 199.1, 201.1, 202.1, 203.1, 207.0, 208.1, 332.C, 508.G, 513.T, 862.T, 875.C, 952.A.

*Stem 22*.—ACCTRAN: 5.u (2), 13.i (8), 42.y (12), 43.a (12), 69.c (15), 71.d (3), 72.f (2), 76.m (10), 81.b (4), 83.g (6), 100.b (3), 103.f (1), 105.r (5), 122.m (6), 133.s (18), 140.w (22), 144.c (2), 145.c (2), 167.e (4), 168.e (4), 170.u (20), 174.d (3), 178.k (5), 179.y (22), 186.a (18), 189.c (10), 206.2, 228.A, 324.C, 331.T, 431.T, 436.A, 437.G, 438.T, 466.C, 471.G, 643.T, 662.G, 680.C, 681.G, 698.C, 702.T, 704.G, 743.T, 783.T, 861.A, 892.T, 1006.T. DELTRAN: 5.u (2), 69.c (15), 72.f (2), 76.m (6), 83.g (6), 100.b (3), 105.r (5), 113.g (6), 122.m (6), 133.s (18), 140.w (22), 144.c (2), 170.u (20), 174.d (3), 184.q (8), 186.a (12), 206.2.

*Stem 23*.—ACCTRAN: 5.p (3), 9.a (20), 42.a (4), 46.a (6), 60.e (8), 70.a (3), 74.y (24), 76.y (2), 79.u (4), 84.v (20), 100.m (8), 163.1, 180.y (24), 186.y (6), 190.m (12), 193.i (8), 194.e (4), 304.T, 475.T, 497.T, 851.A, 1031.T, 1135.C, 1160.G. DELTRAN: 5.p (3), 9.a (14), 14.i (8), 46.f (1), 70.a (3), 74.o (14), 84.q (15), 100.m (8), 127.e (4), 163.1, 178.p (5), 186.y (12), 190.m (12), 194.e (4), 269.T, 475.T, 497.T, 880.C, 893.A, 1200.1

*Stem 24*.—ACCTRAN: 5.a (15), 14.q (8), 48.m (12), 53.c (2), 81.h (2), 88.c (1), 98.u (20), 100.y (12), 103.p (9), 108.y (6), 113.p (9), 148.r (17), 159.q (16), 172.0, 173.y (24), 175.a (12), 179.h (5), 184.y (8), 190.q (4), 191.y (24), 193.j (1), 194.y (20), 207.1, 381.T, 386.G, 508.A, 530.T, 620.A, 680.C, 703.A, 787.-, 821.A. DELTRAN: 5.a (15), 14.q (8), 22.q (8), 46.a (5), 69.w (2), 74.y (10), 98.s (18), 100.s (6), 103.g (1), 108.y (2), 113.h (7), 142.f (3), 145.a (2), 159.c (2),

167.a (4), 179.h (7), 180.u (20), 193.j (9), 194.w (18), 304.T, 381.T, 386.G, 620.A, 680.C, 703.A, 787.-, 821.A, 851.A.

*Stem 25*.—ACCTRAN: 1.q (16), 22.y (8), 45.g (6), 58.g (4), 60.x (19), 63.l (11), 75.c (3), 79.a (20), 85.d (3), 89.s (4), 99.g (6), 172.3, 189.y (12), 193.w (13), 274.G, 275.A, 332.A, 361.T, 387.A, 393.C, 502.T, 643.G, 816.C, 862.C, 892.T, 1199.0. DELTRAN: 1.q (16), 4.a (8), 22.y (8), 58.g (4), 60.x (19), 63.l (11), 71.a (3), 75.c (1), 76.y (6), 79.a (20), 84.v (5), 85.d (3), 89.s (4), 99.g (6), 172.3, 173.y (24), 175.a (8), 189.y (22), 190.q (4), 191.y (24), 193.w (13), 274.G, 275.A, 361.T, 387.A, 393.C, 478.-, 502.T, 643.G, 816.C, 862.C, 892.T, 1199.0.

*Stem 26*.—ACCTRAN: 17.e (4), 21.m (12), 22.e (12), 27.s (6), 43.h (5), 47.m (12), 72.a (2), 81.a (5), 103.c (4), 108.r (1), 113.a (6), 142.t (19), 147.g (6), 178.q (1), 179.a (2), 181.y (24), 182.y (24), 184.a (16), 198.0, 205.0, 266.T, 318.G, 507.T, 705.A, 816.T, 835.A, 851.C, 855.T, 877.T. DELTRAN: 21.m (12), 47.m (12), 53.a (2), 72.a (2), 75.f (2), 76.y (6), 84.v (5), 103.d (2), 142.t (11), 175.m (4), 189.m (10), 198.0, 205.0, 207.0, 318.G, 478.-, 508.G, 816.T, 851.C, 855.T, 877.T, 1031.T, 1037.A, 1135.C, 1202.1.

*Stem 27*.—ACCTRAN: 3.y (24), 60.a (4), 63.w (22), 69.x (1), 79.m (8), 84.y (3), 85.n (13), 87.b (1), 89.m (10), 95.w (2), 122.a (18), 165.a (8), 175.y (12), 189.y (12), 193.a (8), 304.C, 333.G, 484.T, 1082.A, 1176.T. DELTRAN: 3.y (24), 46.a (5), 60.a (4), 63.w (22), 69.x (3), 74.y (10), 79.m (8), 84.y (3), 85.n (13), 87.b (1), 89.m (10), 95.w (2), 122.a (18), 127.g (2), 145.a (2), 175.y (12), 189.y (12), 484.T, 1137.T, 1176.T.

*Stem 28*.—ACCTRAN: 22.a (8), 47.p (3), 60.d (9), 65.f (3), 84.c (1), 87.d (1), 98.f (3), 108.x (1), 130.i (8), 397.C, 821.A, 901.C, 1035.C, 1036.A, 1038.T, 1072.G, 1074.A, 1095.T, 1134.C. DELTRAN: 5.q (2), 47.m (12), 53.m (9), 65.d (1), 98.b (1), 165.f (5), 186.i (4), 397.C, 478.-, 821.A, 893.A, 901.C, 1035.C, 1036.A, 1037.A, 1074.A, 1095.T, 1134.C.

*Stem 29*.—ACCTRAN: 9.d (17), 35.m (12), 46.y (16), 60.c (1), 64.k (4), 69.u (2), 70.m (4), 71.b (3), 79.u (2), 80.b (1), 100.b (3), 103.e (2), 134.a (24), 142.a (8), 160.1, 165.o (9), 175.a (8), 180.d (3), 184.y (8), 189.g (3), 385.G, 389.T, 484.T, 507.A, 557.C, 819.C, 950.T, 952.A, 1046.T. DELTRAN: 3.m (12), 4.a (8), 9.d (11), 46.y (9), 60.c (2), 71.b (7), 100.b (1), 122.r (1), 134.a (24), 142.a (8), 160.1, 165.m (7), 167.a (4), 175.a (7), 180.d (3), 189.c (2).

*Stem 30*.—ACCTRAN: 2.a (8), 3.y (12), 5.q (1), 9.a (3), 14.a (8), 42.a (4), 43.s (6), 65.d (2), 71.a (1), 72.e (2), 73.x (1), 75.a (3), 78.d (3), 79.a (20), 80.c (1), 88.g (5), 89.q (7), 98.b (4), 100.a (1), 108.a (23), 122.s (1), 130.a (8), 145.a (12), 149.a (1), 179.a (2), 180.g (3). DELTRAN: 3.s (6), 43.s (6), 75.a (3), 79.a (20), 89.s (4), 100.a (1), 108.a (22), 145.a (12), 385.G, 389.T, 557.C, 744.G, 819.C, 880.C, 952.A, 1200.1.

*Stem 31*.—ACCTRAN: 35.a (12), 53.k (4), 62.m (12), 87.c (1), 88.h (1), 122.y (6), 157.y (24), 165.q (2), 180.i (2), 197.y (24), 881.C. DELTRAN: 53.k (2), 80.c (1), 87.c (1), 88.d (1), 89.q (2), 122.y (7), 151.a (5), 157.y (24), 165.q (4), 197.y (24).

*Stem 32*.—ACCTRAN: 2.i (8), 27.y (6), 53.f (5), 64.a (10), 69.v (1), 71.g (6), 72.a (4), 80.h (5), 83.b (1), 84.a (2), 89.m (4), 103.g (2), 172.0, 189.c (4).

DELTRAN: 9.c (1), 27.u (2), 53.h (3), 71.g (5), 72.a (2), 80.e (2), 83.b (1), 89.m (4), 172.0.

*Stem 33*.—ACCTRAN: 47.m (3), 60.b (1), 62.a (12), 70.d (9), 71.m (6), 73.y (1), 75.d (3), 89.i (4), 98.a (1), 101.c (2), 105.w (2), 159.y (24), 180.a (8), 186.i (8), 475.T, 507.T, 538.T, 620.A, 903.G, 1051.A, 1133.T. DELTRAN: 9.a (2), 71.j (3), 89.j (3), 180.a (3), 475.T, 538.T, 950.T, 1046.T, 1051.A, 1133.T, 1137.T.

*Stem 34*.—ACCTRAN: 4.g (6), 5.i (8), 17.e (4), 27.u (4), 36.m (12), 40.m (12), 58.a (3), 60.a (1), 65.a (3), 69.y (3), 75.e (1), 78.a (3), 79.c (2), 165.y (8), 218.T, 310.T, 390.T, 397.A, 438.C, 495.G, 509.G, 527.G, 529.G, 539.T, 592.A, 605.T, 607.C, 615.A, 620.T, 836.G, 855.T, 881.T, 892.T, 901.A, 1049.T, 1072.A, 1077.C, 1097.T, 1146.G, 1156.A, 1168.T. DELTRAN: 3.y (6), 4.g (6), 5.i (8), 17.e (4), 36.m (12), 40.m (12), 58.a (3), 60.a (2), 64.e (4), 65.a (3), 69.y (4), 75.e (4), 78.a (3), 79.c (2), 165.y (8).

*Stem 35*.—ACCTRAN: 2.m (4), 3.m (12), 5.s (2), 48.m (12), 57.d (3), 64.k (10), 71.p (3), 89.g (2), 103.h (1), 135.y (24), 164.f (5), 167.g (6), 185.g (6), 190.m (12), 385.A, 431.T, 530.T, 703.A, 835.C, 862.C, 875.C, 903.T, 952.C, 1037.C, 1038.A, 1045.G, 1048.G, 1094.T, 1107.G, 1132.G, 1199.0. DELTRAN: 57.d (3), 64.k (6), 71.p (6), 89.g (3), 98.a (1), 101.c (2), 103.h (3), 105.w (2), 385.A, 431.T, 530.T, 620.A, 703.A, 835.C, 862.C, 875.C, 881.C, 903.T, 952.C, 1199.0.

*Stem 36*.—ACCTRAN: 1.i (8), 42.y (24), 43.a (18), 45.u (8), 47.q (1), 60.d (1), 73.w (1), 80.p (8), 86.x (23), 124.w (2), 178.e (4), 181.m (12), 191.y (24), 862.T, 950.C, 1038.C, 1097.C. DELTRAN: 42.q (16), 43.i (10), 53.g (1), 60.d (1), 62.h (7), 64.d (1), 70.m (9), 73.x (1), 84.a (1), 86.g (6), 186.a (8), 191.y (24), 507.A, 862.T, 1038.C, 1097.C.

*Stem 37*.—ACCTRAN: 36.q (16), 53.b (4), 58.a (3), 60.h (4), 65.i (5), 73.v (1), 88.m (5), 165.m (4), 178.i (4), 185.d (3), 442.G, 644.G, 1072.A, 1077.C, 1137.A, 1145.T. DELTRAN: 1.i (8), 3.y (6), 36.q (16), 58.a (3), 60.h (4), 80.m (8), 88.m (9), 181.i (8), 442.G, 644.G, 1046.T, 1077.C, 1145.T.

*Stem 38*.—ACCTRAN: 1.q (8), 2.a (8), 5.e (12), 38.q (16), 45.m (8), 60.s (11), 62.y (12), 71.w (16), 86.g (17), 124.y (2), 128.i (8), 323.G, 641.G, 881.T, 1045.G, 1076.C, 1097.T, 1138.G, 1199.0. DELTRAN: 60.s (11), 62.y (17), 71.p (9).

*Stem 39*.—ACCTRAN: 53.j (8), 60.v (3), 65.v (13), 69.t (2), 70.k (2), 72.f (5), 86.b (5), 87.f (3), 89.u (8), 101.e (4), 103.a (6). DELTRAN: 53.j (3), 60.v (3), 65.v (18), 69.t (1), 70.k (2), 72.f (5), 73.v (2), 80.p (3), 86.b (5), 87.f (3), 89.u (8), 101.e (4), 103.a (4), 128.i (8).

*Stem 40*.—ACCTRAN: 3.i (16), 22.i (8), 58.g (3), 65.b (2), 69.u (1), 70.s (6), 78.g (3), 88.d (4), 100.b (1), 103.d (3), 124.u (2), 134.o (14), 160.0, 328.C, 386.G, 660.T, 702.T, 705.A, 1046.C, 1082.C, 1095.C, 1107.G, 1108.T, 1110.G, 1167.T, 1174.G, 1175.C. DELTRAN: 3.m (6), 42.y (8), 43.g (2), 58.g (3), 65.c (1), 70.s (6), 78.g (3), 86.w (16), 134.o (14), 180.i (5).

*Stem 41*.—ACCTRAN: 2.f (3), 9.j (9), 67.b (1), 69.s (2), 70.u (2), 73.x (1), 79.h (7), 80.a (15), 83.a (1), 87.f (3), 105.x (1), 108.c (2), 134.q (2), 145.k (10), 160.3, 180.p (7), 181.p (3), 189.o (12). DELTRAN: 1.i (8), 9.j (7), 53.f (1), 67.b (1), 69.s (2), 70.u (2), 79.h (7),

80.a (4), 83.a (1), 87.f (3), 105.x (1), 108.c (2), 134.q (2), 145.k (10), 160.3, 178.e (4), 181.p (15), 189.o (12).

*Stem 42.*—ACCTRAN: 15.a (24), 17.e (4), 35.s (6), 48.m (12), 58.g (3), 63.y (24), 65.a (3), 70.a (12), 72.h (3), 78.a (3), 96.i (8), 101.b (1), 125.a (24), 133.s (18), 139.c (2), 148.m (12), 151.k (10), 152.m (12), 165.m (2), 184.s (6), 186.y (24), 378.G, 472.T, 553.T, 615.A, 628.T, 663.G, 783.T, 1000.G. DELTRAN: 2.a (5), 9.a (3), 15.a (24), 17.e (4), 35.s (18), 48.m (12), 53.o (2), 58.g (3), 63.y (24), 65.a (3), 70.a (3), 71.a (1), 72.h (5), 78.a (3), 84.c (1), 96.i (8), 101.b (1), 125.a (24), 133.s (18), 139.c (2), 148.m (12), 151.k (5), 152.m (12), 184.s (6), 378.G, 472.T, 507.A, 615.A, 628.T, 663.G, 783.T, 950.T, 1000.G.

*Stem 43.*—ACCTRAN: 4.u (20), 8.h (7), 9.y (4), 10.y (24), 17.m (12), 45.y (12), 46.a (8), 48.y (24), 58.f (2), 71.j (5), 87.i (5), 98.k (5), 100.h (3), 103.i (2), 122.q (1), 130.y (16), 142.r (9), 143.i (8), 148.f (5), 149.m (11), 151.f (5), 161.e (4), 167.e (4), 168.y (24), 175.y (16), 189.a (3), 357.A, 408.G, 605.T, 643.T, 680.C, 702.T, 703.T, 880.A, 1031.T, 1055.A, 1059.G, 1061.C, 1076.C, 1082.A, 1109.C, 1137.A, 1161.C, 1167.T, 1174.G. DELTRAN: 4.u (12), 8.h (7), 9.y (10), 10.y (24), 46.a (15), 47.p (3), 58.f (2), 65.e (1), 80.a (1), 84.c (1), 87.e (1), 100.h (5), 130.g (6), 142.r (9), 143.g (6), 149.i (8), 161.e (4), 168.y (24), 175.y (17), 184.s (6), 357.A, 408.G, 484.C, 605.T, 643.T, 680.C, 702.T, 703.T.

*Stem 44.*—ACCTRAN: 2.m (4), 3.a (12), 4.y (4), 8.y (17), 14.a (8), 42.y (20), 43.a (12), 47.y (9), 53.u (6), 58.m (7), 60.g (3), 75.e (1), 83.b (1), 88.c (1), 100.i (1), 142.u (3), 151.s (13), 167.m (8), 179.g (4), 182.g (6), 293.G, 553.T, 615.A, 744.A, 1200.0. DELTRAN: 53.u (8), 58.j (4), 60.g (2), 78.g (3), 151.g (1), 167.m (8), 293.G, 553.T, 615.A.

*Stem 45.*—ACCTRAN: 5.g (9), 60.l (5), 65.e (1), 69.y (2), 72.a (2), 78.y (18), 79.x (1), 87.m (4), 88.k (8), 98.b (9), 108.u (3), 122.r (1), 143.g (2), 145.u (8), 148.a (5), 149.i (4), 165.a (5), 167.y (12), 184.m (4), 702.C, 892.T. DELTRAN: 5.g (10), 17.m (12), 47.y (9), 60.l (5), 69.y (4), 71.j (1), 72.a (2), 78.y (18), 79.x (3), 87.m (8), 88.k (8), 89.x (1), 103.i (4), 108.u (2), 122.r (1), 130.y (18), 145.u (8), 165.a (5), 184.m (6).

*Stem 46.*—ACCTRAN: 5.w (2), 25.i (2), 34.i (8), 58.a (2), 65.d (1), 100.i (4), 103.a (2), 142.p (7), 147.m (12), 172.2, 742.T, 816.T, 1045.T, 1053.C, 1165.C. DELTRAN: 21.y (8), 89.m (4), 100.g (4), 142.m (4), 145.s (6), 147.k (10), 161.d (3), 172.2, 466.G, 742.T, 816.T, 1077.C, 1165.C.

*Stem 47.*—ACCTRAN: 2.e (4), 3.a (12), 4.a (8), 17.g (2), 31.c (2), 35.s (18), 70.c (2), 71.p (6), 78.b (1), 128.f (5), 142.s (3), 151.g (10), 152.a (8), 161.i (5), 169.p (15), 186.m (6), 189.u (17), 1046.T, 1134.C, 1169.T. DELTRAN: 4.e (4), 17.d (3), 27.g (6), 35.m (12), 65.d (1), 148.a (10), 151.i (4), 152.a (8), 161.g (3), 167.a (4), 189.u (20), 1045.T, 1046.T, 1134.C, 1169.T.

*Stem 48.*—ACCTRAN: 5.r (5), 44.f (5), 47.y (24), 53.b (3), 58.f (5), 73.s (6), 80.a (1), 88.a (1), 95.w (2), 96.b (1), 99.e (2), 147.k (2), 165.m (12), 186.u (8), 508.G, 646.C, 703.A, 952.A, 1047.T, 1076.A. DELTRAN: 5.s (2), 17.e (1), 44.e (4), 47.m (12), 58.e (1),

78.b (1), 80.b (1), 142.o (2), 165.i (8), 169.i (8), 186.s (6), 508.G, 646.C, 703.A.

*Stem 49.*—ACCTRAN: 25.a (8), 27.w (10), 30.f (5), 34.k (2), 42.c (2), 43.m (3), 59.d (3), 60.i (2), 63.d (3), 65.e (1), 72.e (1), 73.k (8), 75.a (2), 83.e (3), 86.b (1), 89.o (2), 95.u (2), 96.d (2), 100.b (7), 127.i (8), 134.a (5), 137.a (24), 142.u (2), 145.y (4), 169.y (9), 484.C, 998.C. DELTRAN: 27.m (6), 31.c (2), 44.f (1), 60.g (2), 73.r (3), 83.b (1), 89.o (2), 95.x (1), 96.b (1), 99.d (3), 100.c (4), 142.u (6), 161.i (2), 169.y (16), 484.C, 998.C.

*Stem 50.*—ACCTRAN: 2.g (2), 4.e (4), 5.s (1), 31.g (4), 44.g (1), 45.a (12), 46.y (8), 53.i (7), 64.q (13), 69.s (2), 80.b (1), 87.h (3), 88.g (6), 89.p (1), 94.b (1), 128.a (5), 142.w (2), 147.a (10), 151.a (6), 161.s (10), 165.y (12), 189.i (12), 193.y (24), 194.s (18), 269.T, 549.A, 628.T, 705.A. DELTRAN: 2.g (2), 17.g (2), 31.g (4), 44.g (1), 45.a (12), 46.y (9), 53.i (5), 64.q (12), 69.s (2), 70.c (2), 71.p (7), 87.h (3), 88.g (4), 89.p (1), 94.b (1), 142.w (2), 147.a (10), 151.a (8), 161.s (10), 165.y (16), 189.i (12), 193.y (24), 194.s (18).

*Stem 51.*—ACCTRAN: 17.m (6), 35.m (6), 72.a (3), 75.d (1), 78.c (1), 83.a (1), 89.e (8), 100.u (12), 103.d (3), 145.i (12), 162.3, 189.y (4), 501.C, 522.C, 661.C, 943.T. DELTRAN: 5.r (1), 17.m (8), 25.i (8), 43.j (3), 53.b (2), 71.p (7), 72.a (4), 78.c (1), 80.a (1), 88.a (2), 89.e (8), 100.u (14), 103.d (3), 128.f (5), 134.f (5), 145.i (10), 165.m (4), 189.y (4).

*Stem 52.*—ACCTRAN: 2.a (4), 15.q (8), 25.m (4), 34.a (8), 35.y (6), 43.e (5), 69.q (4), 80.l (10), 88.d (2), 99.a (2), 108.a (4), 190.y (24), 191.y (24), 269.T, 323.G, 331.T, 408.G, 681.G, 697.A, 698.C, 702.C, 784.C, 1052.G, 1053.T, 1082.C, 1085.C, 1137.C, 1146.C. DELTRAN: 2.a (4), 4.a (4), 5.w (2), 15.q (8), 25.m (12), 34.a (6), 35.y (12), 43.e (8), 53.e (1), 58.a (3), 64.d (1), 69.q (4), 70.c (2), 72.d (1), 73.y (4), 80.l (9), 88.d (1), 100.i (2), 108.a (4), 145.u (2), 147.m (2), 151.g (2), 190.y (24), 191.y (24).

*Stem 53.*—ACCTRAN: 2.q (8), 4.j (1), 5.y (2), 8.e (4), 60.c (4), 75.a (2), 125.s (6), 148.k (10), 151.u (4), 189.a (3), 475.T, 1045.C, 1057.C, 1137.A, 1161.A, 1184.G. DELTRAN: 3.m (12), 34.i (2), 46.q (1), 147.m (2), 151.u (8), 475.T.

*Stem 54.*—ACCTRAN: 2.s (2), 3.s (6), 8.y (20), 14.g (6), 17.a (4), 25.a (8), 27.y (12), 32.e (4), 34.u (12), 43.g (3), 45.s (6), 48.m (12), 64.a (3), 65.i (5), 69.v (1), 72.a (3), 87.b (3), 88.a (1), 100.g (2), 134.a (5), 144.k (10), 145.y (4), 147.y (12), 148.m (2), 151.y (4), 152.y (16), 176.a (24), 269.T, 336.C, 358.A, 368.T, 386.T, 389.G, 393.G, 439.C, 549.A, 557.C, 663.G, 698.C, 893.T, 900.T, 998.C. DELTRAN: 64.a (4), 65.i (6), 69.v (1), 72.a (4), 73.y (4), 87.b (3), 88.a (2), 125.s (6), 144.k (10), 145.y (6), 151.y (4), 152.y (16), 176.a (24).

*Stem 55.*—ACCTRAN: 25.m (4), 27.a (12), 43.m (3), 45.a (12), 46.y (8), 64.p (12), 65.c (1), 72.g (3), 73.r (7), 79.f (5), 84.c (2), 87.j (5), 88.g (5), 98.c (2), 100.o (6), 137.q (8), 145.s (2), 476.C, 477.T, 508.G, 646.C. DELTRAN: 17.e (4), 25.m (12), 46.y (8), 60.d (1), 75.a (3), 87.i (4), 88.g (4), 100.o (8), 137.q (8), 476.C, 477.T, 508.G, 646.C.

*Stem 56.*—ACCTRAN: 2.a (16), 4.g (3), 5.m (12), 17.y (20), 69.q (4), 80.c (1), 88.j (3), 89.e (8), 91.e

- (4), 100.q (2), 125.y (6), 133.i (8), 142.m (3), 145.m (6), 148.a (10), 220.G, 246.C, 378.G, 392.G, 397.C, 703.T, 821.T, 901.T. DELTRAN: 2.a (4), 4.g (2), 5.m (8), 8.e (4), 17.y (20), 53.e (1), 69.q (4), 71.j (1), 88.j (3), 89.e (8), 91.e (4), 100.q (2), 133.i (8), 145.m (6), 148.a (10).
- Stem 57.*—ACCTRAN: 15.a (16), 21.q (8), 44.i (8), 46.y (8), 58.j (5), 64.a (3), 71.c (7), 80.w (14), 99.a (2), 148.y (6), 191.y (24), 198.2, 206.1, 207.0, 269.T, 478., 680.A, 1054.T, 1055.A, 1176.T. DELTRAN: 46.q (1), 64.c (2), 71.h (1), 80.r (10), 100.a (2), 148.y (6), 206.1, 207.0, 269.T.
- Stem 58.*—ACCTRAN: 45.y (12), 58.k (1), 60.y (18), 72.e (1), 87.g (2), 89.p (3), 105.u (4), 121.i (8), 143.h (7), 151.a (16), 152.a (8), 186.s (10), 197.y (24), 615.A, 680.C, 1006.T. DELTRAN: 34.a (6), 45.y (12), 58.i (5), 60.x (19), 80.s (1), 89.j (1), 121.i (8), 151.a (12), 152.a (8), 197.y (24), 1006.T.
- Stem 59.*—ACCTRAN: 1.i (8), 17.y (20), 44.y (16), 69.g (14), 70.d (3), 72.f (1), 121.y (16), 122.y (24), 123.y (24), 143.m (5), 146.3, 160.3, 186.y (6), 189.f (5), 1134.C. DELTRAN: 17.y (24), 44.y (24), 46.y (8), 58.k (2), 60.y (1), 69.r (3), 70.d (3), 71.c (5), 73.w (2), 75.f (1), 89.m (3), 105.w (2), 121.y (16), 122.y (24), 123.y (24), 143.m (12), 146.3, 160.3, 186.y (6), 189.f (5).
- Stem 60.*—ACCTRAN: 4.a (8), 5.j (11), 13.g (6), 39.i (8), 40.f (5), 53.i (4), 58.p (5), 64.c (2), 65.a (1), 75.e (1), 116.d (3), 142.a (8), 143.q (4), 149.k (10), 162.3, 165.g (6). DELTRAN: 4.a (8), 5.m (8), 13.e (4), 53.h (4), 58.m (2), 65.a (1), 75.e (1), 142.a (8), 149.k (10), 162.3, 191.y (24), 478., 680.C, 1134.C.
- Stem 61.*—ACCTRAN: 1.a (8), 14.g (6), 34.g (6), 39.s (10), 49.m (12), 64.g (4), 69.a (6), 72.q (11), 73.w (1), 89.m (3), 143.y (8), 149.s (8), 174.y (24), 363.C, 385.G, 466.A, 475.T, 507.C, 615.G, 744.C, 850.A, 873.A, 892.A, 950.T, 1054.A, 1055.C, 1082.C, 1161.C, 1176.A. DELTRAN: 39.m (12), 69.f (12), 149.q (6), 174.y (24), 363.C, 475.T, 507.C, 744.C, 850.A, 892.A, 950.T, 1077.C, 1082.C, 1161.C.
- Stem 62.*—ACCTRAN: 5.i (1), 21.y (8), 27.a (12), 29.i (8), 53.h (1), 60.w (2), 67.c (2), 84.c (2), 87.i (2), 88.g (5), 103.f (3), 116.a (3), 484.C, 502.T, 1073.T, 1076.T, 1137.C, 1194.A. DELTRAN: 21.y (8), 58.o (2), 67.c (2), 72.m (8), 103.e (4), 143.q (4), 385.G, 484.C, 502.T, 873.A, 1194.A.
- Stem 63.*—ACCTRAN: 70.c (1), 84.e (2), 87.m (4), 88.h (1), 103.g (1), 105.y (4), 501.C, 645.G, 851.C, 1062.G, 1085.C, 1132.G, 1133.T. DELTRAN: 70.c (1), 72.q (4), 87.i (2), 88.h (5), 103.f (1), 143.y (8), 501.C, 645.G, 851.C.
- Stem 64.*—ACCTRAN: 58.o (1), 75.g (2), 84.g (2), 87.p (3), 149.y (6), 870.G. DELTRAN: 60.w (2), 75.g (2), 105.y (2), 165.g (6), 870.G.
- Stem 65.*—ACCTRAN: 13.a (6), 14.a (6), 29.a (8), 34.a (6), 39.a (18), 40.a (5), 49.a (12), 60.u (2), 80.y (2), 116.o (14), 128.i (8), 159.q (16), 165.y (18), 189.m (7), 475.C. DELTRAN: 13.a (4), 39.a (12), 69.a (5), 80.y (6), 116.o (14), 159.q (16), 165.y (18), 189.m (7).
- Stem 66.*—ACCTRAN: 5.a (8), 27.y (24), 53.f (2), 64.a (6), 65.c (2), 67.a (2), 70.f (3), 71.a (2), 72.r (1), 73.v (1), 84.a (6), 87.h (8), 88.f (2), 89.k (2), 103.a (6), 116.p (1), 149.q (8). DELTRAN: 53.f (2), 64.a (2), 67.a (2), 71.a (2), 73.v (1), 87.h (1), 88.f (2), 89.k (2), 103.a (5).
- Stem 67.*—ACCTRAN: 58.f (9), 60.y (4), 75.k (4), 87.c (5), 88.a (5), 128.a (8), 172.3, 184.u (4). DELTRAN: 5.a (12), 27.u (20), 58.f (9), 184.u (4), 475.C.
- Stem 68.*—ACCTRAN: 53.a (5), 65.a (2), 70.a (5), 72.p (2), 83.d (3), 135.i (8), 136.i (8), 165.q (8), 174.m (12), 184.q (4), 334.G, 336.C, 535.T, 645.A, 702.C, 705.T, 821.T, 866.G, 1006.C, 1008.A. DELTRAN: 53.a (5), 70.a (2), 83.d (3), 172.3, 174.m (12), 184.q (4).
- Stem 69.*—ACCTRAN: 16.i (8), 60.u (4), 73.w (1), 75.f (5), 83.e (1), 87.k (8), 88.m (12), 123.u (4), 159.m (4), 174.a (12), 184.m (4), 189.a (12). DELTRAN: 123.u (4), 159.m (4), 184.m (4), 189.a (12).
- Stem 70.*—ACCTRAN: 89.f (5), 116.u (5), 122.p (9), 135.a (8), 136.a (8), 149.s (2), 164.m (12), 165.a (16), 178.k (10), 180.i (8), 181.q (16), 184.k (2). DELTRAN: 16.i (8), 72.p (1), 89.f (5), 116.u (6), 122.p (9), 149.s (2), 165.a (24), 178.k (10), 181.q (16), 184.k (2).
- Stem 71.*—ACCTRAN: 70.a (2), 71.f (3), 73.m (10), 75.a (4), 122.u (4), 165.a (6), 172.0, 184.a (24), 189.a (5), 336.C, 478.A, 679.T, 702.T, 703.T, 742.G, 881.C, 900.T, 903.A. DELTRAN: 58.p (1), 70.a (2), 71.f (3), 73.m (10), 75.a (4), 122.u (4), 172.0, 189.a (5).
- Stem 72.*—ACCTRAN: 1.i (8), 29.m (4), 48.m (12), 53.g (1), 58.y (9), 67.e (2), 70.f (2), 83.c (2), 89.h (5), 105.r (3), 149.q (2), 165.m (6), 189.k (5), 224.T, 442.G, 466.G, 854.T. DELTRAN: 1.i (8), 13.g (2), 29.m (12), 48.m (12), 53.g (1), 58.y (10), 67.e (2), 70.f (2), 80.w (4), 83.c (2), 89.h (5), 105.r (5), 165.m (12), 189.k (5), 224.T, 442.G, 466.G, 854.T, 1137.C.
- Stem 73.*—ACCTRAN: 3.i (8), 5.m (3), 13.e (2), 14.i (2), 34.i (2), 35.m (12), 36.m (12), 39.y (6), 40.i (3), 42.m (12), 58.m (3), 71.a (2), 88.a (1), 103.a (2), 116.k (7), 127.g (6), 149.y (6), 164.i (8), 172.0, 189.a (5), 619.T, 644.G, 698.A, 870.T, 875.C, 900.T, 903.A, 1031.A, 1045.T, 1052.C, 1072.C, 1150.G. DELTRAN: 69.a (5), 71.a (2), 149.y (8), 189.a (5), 619.T, 644.G, 698.A, 870.T, 875.C, 900.T, 903.A.
- Stem 74.*—ACCTRAN: 64.a (6), 70.f (2), 72.u (4), 73.s (4), 80.y (2), 89.o (2), 108.g (6), 143.i (16), 178.i (8), 184.a (24), 336.C, 385.A, 502.A, 615.A, 703.T, 704.A, 705.T, 821.T, 865.G, 873.G, 893.T. DELTRAN: 64.a (2), 70.f (2), 72.u (16), 73.s (4), 80.y (6), 89.o (2), 108.g (6), 127.g (6), 143.i (4), 164.i (8), 178.i (8), 184.a (24).
- Stem 75.*—ACCTRAN: 13.m (6), 48.i (8), 58.q (1), 69.r (11), 72.a (5), 75.d (1), 80.e (18), 105.w (2), 332.C, 336.C, 389.G, 390.T, 431.T, 557.A, 605.T, 743.T, 805.A, 903.T, 1182.T. DELTRAN: 1.d (3), 13.m (8), 73.x (1), 80.i (10), 89.p (3), 332.C, 336.C, 389.G, 431.T, 605.T, 743.T, 805.A, 903.T, 1054.T, 1182.T.
- Stem 76.*—ACCTRAN: 3.d (3), 13.q (4), 40.m (7), 128.f (5), 165.a (6), 184.g (18), 190.y (24), 313.T, 328.C, 438.T, 538.T, 539.T, 662.G, 783.T, 819.G, 1036.T, 1071.G, 1073.A, 1096.T, 1109.C, 1137.A, 1145.T, 1147.T. DELTRAN: 5.j (3), 27.m (12), 103.c (2), 116.d (3), 313.T, 328.C, 438.T, 557.A, 615.A, 662.G, 783.T.
- Stem 77.*—ACCTRAN: 1.d (5), 17.q (8), 34.e (4), 39.a (8), 43.i (4), 58.m (4), 64.g (4), 69.j (8), 72.m (12), 80.i (4), 83.d (3), 84.d (3), 87.k (4), 88.q (15),

89.x (8), 95.w (2), 103.d (1), 164.m (12), 172.3, 189.y (19), 386.G, 390.C, 397.C, 464.G, 508.G, 620.G, 668.A, 900.T, 1198.1, 1199.0. DELTRAN: 17.q (8), 64.g (4), 69.j (8), 72.k (6), 75.d (1), 84.c (2), 87.i (2), 88.k (8), 143.q (4), 172.3, 189.y (19), 190.y (24).

*Stem 78.*—ACCTRAN: 1.a (3), 3.a (3), 17.m (4), 21.y (8), 31.y (24), 40.y (12), 58.f (7), 64.k (4), 65.f (5), 69.g (3), 71.f (3), 75.a (3), 79.e (4), 128.a (5), 148.q (8), 184.y (18). DELTRAN: 1.a (3), 13.q (4), 17.m (4), 21.y (8), 40.y (24), 58.f (7), 64.k (4), 65.f (5), 69.g (3), 71.f (3), 75.a (3), 79.e (4), 148.q (8).

*Stem 79.*—ACCTRAN: 1.m (4), 15.y (24), 27.a (12), 40.a (5), 53.w (14), 58.s (2), 64.a (2), 73.y (1), 79.b (1), 80.a (4), 86.b (1), 165.s (12), 167.q (8), 557.C, 646.A, 744.G, 820.T, 821.T, 1051.A, 1053.C, 1055.T, 1060.T, 1062.C, 1075.C, 1077.A, 1085.C, 1095.C, 1157.A, 1176.C. DELTRAN: 1.m (9), 15.i (8), 53.v (14), 58.s (6), 72.a (4), 79.b (1), 80.a (8), 165.s (18), 167.q (8), 390.T, 466.G, 557.C, 744.G, 821.T.

*Stem 80.*—ACCTRAN: 4.m (12), 5.g (3), 21.y (8), 39.m (4), 43.s (6), 48.a (8), 58.u (2), 65.e (4), 70.e (1), 71.m (10), 81.b (1), 88.k (9), 89.u (5), 91.e (4), 98.e (4), 103.a (2), 105.u (2), 116.e (1), 121.i (16), 143.s (2), 149.a (10), 159.q (16), 191.a (24), 269.C, 369.G, 502.A, 541.A, 646.C, 1006.C. DELTRAN: 4.m (12), 21.y (8), 39.m (12), 58.u (2), 71.h (5), 159.f (5), 191.a (24).

*Stem 81.*—ACCTRAN: 8.g (6), 31.m (12), 49.y (24), 79.g (5), 86.a (1), 108.e (4), 133.f (5), 143.u (2), 179.m (12). DELTRAN: 8.g (6), 15.y (16), 31.m (12), 49.y (24), 65.e (4), 71.m (5), 79.g (5), 88.k (8), 89.u (5), 98.e (4), 105.u (2), 108.e (4), 121.i (16), 133.f (5), 143.u (8), 159.q (11), 269.C, 369.G, 541.A, 615.A, 646.C, 1006.C.

*Stem 82.*—ACCTRAN: 15.i (16), 27.s (18), 34.g (6), 35.m (12), 45.s (6), 70.i (4), 87.q (10), 135.g (6), 169.q (16), 178.i (8), 180.g (6), 190.y (24). DELTRAN: 5.g (6), 34.g (6), 43.s (6), 70.i (5), 81.b (1), 86.b (1), 87.q (10), 91.e (4), 116.e (4), 135.g (6), 149.a (10), 169.q (16), 178.i (8), 180.g (6).

*Stem 83.*—ACCTRAN: 17.a (4), 29.i (8), 35.e (4), 37.i (8), 42.m (12), 43.u (8), 44.a (8), 52.i (8), 65.e (3), 71.h (5), 73.m (11), 75.y (19), 87.m (6), 88.h (6), 103.g (4), 111.x (23), 114.m (12), 124.m (12), 135.m (12), 174.m (12), 222.G, 224.T, 304.T, 310.A, 380.G, 478.A, 484.C, 502.T, 522.C, 553.T, 821.A, 861.A, 873.T, 1031.T, 1034.T, 1051.T, 1053.C, 1077.A, 1095.T, 1114.T, 1137.A, 1146.G, 1151.T, 1174.T. DELTRAN: 52.i (8), 73.s (2), 75.s (12), 111.x (23), 114.m (12), 135.i (8), 174.m (12), 304.T, 310.A, 380.G, 484.C, 502.T, 522.C, 861.A, 873.T.

*Stem 84.*—ACCTRAN: 4.a (8), 5.y (4), 8.q (16), 21.y (8), 27.y (12), 52.m (4), 58.i (2), 59.g (6), 72.a (4), 80.s (4), 89.j (6), 105.q (4), 111.y (1), 112.a (24), 143.a (7), 148.a (24), 163.1, 166.y (24), 174.y (12), 186.a (18), 362.T, 433.C, 501.C, 507.C, 615.C, 641.G, 643.G, 680.T, 785.T, 821.T, 892.T, 893.A. DELTRAN: 52.m (4), 59.g (6), 64.a (2), 72.a (4), 148.a (24), 166.y (24), 174.y (12), 186.a (18).

*Stem 85.*—ACCTRAN: 53.a (4), 65.h (3), 69.x (3), 70.g (6), 73.s (6), 75.s (6), 78.b (1), 84.c (2), 86.b (1), 121.a (8), 124.y (12), 135.i (4), 142.g (2), 144.d (3), 178.c (2), 185.y (24). DELTRAN: 4.a (8), 8.m (12),

21.y (8), 69.w (2), 70.g (6), 103.f (5), 121.d (5), 142.g (2), 178.c (2), 185.q (16).

*Stem 86.*—ACCTRAN: 52.s (6), 60.m (12), 70.r (11), 73.y (6), 80.v (3), 89.o (5), 110.y (24), 114.a (12), 118.y (24), 142.f (1), 178.o (12). DELTRAN: 27.y (24), 46.y (8), 52.s (6), 60.m (11), 70.r (11), 73.y (6), 80.v (3), 89.o (5), 110.y (24), 111.y (1), 112.a (24), 114.a (12), 142.f (1), 178.o (12).

*Stem 87.*—ACCTRAN: 11.e (4), 30.m (12), 53.d (1), 60.e (2), 65.a (1), 69.y (4), 71.a (2), 72.a (3), 86.y (24), 87.b (3), 89.a (12), 103.a (2), 133.y (24), 151.y (8), 152.m (4), 158.p (15), 176.f (19), 184.u (4), 323.G, 362.G, 378.G, 389.G, 390.T, 438.T, 466.A, 487.C, 501.C, 504.G, 508.G, 606.T, 614.A, 646.A, 698.A, 702.T, 784.C, 805.A, 893.T, 903.T. DELTRAN: 72.d (1), 86.x (23), 87.f (1), 89.g (2).

*Stem 88.*—ACCTRAN: 62.e (4), 70.d (3), 73.u (3), 75.m (7), 80.r (5), 83.e (4), 88.c (1), 125.h (17), 135.s (18), 136.s (18). DELTRAN: 11.e (4), 30.m (12), 44.i (8), 58.j (6), 62.e (4), 70.d (3), 75.m (6), 83.e (4), 125.h (17), 135.s (18), 136.s (18), 151.y (12), 152.m (4), 158.p (15), 184.u (4), 323.G, 378.G, 389.G, 390.T, 478., 487.C, 501.C, 504.G, 508.G, 606.T, 614.A, 646.A, 680.A, 698.A, 784.C, 805.A, 893.T, 903.T.

*Stem 89.*—ACCTRAN: 7.i (8), 34.y (8), 36.m (12), 40.g (2), 48.y (24), 51.y (24), 55.2, 75.q (9), 86.x (23), 87.u (16), 89.i (4), 96.y (24), 99.y (22), 103.e (2), 107.q (16), 120.u (20), 125.a (24), 132.m (12), 133.y (24), 139.q (16), 149.y (24), 151.y (8), 154.m (12), 163.1, 332.C, 389.T, 393.G, 442.T, 466.A, 634.T, 703.A, 821.T, 1046.A, 1077.A, 1108.A, 1137.A, 1169.T, 1194.A. DELTRAN: 15.m (12), 34.y (18), 48.y (24), 51.y (24), 55.2, 58.e (1), 75.q (10), 86.r (17), 87.t (9), 96.y (24), 99.w (22), 100.a (2), 103.e (4), 107.q (16), 120.u (20), 125.a (24), 132.i (8), 133.y (24), 139.q (16), 149.y (24), 151.y (12), 152.y (16), 154.m (12), 163.1.

*Stem 90.*—ACCTRAN: 3.g (6), 5.m (8), 26.y (24), 43.a (12), 46.m (4), 64.a (3), 69.y (4), 71.i (1), 72.a (3), 73.t (1), 89.f (3), 94.d (3), 95.v (3), 107.u (4), 148.y (6), 183.q (16), 184.a (24). DELTRAN: 26.y (24), 43.g (6), 64.a (4), 69.y (8), 72.a (4), 107.s (2), 148.y (6), 160.1, 184.a (24), 198.4.

*Stem 91.*—ACCTRAN: 4.y (16), 15.m (4), 21.a (24), 25.m (12), 40.a (6), 88.e (1), 139.y (8), 176.i (16), 183.y (8). DELTRAN: 3.g (6), 4.y (16), 21.a (16), 25.m (12), 40.a (3), 43.a (6), 95.x (1), 139.u (4), 183.y (24), 381.T, 389.T, 393.G, 442.T, 634.T, 787., 821.T.

*Stem 92.*—ACCTRAN: 5.y (12), 7.m (4), 11.g (6), 13.g (6), 15.a (12), 29.y (24), 31.s (18), 32.m (12), 36.a (12), 45.s (6), 58.i (4), 65.a (1), 132.i (4), 172.0, 213.T, 328.C, 369.G, 380.G, 431.T, 467.G, 475.T, 489.T, 498.C, 499.T, 680.C, 741.C, 783.T. DELTRAN: 58.i (4), 65.a (1), 86.x (6), 88.e (2), 107.u (2), 172.0.

*Stem 93.*—ACCTRAN: 3.m (6), 5.g (6), 7.a (8), 8.m (12), 18.s (18), 25.y (12), 27.a (6), 34.m (12), 46.y (12), 65.d (2), 86.d (20), 120.r (3), 132.y (12), 175.m (12), 197.y (24), 215.A, 265.C, 269.A, 336.C, 378.G, 466.T, 615.T, 703.T, 782.A, 819.G, 853.G, 862.C, 1006.T. DELTRAN: 65.d (2), 86.d (14), 94.d (3), 95.v (2), 120.r (3), 132.y (16), 139.y (4), 175.m (12), 197.y (24).

*Stem 94.*—ACCTRAN: 27.m (6), 30.y (24), 42.g (6), 45.a (12), 120.y (4), 142.g (2), 164.s (18). DEL-

TRAN: 5.m (8), 15.q (4), 21.y (8), 27.m (12), 30.y (24), 40.g (3), 42.g (6), 45.a (12), 120.y (4).

*Stem 95.*—ACCTRAN: 2.m (12), 3.y (18), 5.i (4), 8.i (8), 27.y (12), 36.a (12), 43.g (6), 87.t (1), 94.e (1), 107.y (4), 139.k (6), 142.a (6), 151.m (12), 164.y (6), 183.a (16). DELTRAN: 80.i (1), 94.e (4), 95.v (3), 107.y (6), 132.m (4), 139.k (6), 142.a (8), 151.m (12), 164.y (24).

*Stem 96.*—ACCTRAN: 1.y (24), 3.a (6), 4.a (8), 7.a (8), 15.y (8), 28.m (12), 32.y (24), 35.y (24), 36.y (12), 40.y (18), 46.i (12), 59.e (4), 80.g (2), 87.w (2), 94.a (3), 95.y (3), 107.s (2), 132.g (6), 168.i (8), 172.0. DELTRAN: 59.e (4), 80.g (1), 87.w (3), 89.f (3), 132.g (2), 168.i (8), 172.0, 183.q (16).

*Stem 97.*—ACCTRAN: 4.s (10), 5.y (4), 26.y (24), 47.m (12), 50.y (12), 57.c (2), 62.k (10), 65.f (4), 67.d (3), 69.p (5), 71.o (5), 72.k (7), 73.t (1), 83.d (3), 87.a (4), 89.q (4), 100.m (12), 102.c (2), 113.d (3), 262.C, 323.G, 357.C, 368.T, 373.A, 473.T, 484.C, 507.C, 513.T, 545.G, 619.T, 784.A, 852.T, 872.G, 879.T, 885.T, 950.T, 952.A, 1038.T, 1050.C, 1053.C, 1094.T, 1134.T, 1165.C, 1175.G, 1176.T, 1196.1, 1200.1. DELTRAN: 4.m (4), 26.m (12), 34.q (10), 64.k (2), 71.o (6), 83.c (2), 87.a (10), 89.q (8), 100.e (2), 152.m (4), 160.1, 262.C, 323.G, 332.A, 368.T, 373.A, 381.T, 397.C, 466.G, 473.T, 475.T, 484.C, 507.C, 513.T, 619.T, 784.A, 787., 852.T, 872.G, 879.T, 885.T, 952.A.

*Stem 98.*—ACCTRAN: 40.g (2), 44.m (12), 46.m (4), 53.b (1), 58.q (12), 71.p (1), 75.e (3), 80.o (6), 84.i (3), 88.i (3), 89.t (3), 108.c (2), 151.y (8), 172.0, 186.q (8), 222.G, 442.T, 489.T, 705.A, 706.T, 862.A. DELTRAN: 40.g (3), 44.m (12), 47.m (12), 50.y (12), 53.b (1), 58.q (13), 71.p (1), 75.e (2), 80.o (7), 88.i (2), 89.t (3), 103.c (2), 108.c (2), 151.y (12), 186.q (8), 222.G, 442.T, 489.T, 705.A, 706.T, 862.A.

*Stem 99.*—ACCTRAN: 8.m (12), 13.m (12), 21.a (8), 33.y (24), 34.g (10), 42.e (4), 43.u (8), 50.a (12), 63.v (21), 64.y (9), 65.a (1), 69.y (4), 71.a (8), 72.a (3), 79.r (17), 80.a (4), 81.r (17), 84.y (8), 85.y (24), 87.m (2), 124.y (24), 126.y (24), 141.y (24), 152.a (3), 160.2, 178.u (20), 190.y (24), 212.C, 269.T, 304.T, 331.A, 334.C, 358.A, 360.G, 380.G, 381.C, 386.G, 387.A, 388.C, 389.T, 393.C, 396.C, 437.G, 438.T, 475.A, 481.A, 501.A, 604.T, 620.T, 643.T, 644.T, 681.G, 698.C, 702.C, 748., 784.C, 785.T, 795.T, 837.T, 861.T. DELTRAN: 8.m (12), 13.m (12), 33.y (24), 43.u (8), 50.a (12), 63.v (21), 69.y (9), 71.a (8), 72.a (5), 73.u (1), 79.r (17), 80.a (7), 81.r (17), 84.y (8), 85.y (24), 87.m (2), 100.a (2), 124.y (24), 126.y (24), 141.y (24), 178.u (20), 189.m (12), 190.y (24).

*Stem 100.*—ACCTRAN: 2.i (8), 3.q (12), 5.i (4), 7.y (12), 26.y (24), 34.y (8), 54.y (24), 56.y (24), 59.w (22), 61.d (3), 67.c (2), 70.i (8), 73.c (11), 75.k (3), 96.x (23), 99.h (7), 125.a (24), 128.c (2), 147.u (12), 184.v (3), 186.a (24), 336.C, 385.G, 466.T, 487.A, 490.C, 557.T, 571.C, 572.T, 783.T, 792.C, 816.C, 893.G, 903.T, 1017.T. DELTRAN: 2.i (8), 3.q (16), 5.i (4), 7.y (24), 24.y (8), 26.y (24), 42.a (4), 54.y (24), 56.y (24), 59.w (22), 61.d (3), 65.b (1), 67.c (2), 70.i (8), 73.c (11), 75.k (4), 96.x (23), 99.h (7), 125.a (24), 128.c (2), 133.w (7), 147.u (20), 152.d (3), 184.v (3), 186.a (24), 336.C, 369.G, 381.T, 385.G, 487.A, 490.C,

508.G, 557.T, 571.C, 572.T, 641.G, 643.A, 744.A, 783.T, 784.T, 792.C, 816.C, 903.T, 1017.T.

*Stem 101.*—ACCTRAN: 20.y (24), 42.q (12), 43.i (4), 45.m (12), 71.f (3), 80.c (2), 83.b (1), 87.p (5), 88.i (3), 126.p (15), 143.f (5), 149.f (5), 167.a (12), 333.T, 362.T, 487.C, 530.T, 646.C, 702.T, 705.A, 816.T, 900.T. DELTRAN: 20.y (24), 42.q (12), 71.f (3), 80.c (5), 87.p (5), 88.i (2), 126.p (15), 131.v (21), 135.y (5), 136.m (12), 143.f (5), 147.i (8), 149.f (5), 362.T, 530.T, 646.C, 702.T, 704.T, 705.A, 816.T.

*Stem 102.*—ACCTRAN: 30.g (6), 40.g (2), 42.a (4), 43.i (4), 47.y (24), 50.g (6), 65.f (5), 67.u (18), 71.x (3), 73.e (9), 75.m (6), 78.h (4), 80.e (3), 83.v (21), 85.u (20), 90.d (1), 96.m (12), 97.c (2), 101.d (3), 119.b (1), 127.d (3), 138.y (20), 148.y (4), 151.u (20), 176.w (2), 187.y (24), 317.A, 318.T, 393.T, 475.T, 534.T, 545.G, 605.T, 615.A, 641.G, 646.C, 783.T, 892.T, 1006.T, 1049.T, 1064.T, 1147.A, 1160.C, 1196.1, 1201.1. DELTRAN: 11.e (4), 47.q (16), 55.1, 67.g (6), 71.l (3), 73.e (6), 75.h (1), 77.y (14), 80.g (2), 83.s (16), 90.b (1), 97.c (2), 101.c (2), 105.w (22), 106.1, 109.c (2), 115.y (24), 142.y (7), 148.y (6), 151.h (7), 179.g (6), 187.y (24), 318.T, 393.T, 475.T, 545.G, 605.T, 641.G, 744.A, 783.T, 892.T, 1196.1, 1201.1.

*Stem 103.*—ACCTRAN: 11.y (20), 12.m (12), 14.m (2), 15.y (24), 25.g (6), 32.e (4), 40.i (2), 45.e (4), 50.a (6), 51.y (24), 64.c (1), 65.q (11), 67.y (4), 69.a (2), 71.y (1), 80.a (4), 85.x (3), 88.x (7), 90.t (16), 94.y (21), 96.x (11), 101.s (15), 107.x (23), 114.y (24), 118.y (24), 119.y (23), 127.p (12), 135.a (15), 136.a (12), 146.2, 151.y (4), 163.2, 176.a (22), 317.C, 325.T, 336.C, 436.A, 470.C, 489.C, 490.C, 501.G, 528.G, 541.G, 542.C, 547.C, 620.A, 628.T, 643.C, 724.C, 893.T, 894.T, 903.T, 920.G, 934.C. DELTRAN: 8.m (12), 11.y (20), 14.m (12), 27.g (2), 38.a (24), 40.i (8), 45.e (4), 50.a (6), 51.y (24), 65.q (16), 67.w (16), 71.y (13), 80.a (6), 85.h (7), 90.t (18), 94.s (15), 96.s (18), 101.s (16), 107.u (20), 109.y (22), 111.l (5), 118.y (24), 119.y (24), 125.a (24), 127.p (15), 137.a (12), 146.2, 151.k (3), 163.2, 224.C, 317.C, 325.T, 336.C, 362.T, 436.A, 628.T, 643.C, 646.C, 724.C, 893.T, 894.T, 920.G, 1046.C, 1064.T, 1082.A, 1147.A, 1160.C.

*Stem 104.*—ACCTRAN: 8.s (6), 14.y (12), 18.i (4), 37.a (6), 40.m (4), 43.y (16), 45.m (8), 58.f (5), 60.c (2), 65.r (1), 75.h (5), 87.h (3), 90.u (1), 111.y (13), 335.C, 557.T, 645.G, 703.T, 738.C, 739.C, 740.A, 743.G, 784.A, 785.G, 789.G, 790.G, 815.T, 851.A, 861.T, 890.C, 895.G, 900.C, 1031.T, 1033.C, 1034.T, 1038.T, 1045.C, 1047.T, 1049.C, 1085.C, 1088.C, 1104.G, 1108.T, 1114.T, 1134.T, 1137.T, 1175.G, 1176.A, 1185.G. DELTRAN: 8.s (6), 14.y (12), 37.a (6), 40.m (4), 43.y (16), 47.y (8), 65.r (1), 83.v (3), 111.y (13), 138.y (20), 470.C, 489.C, 501.G, 522.C, 528.G, 534.T, 541.G, 547.C, 557.T, 620.A, 738.C, 739.C, 740.A, 784.A, 789.G, 790.G, 851.A, 890.C, 1006.T.

*Stem 105.*—ACCTRAN: 8.y (6), 12.a (12), 25.a (6), 30.a (6), 32.a (4), 34.a (6), 64.p (13), 65.y (7), 73.a (4), 83.x (2), 84.p (8), 85.h (16), 88.y (1), 94.s (6), 95.h (7), 96.y (1), 97.a (2), 101.u (2), 105.u (2), 114.a (24), 135.y (24), 136.y (24), 152.m (12), 163.4, 176.y (24), 318.C, 497.T, 645.T, 783.C, 901.T. DELTRAN: 15.y (24), 34.a (6), 64.p (13), 65.x (6), 67.y (2), 73.a (4), 83.x (2), 84.p (1), 88.y (1), 95.h (7), 96.x (5), 97.a

(2), 101.u (2), 105.u (2), 107.x (3), 135.y (9), 136.y (24), 151.y (14), 152.m (12), 163.4, 176.y (2), 179.y (18), 184.y (24).

*Stem 106*.—ACCTRAN: 27.a (6), 45.a (12), 58.a (5), 64.q (1), 78.c (5), 80.c (2), 84.g (9), 85.f (2), 87.y (17), 90.k (10), 99.b (1), 101.x (3), 103.c (2), 105.s (2), 127.k (5), 145.f (5), 189.f (5). DELTRAN: 45.a (4), 60.b (1), 64.q (1), 84.g (9), 85.f (2), 87.y (14), 90.m (7), 101.x (3), 167.m (12).

*Stem 107*.—ACCTRAN: 8.a (24), 64.y (8), 84.d (3), 85.b (4), 95.j (2), 96.x (1), 163.0, 167.y (12). DELTRAN: 64.y (8), 65.y (1), 84.d (3), 85.b (4), 95.j (2),

163.0, 318.C, 497.T, 615.A, 645.T, 783.C, 901.T, 934.C.

*Stem 108*.—ACCTRAN: 7.m (12), 18.r (5), 27.a (6), 44.k (10), 64.e (1), 73.d (1), 78.i (1), 83.w (1), 92.c (2), 95.q (16), 111.e (7), 135.q (1), 136.q (4), 137.p (15), 149.e (4), 158.y (24), 186.u (4), 303.A, 362.C, 502.A, 508.G, 522.T, 661.C, 741.A, 742.T, 784.G. DELTRAN: 7.m (12), 18.r (5), 27.a (4), 44.k (10), 47.y (8), 64.e (2), 69.c (2), 73.d (1), 75.m (5), 78.i (5), 83.w (4), 88.q (7), 92.c (2), 95.q (16), 111.e (2), 135.q (1), 136.q (16), 137.p (3), 138.y (20), 149.e (4), 158.y (24), 303.A, 317.A, 502.A, 508.G, 661.C, 784.G, 1006.T.