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an attempt for a genetic interpretation of speciation. *Zeit. Zool. Syst. Evol.* 20:187–197.

WINOGRAD, I. J., B. J. SZABO, T. B. COPLIN, AND A. C. RIGGS. 1988. A 250,00-year climatic record from Great Basin vein calcite: implications for Milankovitch theory. *Science* 242:1275–1280.

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## Phylogenetic Relationships of Phrynosomatid Lizards and Monophyly of the *Sceloporus* Group

JOHN J. WIENS

**The monophyly of the *Sceloporus* group (*Sator*, *Sceloporus*, *Urosaurus*, *Uta*) was reevaluated through a phylogenetic analysis of the iguanian lizard family Phrynosomatidae. Relationships and monophyly of eight phrynosomatid taxa were assessed using 45 characters describing variation in osteology, squamation, soft anatomy, coloration, karyotype, and behavior. Phylogenetic analysis yielded a single tree [length = 66 steps, consistency index = 0.803 (0.772)] that supports the monophyly of the *Sceloporus* group and shows the relationships: ((*Phrynosoma* + sand lizards) + (*Petrosaurus* + (*Uta* + (*Urosaurus* + (*Sator* + (*Sc. merriami* + all other *Sceloporus*)))))).**

THE *Sceloporus* group, consisting of *Sator*, *Sceloporus*, *Urosaurus*, and *Uta* (Etheridge and de Queiroz, 1988), contains many of the more conspicuous and frequently studied species of North American phrynosomatid lizards (formerly sceloporine iguanids; Frost and Etheridge, 1989). The genus *Uta* consists of six species (Ballinger and Tinkle, 1972) from the arid and semiarid regions of the western United States and Mexico. The 11 species of *Urosaurus* (Savage, 1958, plus *Urosaurus lahtelai* Rau and Loomis, 1977) range from southern Wyoming to southern Mexico. *Sceloporus* contains approximately 75 species (Sites et al., 1992) ranging from Canada to Panama. The enigmatic genus *Sator*, considered a synonym of *Sceloporus* by Wyles and Gorman (1978), de Queiroz (1982), and Frost and Etheridge (1989), contains two species from the islands of Cerralvo, Santa Cruz, and San Diego in the Gulf of California.

The *Sceloporus* group first was named by Etheridge and de Queiroz (1988) in their phylogenetic study of relationships within the "Iguanidae." The four genera comprising this taxon have long been regarded as forming a natural group (e.g., Etheridge, 1964; Larsen and Tanner, 1975; Paull et al., 1976) because they possess hooked processes on the clavicles, a feature unique among phrynosomatids (Etheridge, 1964). However, in a recent cladistic analysis of iguanian relationships, Frost and Etheridge

(1989) questioned the monophyly of the *Sceloporus* group. Frost and Etheridge (1989) presented three equally parsimonious topologies for relationships within the Phrynosomatidae; the *Sceloporus* group was paraphyletic in two of these trees (their Topologies 2 and 3), whereas its monophyly was unsupported in a third (Topology 1). Although Frost and Etheridge (1989) mentioned the presence of a hooked clavicle as a possible synapomorphy of the group (it was excluded from their computer analyses because of characterization problems), none of these authors presented a parsimony analysis of phrynosomatid relationships based on all the evidence that they discussed. Herein, the evidence for the monophyly of the *Sceloporus* group is reevaluated.

### METHODS

To test the monophyly of the *Sceloporus* group, a phylogenetic analysis of the Phrynosomatidae was performed. Most characters were initially taken from the literature, and citations and descriptions are given in Appendix I. Most of these characters were reexamined on alcohol-preserved, dry-skeletal, and cleared-and-stained specimens (see Material Examined). Taxa examined included representatives of 76 of the approximately 94 species in the *Sceloporus* group. Cleared-and-stained specimens were prepared

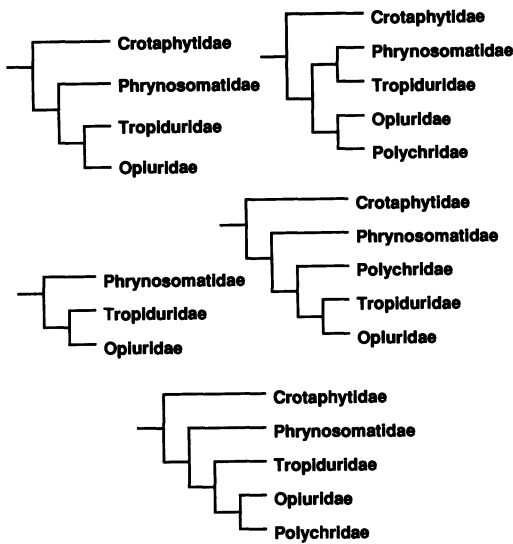


Fig. 1. Possible outgroup relationships of the Phrynosomatidae (from Frost and Etheridge, 1989; their fig. 7).

following a modified version of the technique of Dingerkus and Uhler (1977). Some characters described in the literature were not corroborated by my observations or varied in a way that could not be coded into discrete character states. These characters were not used but are discussed in Appendix I. A total of 23 characters was added to 22 taken or modified from Etheridge and de Queiroz (1988) and/or Frost and Etheridge (1989).

Characters were polarized using outgroup comparison. A "hypothetical ancestor" taxon that summarized the polarity decisions for each character was then reconstructed and used to root the basic tree of ingroup relationships. Frost and Etheridge (1989) discovered five equally parsimonious topologies for the immediate outgroups to the Phrynosomatidae (Fig. 1). For each character, the algorithm of Maddison et al. (1984) was applied to all five topologies and to each of the intrafamilial topologies from Frost and Etheridge (1989). Polarity decisions were considered unequivocal only if they were consistent across all the possible inter- and intrafamilial outgroup topologies. Because of this conservative approach, nearly a third of the characters were left as initially unpolarized. These characters, therefore, had little effect on the rooting of the resulting tree. The monophyly of the ingroup was not questioned because the analysis of Frost and Etheridge (1989) showed the Phrynosomatidae to be united by at least seven synapomorphies [pterygoid teeth lost, scleral ossicle 8 reduced (de Queiroz, 1982),

clavicular flange reduced, posterior process of interclavicle invested by sternum posteriorly, sink-trap nasal apparatus, enlarged posterior lobe of hemipenis, m. retractor lateralis posterior completely divided (Arnold, 1984)].

Eight taxa of Phrynosomatidae were selected as OTUs (operational taxonomic units). Etheridge and de Queiroz (1988) summarized evidence for the monophyly of the "sand lizard" clade (*Callisaurus*, *Cophosaurus*, *Holbrookia*, *Uma*) and all the genera of phrynosomatids except *Sceloporus* (e.g., *Petrosaurus*, *Phrynosoma*, *Sator*, *Urosaurus*, *Uta*). Some of their hypothesized synapomorphies later were rejected, but initially the monophyly of these six taxa was assumed. Additional apomorphies for these genera also were evaluated and included in the analysis, but see Etheridge and de Queiroz (1988), de Queiroz (1989), and Montanucci (1987) for a more extensive list of characters corroborating the monophyly of *Phrynosoma* and/or the sand lizard clade.

Although no unequivocal evidence could be found a priori to suggest that *Sceloporus* was monophyletic, one presumptive synapomorphy unites *Sceloporus* exclusive of *Sceloporus merriami* and *Sator*—the presence of pointed, overlapping dorsal scales. The absence of a second (posterior) series of circumorbital scales also might support this group, but these scales are also absent in some *S. merriami*. Based on this evidence, *Sator*, *S. merriami*, and a clade including all other *Sceloporus* were treated as three separate OTUs. Coding these three taxa separately also allowed limited testing of the monophyly of *Sceloporus* relative to *Sator*.

Because a number of characters varied within *Sceloporus*, certain assumptions were made about the phylogeny of the genus to help determine the ancestral states. Although no rigorous phylogenetic hypothesis for *Sceloporus* is currently available, *S. couchii* and *S. parvus* possess a suite of primitive character states that support their placement as "basal" members of the genus, along with *S. merriami* (Wiens, unpubl.). Characters that varied within *Sceloporus* were optimized by considering these two species to be in an unresolved trichotomy with a clade including all other *Sceloporus* exclusive of *S. merriami*. The phylogeny of sand lizards proposed by Etheridge and de Queiroz (1988) and de Queiroz (1989) and the phylogeny of *Phrynosoma* from Montanucci (1987) were used to help determine primitive character states in these taxa. Variation within terminal taxa was optimized using the algorithm of Fitch (1971) for dichotomous nodes and Maddison (1989; unordered option) for unresolved nodes. Thus, if an OTU con-

tained two species or clades, one with the states “a” and “b” and the other with “b,” the taxon would be optimized and coded as having state “b” ancestrally.

Phylogenetic analysis was performed using version 3.0q of David Swofford’s PAUP (Phylogenetic Analysis Using Parsimony) program. The lengths of all possible topologies were evaluated to guarantee finding the shortest tree using the “Exhaustive Search” option. To minimize a priori assumptions about character evolution, all multistate characters were analyzed as unordered transformation series (a change to or between any of the derived states equally likely), and all characters were weighted equally (weight = 1.0). Character states were optimized using both ACCTRAN (accelerated transformation; favoring reversals over parallelisms/convergences and placement of unordered multistate characters “lower” on a tree; Farris, 1970; Swofford and Maddison, 1987) and DELTRAN (delayed transformation; favoring convergences/parallelisms and placement of multistate character transformations “higher” on a tree; Swofford and Maddison, 1987) optimization routines, to avoid considering apomorphies of uncertain placement as support for a given stem. When a plesiomorphic condition for an OTU could not be determined a priori (e.g., could not be optimized unambiguously), a taxon with two states was coded as being “polymorphic.” However, transformations hypothesized to occur within an OTU were not included in calculations of the tree length and consistency index. Logical impossibilities (e.g., condition of frontal scales in taxa that lack them), taxa with more than three character states, taxa for which data were unavailable, and other uncertainties were coded as “?” (unknown). Manipulation of the data matrix and alternative topologies was done using the MacClade program (version 2.97.9) by W. Maddison and D. Maddison.

## RESULTS AND DISCUSSION

Phylogenetic analysis of 45 characters (Appendix I; Table 1) yielded a single shortest tree (Fig. 2) with a length of 66 steps and a consistency index (Kluge and Farris, 1969) of 0.803 (or 0.772 excluding ingroup synapomorphies and a posteriori autapomorphic character states). This tree confirms the monophyly of the *Sceloporus* group and supports the monophyly of all of its constituent genera. The support for each internode is discussed below. Unless noted otherwise, only the character states that appear on a stem using both ACCTRAN and DEL-

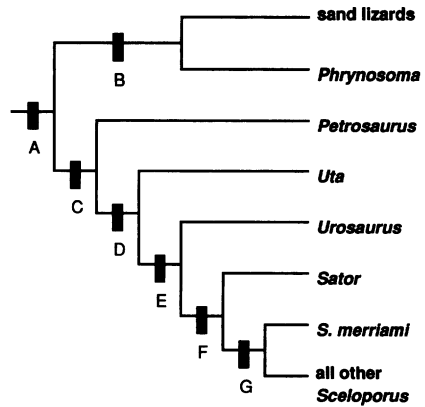


Fig. 2. Hypothesized phylogeny of the Phrynosomatidae [length = 66 steps, consistency index = 0.803 (0.772 excluding uninformative characters)]. See Appendix II for a listing of apomorphies for each stem.

TRAN optimization routines are considered to be unambiguous support for that group. A more complete listing of possible character state assignments to each stem is given in Appendix II.

Two synapomorphies provide additional evidence for the monophyly of the Phrynosomatidae (Internode A): 37.1 (peroneal innervation of the dorsal shank muscle, reversed at Internode E) and 42.1 (diploid chromosome number 34). Nine synapomorphies unite *Phrynosoma* and the sand lizards (Internode B): 6.1 (postfrontal absent), 7.1 (lacrimal absent), 8.1 (scleral ossicle 6 reduced), 10.1 (median process of interclavicle reduced), 27.1 (rostral scale narrow), 28.1 (mental scale reduced), 29.2 (first sublabial posterior to second infralabial), 35.1 (femoral pore row discontinuous), and 38.1 (anterior fibers of retractor lateralis anterior reflected outwards or posteriorly). Etheridge and de Queiroz (1988) considered state 2.1 (anterolateral processes of frontals covered by nasals) to be a synapomorphy of this clade, but neither this character state nor 2.0 can be placed unambiguously on any stem of the tree. Four synapomorphies support the uncontested monophyly of *Phrynosoma* (5.1—skull rugosity acquired, 11.2—sternal fontanelle wide posteriorly, 12.2—two sternal ribs, and 31.2—dorsals heterogeneous), and two synapomorphies diagnose the sand lizard clade [40.2—dark ventrolateral stripe(s) and 41.1—reddish female breeding coloration]. A more extensive list of synapomorphies for the Phrynosomatidae is given in Frost and Etheridge (1989), for *Phrynosoma* in Etheridge and de Queiroz (1988) and Montanucci (1987), and for the sand lizard clade in Etheridge and de Queiroz (1988) and de Queiroz (1989).

TABLE 1. DATA MATRIX FOR PHYLOGENETIC ANALYSIS OF PHRYNOSOMATID LIZARDS. Characters 3, 6, 12, 13, 19, 23, 24, 26, 30-33, 36, and 44 are unpolarized. For all other characters, "0" represents the hypothesized plesiomorphic state. All characters were analyzed as unordered. See Appendix I for description of characters. HYPANC = reconstructed hypothetical ancestor of the Phrynosomatidae.

Taxon	Character																						
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
Crotaphytidae	?	0	1	0	0,1	1	0	0	0	0	?	1	0	0	0	0	0	0	?	0	0	?	?
Opluridae	?	0	0	0,1	0	1	0	0	0	0	?	0,1	?	0	0	?	?	0	?	0	0	0	1
Polychridae	0	0	1	0	0,1	0	0	0	0	0	?	?	0,1	0,1	1	0	0	0	?	0	0	?	?
Tropiduridae	0	0,1	0,1	0	0	0	0	0	0	0	0	0	0,1	0	0,1	0	0	0	?	0	0	0	2
HYPANC	0	0	0,1	0	0	0,1	0	0	0	0	0	0,1	0	0	0	0	0	0	?	0	0	0	1,2
sand lizards	?	1	0	1	0	1	1	1	0	1	1	0	0	0	0	0	0	0,1	?	0,1	0	?	?
<i>Phrynosoma</i>	?	1	0	0	1	0	1	1	0	1	2	0	0	0	1	0	0	?	0	?	0	?	?
<i>Petrosaurus</i>	0	0	0,1	1	0	0	0	1	0	0	1	0	0	0	1	1	1	1	0	1	0	0	0
<i>Uta</i>	0	1	0	1	0	0	0	0	0	0	0	0	0,1	1	1	0	0	1	0	1	1	0	0
<i>Urosaurus</i>	1	0,1	0	1	0	0	0	0	0	1	0,2	1	1	1	1	0	0	1	0,1	1	1	1	2
<i>Sator</i>	0	0	1	0	1	0	0	0	0	1	0	1	1	1	1	0	0	1	1	1	1	0	0
<i>S. merriami</i>	0	1	0	1	0	0	0	?	0	0	1	0	1	1	0	0	0	1	0	1	1	0	1
other <i>Sceloporus</i>	0,1	0,1	0	1	0	0	0	0	0	0	1	0	1	1	0,1	0	0	1	0	1	0	1	1

Taxon	Character																						
	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	
Crotaphytidae	?	0	0	0	0	?	0	0	?	?	?	0	0	0	0	0	0	1	0	0	?	0	
Opluridae	1	0	0	0	0	0	0	1	0,1	?	?	?	0	0	0	0	0	0	0	0	0	?	0
Polychridae	?	0	0	0	?	0	0,1	0	?	?	0	0,1	0,1	0	0	0	0	0	0	0	0	?	1
Tropiduridae	0	0,1	1	0	0	0	1	0,1	1	?	?	?	1	0,1	0	0	0	0	0	0	0	?	0
HYPANC	0,1	0	0,1	0	0	0	0,1	0,1	0,1	?	?	0	0	0,1	0	0	0	0	0	0	0	?	0
sand lizards	0	0	0,2	1	1	2	0	0	?	?	?	0	1	0	1	1	0,1	2	1	1	1	?	0
<i>Phrynosoma</i>	0	0	0	1	1	2	?	2	?	?	0,1	1	0	1	1	0	0	0	1	1	?	?	0
<i>Petrosaurus</i>	1	0	2	0	0	0	0	0	?	?	?	0	0	1	0	0,1	0	1	1	0	0	?	0
<i>Uta</i>	0	1	2	0	0	1	0	1	0	0	0	0	0	1	0	1	0	1	0	1	1	0	0
<i>Urosaurus</i>	0	1	2	0	0	0	0	1	0	0	1	0	0	1	0	0	1	0	1	1	1	0	0
<i>Sator</i>	0	1	2	0	0	0	1	1	0	0	0	0	1	0	?	1	0	0	1	0	1	1	1
<i>S. merriami</i>	0	1	1,2	0	0	0,1	?	1	0	0	0	0	1	0	?	0,1	0	0,1	1	?	?	?	1
other <i>Sceloporus</i>	0	1	1	0	0	0	1	1	1	0	0	1	0	1	0	1	0	0	1	0	1	0	1

Three synapomorphies unite *Petrosaurus* with the *Sceloporus* group (Internode C): 18.1 (frontal scales acquired), 20.1 (interparietal scale enlarged), and 26.2 (double row of circumorbital scales differentiated). All three involve the differentiation/enlargement of dorsal head scales. The independence of these characters is somewhat problematic (Frost and Etheridge, 1989), because these three types of scales also are differentiated convergently and congruently within the sand lizard clade (although their distribution in the outgroups justified their initial coding as independent). A near-equally parsimonious interpretation is that frontals, circumorbitals, and an interparietal became differentiated in the common ancestor of the Phrynosomatidae but were independently reduced in *Phrynosoma* and *Uma* (or dedifferentiated at Internode B and then regained within sand lizards). The presence of six postrostral scales (23.0) is a fourth synapomorphy of this clade but was considered ambiguously placed in the parsimony analysis because the highly modified postrostral scales of *Phrynosoma* and the sand lizards were coded as “unknown” (although they clearly have fewer than six). The presence of an enlarged parietal foramen (4.1) and the loss of the scapular fenestra (15.1) are synapomorphies for Internode C when the data are optimized to favor parallelisms (DELTRAN). The monophyly of *Petrosaurus* is corroborated by six synapomorphies: 9.1 (vertebrae depressed), 12.1 (4 sternal ribs), 16.1 (elongate epipubic cartilage), 17.1 (third metatarsal longer than fourth), 24.1 (7–9 superciliary scales), and 41.1 (red female breeding coloration acquired).

Three unambiguously placed synapomorphies confirm the monophyly of the *Sceloporus* group (Internode D): 21.1 (enlarged frontonasal scales), 25.1 (single row of supraoculars), and 31.1 (keeled dorsal scales). A character that is conspicuously absent from the preceding list is the presence of a hooklike process on the clavicle (14.1); because the presence of clavicular hooks is variable in *Uta*, the derived state is only a synapomorphy for this group under ACCT-RAN optimization (favoring reversals). The presence of “shimmy” burial behavior (40.1) also might support the monophyly of the *Sceloporus* group. Five synapomorphies support *Uta* as the sister taxon of the other members of the *Sceloporus* group (Internode E): 11.1 (heart-shaped sternal fontanelle), 13.1 (xiphisternum fused to sternum), 37.0 (interosseous innervation of dorsal shank muscle, reversed from Internode A), 39.1 (blue belly patches in males), and 44.1 (increase in hip movement during male push-up display). Two synapomorphies support

the monophyly of *Uta*: 29.1 (first sublabial contacts second infralabial) and 40.1 (dark axillary spot).

*Urosaurus* is diagnosed by four synapomorphies: 1.1 (frontal bone contacts postorbital), 22.1 (loss of supranasal scales), 23.2 (two postrostral scales), and 33.1 (keeled dorsals in narrow band). The evolution of arboreality (45.1) is another possible synapomorphy of the genus. The *Sator* + *Sceloporus* clade (Internode F) is united by two synapomorphies, the imbrication of the gular scales (30.1) and the interruption or loss of the gular fold (36.1). The monophyly of *Sator* is corroborated by four derived states: 3.1 (basioccipital constricted), 4.0 (parietal foramen reduced), 5.1 (parietal roof exostosed and rugose) and 19.1 (fused frontal scales). The three osteological characters (3.1, 4.0, 5.1) may be associated with the large size of adult *Sator* relative to members of *Uta*, *Urosaurus*, and primitive *Sceloporus*. Two derived states support the monophyly of *Sceloporus* (excluding *Sator*; Internode G): the presence of four postrostral scales (23.1) and the loss of the posterior series of circumorbitals (26.1). Because of variability in *S. merriami*, PAUP showed 26.1 to be of ambiguous placement, but it is more parsimonious to consider the loss of the second series of circumorbitals to be a polymorphic synapomorphy of *Sceloporus* rather than considering the presence of both states in *S. merriami* to be due to homoplasy. The presence of a scapular fenestra (15.0) is probably another synapomorphy of the genus, but the absence of the fenestra in the likely primitive species *S. couchii* renders its placement at this level ambiguous. Two additional, ambiguously placed synapomorphies of *Sceloporus* are the close approximation of the femoral pore rows medially (34.1) and the loss of arboreality (45.0, a putative reversal from Internode E).

The clade of *Sceloporus* exclusive of *S. merriami* is corroborated by state 32.1, the presence of pointed, imbricate dorsal scales. The complete loss of the posterior series of circumorbitals might also be considered support for this clade (e.g., fixation of the polymorphism from Internode G). Some characters suggest that *S. couchii* might instead be the sister taxon to all other *Sceloporus* (e.g., the absence of scapular fenestra, femoral pore rows well separated medially, and variable presence of six postrostrals in *S. couchii*), but substituting *S. couchii* for *S. merriami* in the analysis does not change the resulting hypothesis of relationships among the genera. *Sceloporus merriami* has one unambiguously placed autapomorphy, 42.2 (diploid chromosome number 46).

The phylogeny recovered in this analysis is largely congruent with the preferred tree of Etheridge and de Queiroz (1988, their fig. 16), although their phylogeny was not the tree supported by their computer analysis of the data (their fig. 17). The only differences between their preferred tree and mine involve the placement of *Petrosaurus* and of *Sator*. The phylogeny depicted in Figure 2 also is consistent with one of the three topologies discovered by Frost and Etheridge (1989; their preferred and most frequently obtained hypothesis, Topology 1) and is identical to the tree of intergeneric relationships proposed by Larsen and Tanner (1975, their fig. 1). The hypothesis of Larsen and Tanner (1975) was based on a somewhat subjective analysis of five characters (dorsal scale carination, gular fold, scapular fenestra, clavicular hooks, and push-up display).

The two inconsistencies with the phylogeny proposed by Etheridge and de Queiroz (1988) merit further discussion. Etheridge and de Queiroz (1988) considered *Petrosaurus* to be the sister taxon to all other Phrynosomatidae, an arrangement that was rejected in all three topologies discovered by Frost and Etheridge (1989). Etheridge and de Queiroz (1988) listed five synapomorphies shared by the *Sceloporus* group and the *Phrynosoma*-sand lizards clade as support for the basal position of *Petrosaurus*: (1) closure of the Meckel's groove, (2) reduction to three sternal ribs, (3) widening of the sternal fontanelle, (4) presence of nasal valves, and (5) "shimmy" burial behavior. According to my observations, characters 1 and 3 vary only within *Petrosaurus*, whereas character 4 varies only between the sand lizards and the other phrynosomatids (see Appendix I). Based on the outgroups of the Phrynosomatidae proposed by Frost and Etheridge (1989), the presence of four sternal ribs is of questionable polarity and an a posteriori autapomorphy of *Petrosaurus* (a conclusion also reached by Frost and Etheridge, 1989). However, I differ from Frost and Etheridge (1989) in that I consider the presence of "shimmy" burial behavior to be derived within phrynosomatids and to be potential evidence supporting the Etheridge and de Queiroz (1988) phylogeny. A parsimony analysis of the available data refutes a basal position for *Petrosaurus*, but I consider the relationships of *Petrosaurus* to remain somewhat problematic because of the possible nonindependence of the synapomorphies at Internode C (see Results) and the potentially conflicting character evidence (character 43).

The results of this analysis also differ from those of several previous studies in showing *Sa-*

*tor* to be the sister taxon of *Sceloporus*, rather than nested within it. Synonymy of *Sator*, therefore, is unnecessary but, nevertheless, is logically consistent with the phylogeny. I advocate retaining *Sator* as a genus separate from *Sceloporus* because I consider the evidence showing *Sator* and *Sceloporus* to be sister taxa to be no more convincing than the evidence supporting the monophyly of *Sceloporus* excluding *Sator*. Furthermore, some characters (fused frontal scales, fused supranasals, arboreality) suggest *Sator* could be the sister taxon of *Urosaurus* rather than *Sceloporus*. My taxonomic decision reflects the uncertainty about the phylogenetic position of *Sator* at this level.

The justification for placing *Sator* in the synonymy of *Sceloporus* rests largely on the supposed relationship between *Sator* and *Sceloporus utiformis* (Wyles and Gorman, 1978; de Queiroz, 1982; but Frost and Etheridge, 1989, did not provide a justification for this synonymy). However, phylogenetic analysis of morphological characters and of the published biochemical data rejects a close relationship between these taxa and suggests that *S. utiformis* is nested within *Sceloporus* as the sister taxon of the *siniferus* species group (Wiens, unpubl.).

This study represents the third cladistic analysis of phrynosomatid lizards in a relatively short period of time. In this paper, I have tried to (1) review and synthesize the character evidence from the two previous phylogenetic studies, (2) bring several new characters to bear on the problem, (3) take advantage of new information on outgroup relationships (Frost and Etheridge, 1989) to polarize characters, and (4) provide a parsimony analysis of all the relevant character data. Regardless, one could still ask what progress has really been made in resolving phrynosomatid phylogeny. To address this question, I examined the topologies of several near shortest trees from my analysis and evaluated the lengths of the topologies of Etheridge and de Queiroz (1988) and Frost and Etheridge (1989) using the data matrix from this study.

Figure 3 shows strict consensus trees of a series of shortest and near-shortest trees (topologies that were rejected because they were only one or more steps longer). These consensus trees show that (1) most of the resolution within the *Sceloporus* group and the proposed phylogenetic position of *Petrosaurus* are not maintained among the trees that are only one step longer than the shortest tree (Fig. 3A), (2) the monophyly of the *Sceloporus* group is not supported in some trees that are three steps longer (Fig. 3B), (3) almost all resolution within the Phrynosomatidae (except for the *Phrynosoma*-sand lizard clade) is lost

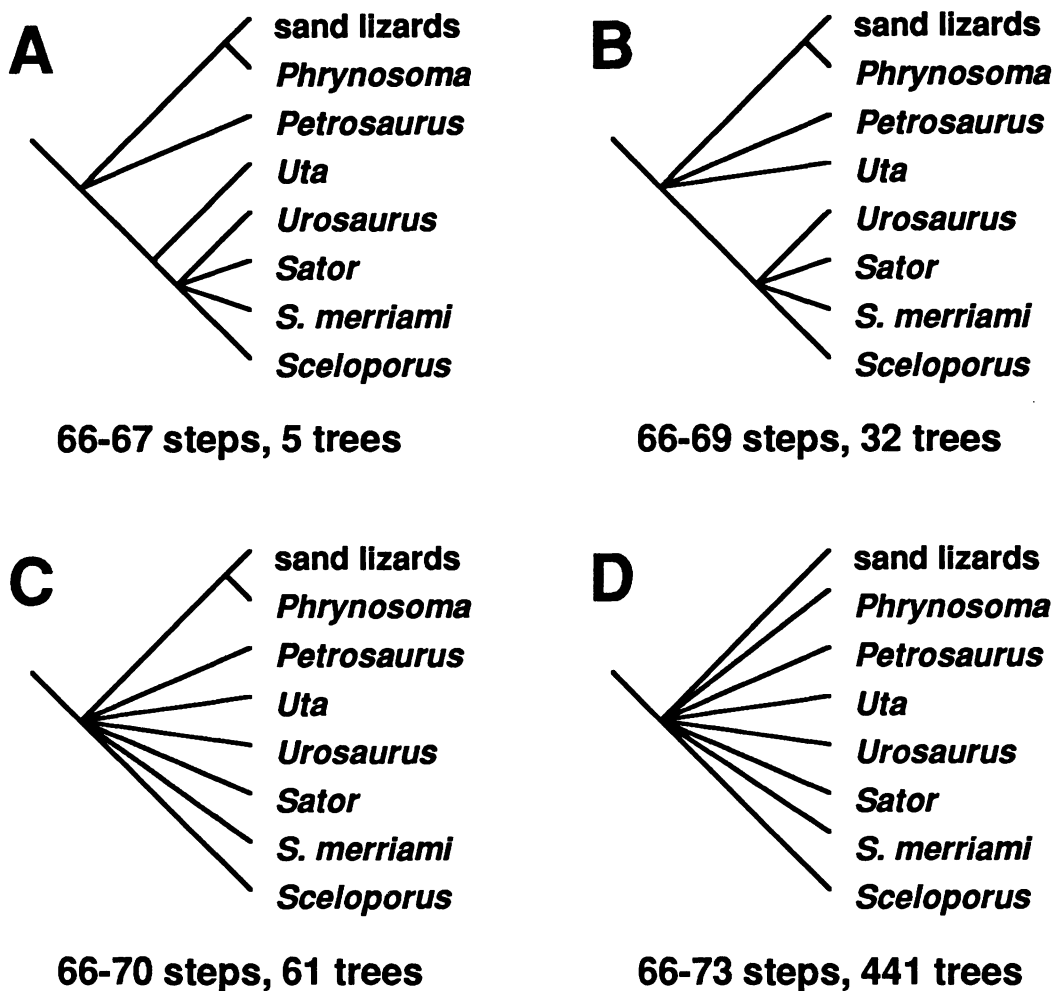


Fig. 3. Strict consensus trees of shortest and near-shortest topologies.

in a strict consensus tree of cladograms that are four steps longer (Fig. 3C), and (4) all resolution is lost in a strict consensus tree of topologies seven steps longer than the shortest tree found (Fig. 3D). Although it is not clear how many steps must separate differing topologies for a given hypothesis of relationships to be considered strongly supported, it is obvious that some of the resolution obtained within the Phrynosomatidae may not be very stable.

Using MacClade, I forced the data from this analysis onto the preferred topology of Etheridge and de Queiroz (1988). Their largely congruent phylogeny has a length of 68 steps, two steps longer than the shortest tree from this study. The trichotomy in Topology 1 of Frost and Etheridge (1989) can be resolved to yield the same topology as my most parsimonious tree, but when my data are forced onto Topologies 2 and 3, they have lengths of 72 and 71 steps,

respectively. These were the two topologies that showed the paraphyly of the *Sceloporus* group. Although most of the differences in tree lengths between the competing phylogenetic hypotheses seem slight, the two topologies that originally called into question the monophyly of the *Sceloporus* group appear to be considerably longer than the most parsimonious solution obtained. I feel these topologies can, therefore, be rejected with some confidence and that the monophyly of the *Sceloporus* group is a reasonable working hypothesis for future systematic and evolutionary studies of phrynosomatid lizards.

#### MATERIAL EXAMINED

Institutional abbreviations follow Leviton et al. (1985). (AA)—cleared-and-stained skeleton; (AP)—cleared-and-stained postcranial skeleton; (DS)—dry skull; (D)—dry skeleton; (W)—alcohol-preserved specimen.

CROTAPHYTIDAE: *Crotaphytus collaris*: KU 16414, 147300 (DS), 7200, 16419, 21004 (D); 182257–182259, 182261 (W). *Crotaphytus*



*insularis*: KU 121747 (DS), 12464–12465, 12167–12168 (W). *Crotaphytus reticulatus*: KU 142725 (DS); 13203, 61449, 121487, 121491 (W). *Gambelia silus*: KU 121754, 121756, 121773–121774 (DS); 121537, 121659, 121677, 121682 (W). *Gambelia wislizenii*: KU 121776, 121779 (DS); 121688–121691 (W).

OPLURIDAE: *Chalarodon madagascariensis*: KU 187756 (DS); 187758–187765 (W). *Oplurus cuvieri*: KU 187766–187768 (W). *Oplurus cyclurus*: AMNH 71462 (DS). *Oplurus fernensis*: KU 187770 (DS); 187769–187772 (W). *Oplurus quadraculatus*: AMNH 71452 (DS).

PHRYNOSOMATIDAE: *Callisaurus draconoides*: KU 13990, 13992–13994 (D); 77722, 77731, 77742, 77748, 77774 (W). *Cophosaurus texanus*: KU 13916, 19562, 73394 (D); 40306, 73049, 73054, 73059, 74409 (W). *Holbrookia laevata*: KU 56081–56084 (W). *Holbrookia maculata*: KU 1893, 19563, 20996 (D); 44135, 44147, 45739–45740, 51711, 51714, 51720 (W). *Holbrookia propinqua*: KU 13919, 13923 (D); 28006–28007, 63471, 63473, 63475, 63477 (W). *Petrosaurus mearnsi*: CAS 16544, 90875 (DS, AP); 43167 (DS); 16451, 90878, 90881–90882 (W); KU 61560 (AA); 176009 (DS); 11404–11410, 31346, 61559, 61561, 90835, 176008–176009 (W); LACM 131520 (D). *Petrosaurus thalassinus*: CAS 3009, 3012 (DS, AP); 3010, 91100, 91102–91103 (W); KU 178967, 182075 (W). *Phrynosoma asio*: KU 37763, 40388–40389, 61484 (W). *Phrynosoma braconieri*: KU 37761 (W). *Phrynosoma cornutum*: KU 20992–20993, 7233 (D); 207086, 207260 (W). *Phrynosoma coronatum*: KU 7230–7231 (D); 78622–78625 (W). *Phrynosoma douglassii*: KU 13943, 13945 (D); 45312–45315, 45317 (W). *Phrynosoma mcallii*: KU 21931 (D); 6998 (W). *Phrynosoma modestum*: KU 473 (DS); *Phrynosoma orbicolare*: KU 61503, 105706 (W). *Phrynosoma platyrhinus*: KU 22237 (D). *Phrynosoma solare*: KU 13941 (D); 40463, 152628 (W). *Phrynosoma taurus*: KU 37802 (W). *Sator angustus*: KU 91476–91477 (W); LACM 13749, 13752 (DS, AP); 134739, 134755, 135475, 135918 (W). *Sator grandaicus*: KU 91480 (D); 91483 (DS, AP); 91478–91479, 91481–91483 (W); LACM 9936, 9961 (DS, AP); 9958, 9962, 9968–9969 (W). *Sceloporus acanthinus*: KU 187162–187163, 190774 (W). *Sceloporus adleri*: KU 143612, 105750, 105760, 105767 (W). *Sceloporus aeneus*: KU 62847 (AA); 62840, 62842, 62844–62845 (W). *Sceloporus anahuacensis*: KU 197023 (W). *Sceloporus asper*: KU 73684 (W). *Sceloporus bicanthalis*: KU 26978, 26988, 26994, 27001 (W). *Sceloporus bulleri*: KU 73687–73688, 73692, 86605 (W). *Sceloporus carinatus*: KU 43659, 116952–116953 (W). *Sceloporus caustus*: KU 29337–29338, 35062 (W). *Sceloporus chrysostictus*: KU 70453 (AA); 74948 (DS, AP); 157365, 157369, 157371, 157397, 171518–171519 (W). *Sceloporus clarki*: KU 44170–44174 (W). *Sceloporus cochiui*: KU 192572 (AA); 192568, 192571 (DS, AP); 192569–192570, 192577, 192579, 192581, 192591–192592, 203248–203249, 203255, 203259 (W). *Sceloporus cozumelae*: KU 70455, 157411 (AA); 70477 (DS, AP); 171454–171455; 171459–171461 (W). *Sceloporus cryptus*: KU 70518–70519, 137730–137731 (W). *Sceloporus cyanogenys*: KU 13971 (D); 24176–24180 (W). *Sceloporus dugesii*: KU 67553, 67557–67558 (W). *Sceloporus edwardtaylori*: KU 43731 (W). *Sceloporus formosus*: KU 71764 (D); 70534, 101132–101134 (W). *Sceloporus gadoviae*: KU 67574 (AA); 61608–61609, 67573, 67575–67578, 68986–68987 (W). *Sceloporus graciosus*: KU 87521–87522 (AA); 87527–87528, 87530, 87532–87533 (W). *Sceloporus graminicus*: KU 182610 (AA); 182608–182609 (DS, AP); 10525–10527, 182606–182607 (W). *Sceloporus horridus*: KU 29166–29168, 68989–68990 (W). *Sceloporus hunsakeri*: KU 78683–78686 (W). *Sceloporus insignis*: KU 102923–102924 (W). *Sceloporus internasalis*: KU 40146–40147 (W). *Sceloporus jalapae*: KU 43719–43723 (W). *Sceloporus jarrovi*: KU 13961, 13965 (D); 44187–44188, 51072–51073 (W). *Sceloporus magister*: KU 29350–29351, 38164, 80295 (W). *Sceloporus malachiicus*: KU 88667 (D); 200567–200568, 200571, 203006 (W). *Sceloporus megalopidurus*: KU 59679 (AA); 59688–59692 (W). *Sceloporus melanorhinus*: KU 29140–29141, 29570, 62833–62835 (W). *Sceloporus merriami*: KU 128835–128836 (AA); KU 13967 (D); 39947, 61655, 118901 (DS, AP); 47059–47069, 51777–51783, 128837–128840 (W). *Sceloporus mucronatus*: KU 39885–39886, 61659, 61662 (W). *Sceloporus nelsoni*: KU 44838–44839, 78671–78673 (W). *Sceloporus occidentalis*: KU 1898 (D); 88172–88173, 192064–192065 (W). *Sceloporus ochoterenaei*: KU 37736, 61682 (W). *Sceloporus olivaceus*: KU 16418 (D); 126991–126993, 176471 (W). *Sceloporus orcutti*: KU 49690–49691, 12682, 61691 (W). *Sceloporus ornatus*: KU 33975–33976, 37725–37726 (W). *Sceloporus palaciosi*: KU 197024–197025 (W). *Sceloporus parvus*: KU 33991 (AA); 33503, 33611–33614, 33989–33990, 38102, 39889–39890 (W). *Sceloporus poinsettii*: KU 9123, 13968 (D); 3755–3758 (W). *Sceloporus pyrocephalus*: KU 62853 (AA); 62854 (DS, AP); 29593, 29600, 29619, 63401 (W). *Sceloporus salvini*: KU 87372 (W). *Sceloporus scalaris*: KU 102928 (DS, AP); 102929–102937 (W). *Sceloporus serrifer*: KU 94091–94094 (W). *Sceloporus siniferus*: KU 43863 (DS, AP); 43830, 43852–43853, 43857, 43860 (W). *Sceloporus smaragdinus*: KU 59643, 145792–145793, 145795 (W). *Sceloporus squamosus*: KU 85857 (AA); 184227 (DS, AP); 18249–18253 (W). *Sceloporus stejnegeri*: KU 182604 (W). *Sceloporus taeniocnemis*: KU 187164–187165, 187168–187169 (W). *Sceloporus teapensis*: KU 59714 (AA); 55806 (DS, AP); 171499–171502 (W).

*Sceloporus torquatus*: KU 38159–38160, 91414 (W). *Sceloporus undulatus*: KU 2206 (D); 207261–207265, 206270–206271 (W). *Sceloporus utiformis*: KU 73737 (AA); 27193, 29623, 29629, 63403, 73733–73736, 182654 (W). *Sceloporus variabilis*: KU 7229 (D); 187174 (DS, AP); 37791, 44874, 59734, 87395, 87482, 116961 (W). *Sceloporus virgatus*: KU 74454 (AA); 74466 (DS, AP); 49531, 74455, 74460 (W). *Sceloporus woodi*: KU 69001–69002 (W). *Uma inornata*: KU 90961, 95849 (D); 90821–90825 (W). *Uma notata*: KU 61507, 61518–61520, 154465 (W). *Urosaurus auriculatus*: LACM 132538, 132540 (DS, AP); 132539, 132542, 132545, 132549 (W); UMMZ 84222 (7 specimens, W; 3 specimens, AA) (W); USNM 15896 (DS, AP); 5903 (W). *Urosaurus bicarinatus*: KU 29256 (AA); 29255, 61525 (DS, AP); 27184–27185, 29249–29254, 29258, 29665 (W); LACM 97732, 97736 (DS, AP); 97734–97735, 97737–97738 (W). *Urosaurus darionensis*: LACM 19139, 19166 (DS, AP); 19140, 19153, 19158, 19170 (W); UMMZ 84224 (7 specimens, W; 3 specimens, AA); USNM 24416 (DS, AP); 24417 (W). *Urosaurus gadovi*: KU Anatomy 83 (DS, AP); KU 29236 (AA); 29239, 29671 (DS, AP); 29237–29238, 29240, 29242–29248, 29662–29664, 29667–29670, 29672, 62836 (W). *Urosaurus graciosus*: KU 72740, 72746, 14242 (DS, AP); 11610, 72729, 72731–72739, 72741–72742 (W); LACM 19040, 19066 (DS, AP); 19038, 19042, 19076, 19083, (W); SDSNH 63124, 63180, 63195, 65442 (D). *Urosaurus lahleli*: SDSNH 41369, 41421, 41422, 41432 (AA), 66729 (D); 41298, 41386, 41407, 41428, 41437, 41441 (W). *Urosaurus microscutatus*: KU 91505–91507 (W); LACM 128137, 128172 (DS, AP); 128116, 128137, 128157, 128174 (W); SDSNH 49909, 49912, 49923, 57453 (AA); 64076, 66278 (D); 49908, 49924, 49926, 55384, 55451, 62929 (W). *Urosaurus nigricaudus*: KU 78732, 78754 (DS, AP); 78700–78715 (W); SDSNH 65036–65037 (D); UMMZ 181141 (D). *Urosaurus ornatus*: KU 14879 (AA); 13935–13936, 13938 (D); 77868 (DS, AP); 40469, 40472, 40474–40475, 40477, 74482, 74501, 74585–74586, 74594, 74596–74597 (W); SDSNH 63219, 63240, 63245, 66265 (D); UMMZ 181779–181780, 181990, 181992 (D). *Uta antiqua*: CAS 14099, 14100 (DS, AP); 14098, 14101, 14108–14109 (W). *Uta nolasensis*: CAS 14251, 14252 (DS, AP); 14245–14246, 14249–14250 (W). *Uta palmeri*: CAS 14123, 14124 (DS, AP); 14122, 14128, 14130–14131 (W); KU 91525 (DS, AP); 91514–91524, 91526–91528 (W). *Uta squamata*: CAS 149025, 149032 (DS, AP); 149020, 149034, 149038, 149041 (W); KU 91529–91533. *Uta stansburiana*: KU 194136–194137 (AA); 7215 (D); 73395–73396 (DS); 194130 (DS, AP); 45803, 45876, 45895, 47673, 179542, 179547, 179549–179550, 194094, 194098, 194128–194129 (W). *Uta stellata*: CAS 14297–14298 (DS, AP); 14295–14296, 14299–14300 (W); LACM 74268 (DS, AP); 5645, 5647, 5650, 5653 (W).

POLYCHRIDAE: *Anolis carolinensis*: KU 691051 (D); 50779–50781 (W). *Anolis equestris*: KU 61391 (D). *Anolis frenatus*: KU 77668 (D). *Anolis nebulosus*: KU 44124–44125, 47405–47406 (W). *Anolis oculatus*: KU 100545, 100547, 100549–100550 (W). *Anolis petersii*: KU 187448 (D). *Chamaelinorops barbouri*: KU 24546–24547 (W). *Diplolaemus darwini*: KU 160897 (D). *Lioisaurus catamarcensis*: KU 160900 (W). *Pristidactylus scapulatus*: KU 160888 (W). *Pristidactylus torquatus*: KU 161950–161952 (W). *Polychrus acutirostris*: KU 73436–73438 (W). *Polychrus liogaster*: KU 133872–133873 (W). *Polychrus gutturosus*: KU 76074 (W). *Polychrus marmoratus*: KU 124618, 127224–127225 (W).

TROPIDURIDAE: *Leiocephalus barahonensis*: KU 93330–93332 (W). *Leiocephalus carinatus*: KU 206535 (W). *Leiocephalus loxogrammus*: KU 192293 (D). *Leiocephalus melanochlorus*: KU 93299–93302 (W). *Leiocephalus personatus*: KU 93322–93326 (W). *Leiocephalus schreibersi*: KU 93358 (AA); 93354–93357 (W). *Liolaemus elongatus*: KU 161108–161109 (D). *Liolaemus multiformis*: KU 163537 (AA). *Liolaemus perigracialis*: KU 190410–190414 (W). *Liolaemus silvanae*: KU 190418 (DS); 190418–190421 (W). *Liolaemus stolmanni*: KU 163589, 163592, 163595 (W). *Liolaemus walkei*: KU 139259, 139262 (W). *Phymaturus palluma*: KU 161972 (AA); 160923 (D); 161957–161960 (W). *Phymaturus patagonicus*: KU 160926–160929 (W). *Proctotretus pectinatus*: KU 187793, 187795–187797 (W). *Stenocercus apurimicus*: KU 134284 (DS, AP). *Stenocercus chrysopygus*: KU 133906 (DS). *Stenocercus formosus*: KU 134110 (DS, AP); 134109, 134112, 134114 (W). *Stenocercus melanopygus*: KU 134058 (DS); 134037, 134051, 134067, 134082 (W). *Tropidurus occipitalis*: KU 142714 (DS); 142721 (DS, AP); 134654–134655, 163630–163631 (W). *Tropidurus tigris*: KU 163753 (DS). *Uranosodon superciliosus*: KU 128215, 135269 (D); 128216–128218 (W).

## APPENDIX I. LIST OF CHARACTERS

*Osteology*.—A total of 17 osteological characters were coded. The following characters used by Etheridge and de Queiroz (1988) and/or Frost and Etheridge (1989) were excluded from this analysis: distinctness of osseous labyrinth, length of dentary, development of secondary cusps of posterior marginal teeth, closure of Meckel's groove, width of

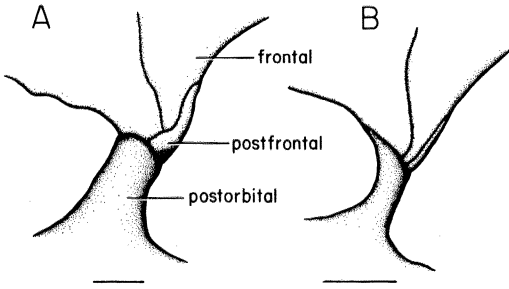


Fig. 4. Dorsal view of right side of skull roof (anterior to the right), showing relationships between frontal and postorbital (character 1). (A) *Sator angustus* LACM 134749 (character 1.0); (B) *Urosaurus auriculatus* LACM 132540 (character 1.1). Scale equals 2 mm.

sternal fontanelle, and number of cervical ribs. The first three (osseous labyrinth, dentary, marginal teeth) appear to vary continuously both within and between terminal taxa. The relatively open Meckel's groove and very narrow sternal fontanelle are unique to *Petrosaurus thalassinus* among phrynosomatids. Given the well-corroborated monophyly of *Petrosaurus*, these characters are phylogenetically uninformative (equally consistent with any topology) for this analysis. According to Frost and Etheridge (1989), the number of cervical ribs varies only between *Petrosaurus* and other phrynosomatids, but according to my observations, both species of *Petrosaurus* have the widespread phrynosomatid condition (first pair of ribs on vertebra number 4).

1. Frontal-postorbital contact (Fig. 4): (0) well-developed postfrontal preventing contact of frontal and postorbital; (1) frontal contacting postorbital. Taxa lacking postfrontals were coded as unknown ("?") for this character.
2. Frontal, anterolateral processes (Etheridge, 1964; Etheridge and de Queiroz, 1988): (0) exposed dorsally, not covered by nasals; (1) covered by nasals. Intermediate conditions and inter- and intraspecific variation are present in *Sceloporus*, *Urosaurus* and some outgroup taxa.
3. Basioccipital: (0) not distinctly constricted anterior to sphenoccipital tubercle; (1) distinctly constricted anterior to sphenoccipital tubercle. Unpolarized.
4. Parietal foramen (modified from Etheridge and de Queiroz, 1988, and Frost and Etheridge, 1989): (0) small, circular, in both parietal and frontal; (1) large, roughly rectangular or triangular, mostly in parietal.
5. Skull rugosity (modified from Etheridge and de Queiroz, 1988, and Frost and Etheridge, 1989): (0) absent or indistinct; (1) roof of parietal rugose and heavily exostosed (in adults).
6. Postfrontal (Etheridge and de Queiroz, 1988; Frost and Etheridge, 1989): (0) present; (1) absent. Unpolarized.
7. Lacrimal (Etheridge and de Queiroz, 1988; Frost and Etheridge, 1989): (0) present; (1) absent.
8. Scleral ossicle 6 (de Queiroz, 1982; Etheridge and de Queiroz, 1988): (0) approximately same size as other ossicles; (1) reduced or absent. I have not rechecked the distribution of this character.
9. Vertebrae (Etheridge, 1964; Etheridge and de Queiroz, 1988; Frost and Etheridge, 1989): (0) not depressed; (1) depressed, neural spines short.
10. Interclavicle, median process (Etheridge, 1964; Etheridge and de Queiroz, 1988): (0) normal length, extending to or close to sternal fontanelle (if present); (1) reduced, not extending close to sternal fontanelle.
11. Sternal fontanelle shape (Fig. 5; Etheridge, 1964): (0) roughly ovoid; (1) "heart-shaped," narrow posteriorly, wide anteriorly; (2) narrow anteriorly, wide posteriorly.
12. Sternal ribs (Fig. 5; Etheridge and de Queiroz, 1988; Frost and Etheridge, 1989): (0) three; (1) four; (2) two. Contrary to previous reports, some species of *Urosaurus* (e.g., *U. bicarinatus*, *U. gadovi*, *U. nigricaudus*) typically have two sternal ribs, and the genus was coded as having both 12.0 and 12.2. Unpolarized.
13. Sternum-xiphisternum (Fig. 5; Etheridge, 1964): (0) articulating; (1) fused. Unpolarized.
14. Clavicular hooks (Etheridge and de Queiroz, 1988): (0) posterior flange on clavicle absent or not recurved; (1) clavicular flange re-

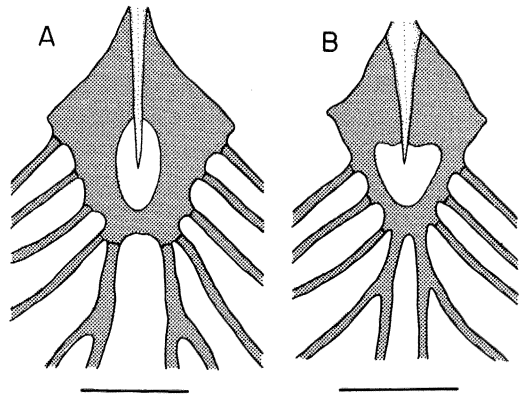


Fig. 5. Ventral view of sternum, showing sternal fontanelle shape (character 11), number of sternal ribs (character 12), and relationship between sternum and xiphisternum (character 13). (A) *Petrosaurus mearnsi* KU 61560 (characters 11.0, 12.1, 13.0); (B) *Urosaurus bicarinatus* KU 29255 (characters 11.1, 12.0, 13.1). Scale equals 5 mm.

curved, hooklike. Because species of *Uta* show continuous inter- and intraspecific variation in the development of the clavicular hook, the genus was coded as having both states.

15. Scapular fenestra (Etheridge and de Queiroz, 1988; Frost and Etheridge, 1989): (0) present; (1) absent. Because *Sceloporus couchii* (one of the presumed primitive species) lacks a scapular fenestra, *Sceloporus* (exclusive of *S. merriami*) was coded as having both character states.
16. Epipubic cartilage (Fig. 6): (0) not extending well anterior to level of pubic symphysis; (1) elongate, extends past pubic symphysis.
17. Metatarsal lengths: (0) IV > III; (1) III > IV.

*Squamation*.—A total of 16 characters involving squamation were coded. Because of intrageneric variability, I was unable to objectively codify an increase in the size of the dorsals between *Uta* and *Sceloporus*, *Sator*, and *Urosaurus* noted by Larsen and Tanner (1975) and cited subse-

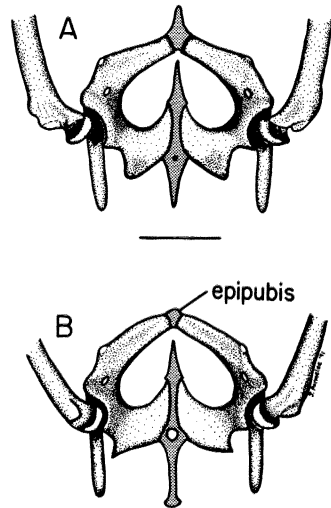


Fig. 6. Ventral view of pelvic girdles showing variation in length of the epipubic cartilage (character 16). (A) *Petrosaurus mearnsi* KU 61560 (character 16.1); (B) *Uta palmeri* CAS 14123 (character 16.0). Scale equals 5 mm.

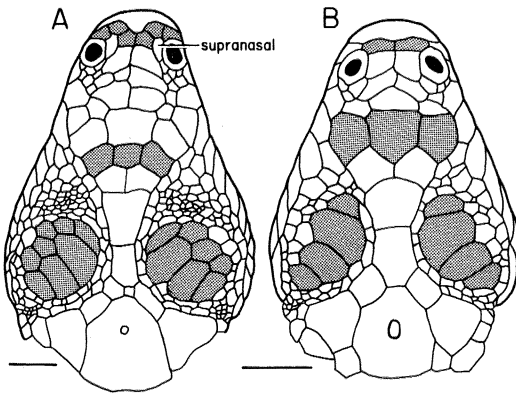


Fig. 7. Dorsal view of cephalic scales, with postrostrals (character 23), frontonasals (character 21), and supraoculars (character 25) stippled. (A) *Petrosaurus mearnsi* CAS 90878 (characters 21.0, 22.0, 23.0, 25.0); (B) *Urosaurus ornatus* KU 74482 (characters 21.1, 22.1, 23.2, 25.1). Scale equals 2 mm.

quently by Etheridge and de Queiroz (1988) and Frost and Etheridge (1989). Etheridge and de Queiroz (1988; from R. Montanucci, pers. comm.), Frost and Etheridge (1989), and Montanucci (1987) cited the presence of a row of enlarged chinshields increasing in size posteriorly as a synapomorphy of *Phrynosoma* plus the sand lizards. Like Montanucci (1987), I question the homology of these scales between these two clades, and suspect the character could be redundant with state 29.2 of this analysis. Montanucci (1987) also mentioned the presence of anteriorly "tilted" supralabials as another synapomorphy of the *Phrynosoma*-sand lizards clade. Although the tilt is obvious in the sand lizards and some *Phrynosoma* (e.g., *P. orbiculare*), it appears to vary continuously in other *Phrynosoma* and other genera (e.g., *Petrosaurus*). This character also was excluded.

18. Frontal scales—1 (Frost and Etheridge, 1989): (0) undifferentiated, small scales between orbits; (1) present, large scale or pair of scales between orbits. Frost and Etheridge (1989) suggested that this character may not be independent of the development of the interparietal, but the distribution of these characters in the Tropiduridae suggests their initial coding as independent; *Tropidurus* have a well-developed interparietal but lack differentiated frontal scales, whereas some *Liolaemus* have well-developed frontal scales but do not have an enlarged interparietal.

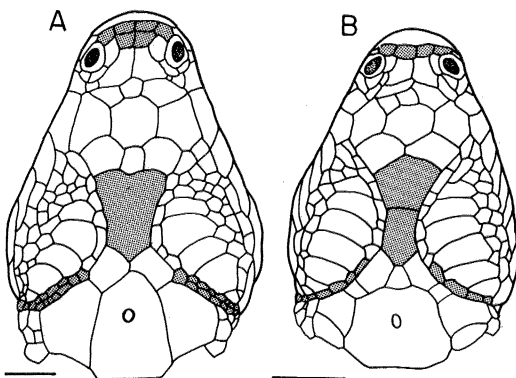


Fig. 8. Dorsal view of cephalic scales, with postrostrals (character 23), frontals (character 19), and circumorbitals (character 26) stippled. (A) *Sator grandaevus* KU 91484 (characters 19.1, 23.0, 26.2); (B) *Sceloporus gadoviae* KU 67573 (characters 19.0, 23.1, 26.1). Scale equals 2 mm.

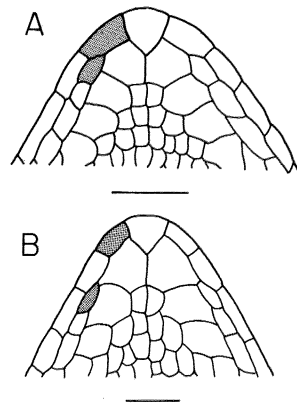


Fig. 9. Ventral view of chin scales, with first infralabial (contacting mental) and first sublabial stippled. (A) *Urosaurus nigricaudus* KU 78748 (character 29.0); (B) *Uta squamata* KU 91531 (character 29.1). Scale equals 2 mm.

19. Frontal scales—2 (Fig. 8): (0) paired; (1) usually fused, single scale between orbits. Taxa lacking differentiated frontal scales were coded as unknown. One individual of *Sator grandaevus* (KU 91478) examined has divided frontals, but the genus was coded as having 19.1. Unpolarized.

20. Interparietal scale (Etheridge and de Queiroz, 1988; Frost and Etheridge, 1989): (0) small or absent; (1) large, as wide as interorbital distance.

21. Frontonasals (Fig. 7; Ballinger and Tinkle, 1972): (0) small, undifferentiated; (1) enlarged.

22. Supranasals (Fig. 7; Savage, 1958): (0) present, usually four scales between nasal scales; (1) absent, two scales between nasals. Some individuals of *Sator* may have the supranasals fused to the posterior postrostrals; this was not considered to be homologous to the condition observed in *Urosaurus*, in which the supranasals appear to be fused to the internasals. Taxa with poorly differentiated head scales (e.g., *Phrynosoma* and the sand lizards) were coded as unknown for this character.

23. Postrostrals (Figs. 7, 8): (0) six; (1) four; (2) two. The pair of scales contacting both the rostral and first supralabial are considered to be lorilabials and are not counted as postrostrals. The species of *Sator* usually have four small scales contacting the rostral and two small scales posterior to these. Because an identical condition occurs frequently in *Petrosaurus* and *Uta*, all three taxa are considered as having six postrostrals. The scales in the rostral region of *Phrynosoma* and the sand lizards are highly modified, and the number of postrostrals could not be determined with certainty (coded as "?"). Some individuals of *S. couchii* have state 23.0. Unpolarized.

24. Superciliaries (Ballinger and Tinkle, 1972): (0) four to six; (1) seven to nine. Unpolarized.

25. Supraoculars (Fig. 7; Ballinger and Tinkle, 1972): (0) two or more rows or undifferentiated; (1) single row. Because the number of rows of supraoculars is unclear in some taxa, the derived state might also be characterized as an enlargement of the median row of supraoculars. Some individuals of *Uta* species have the primitive condition.

26. Circumorbitals: (0) undifferentiated; (1) single row; (2) double row posteriorly. Some *Sator angustus* may have 23.1, but the genus was coded as having state 23.2. Unpolarized.

27. Rostral scale: (0) wider than internarial distance; (1) equal to or narrower than internarial distance.

28. Mental scale: (0) larger than labials; (1) reduced, roughly same size as labials. Etheridge and de Queiroz (1988) listed the presence of a median triangular "postmental" scale as a synapomorphy of the sand lizard clade. I suspect that this scale represents the mental scale that has been occluded from the margin of the lower jaw by the infralabials. Regardless, the mental scale is clearly reduced in the sand lizards relative to other phrynosomatids (except *Phrynosoma*) and the outgroups.

29. Sublabials (Fig. 9; Smith, 1946): (0) first (anteriormost) sublabial contacts first (anteriormost) infralabial; (1) first sublabial contacts second infralabial; (2) first sublabial posterior to second infralabial. Some individuals of *Petrosaurus mearnsi* have state 28.1.

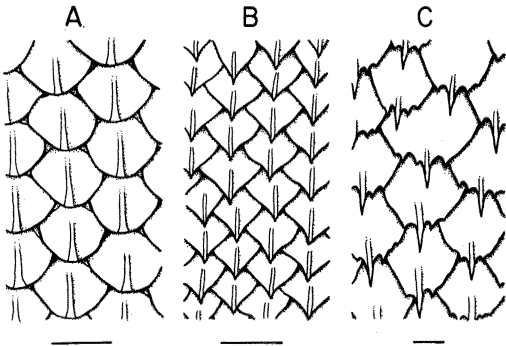


Fig. 10. Dorsal scales of (A) *Sator grandaevus* KU 91478 (character 32.0); (B) *Sceloporus couchii* KU 203249 (character 32.1); (C) *Sceloporus malachiticus* KU 96705 (character 32.1). Scale equals 2 mm.

- 30. Gular scales: (0) granular, nonimbricate; (1) imbricate. This character may appear to be equivalent to the presence or absence of a gular fold (character 36), but two lines of evidence suggest their independence. First, the scales adjacent to the gular fold are imbricate in phrynosomatids that have well-developed gular folds; these scales are termed the mesoptychials by Smith (1946). Furthermore, the imbrication of these scales does not seem to prevent the possibility of throat folds, as *Sator* has imbricate gular scales but a distinct antegular fold (which has long been mistaken for a gular fold; Frost, pers. comm., in Etheridge and de Queiroz, 1988). *Uta squamata*, *Urosaurus clarionensis*, and *Sceloporus merriami* appear to have intermediate conditions and were coded as unknown. The highly modified gular scales of *Phrynosoma* also were coded as unknown for this character. Unpolarized.
- 31. Dorsals—1 (Etheridge and de Queiroz, 1988; Montanucci, 1987): (0) smooth, granular; (1) keeled; (2) heterogeneous; smooth, keeled, and enlarged spinous scales. Unpolarized.
- 32. Dorsals—2 (Fig. 10): (0) rounded, nonoverlapping posteriorly; (1) pointed, overlapping posteriorly. Taxa with smooth, granular dorsal scales were coded as unknown. Unpolarized.
- 33. Dorsals—3 (Fig. 11): (0) keeled dorsals in wide band extending laterally to just above insertion of hindlimb; (1) keeled dorsals in narrow band restricted to vertebral region. Taxa lacking both keeled dorsals and granular lateral scales were coded as unknown. Unpolarized.

*Miscellaneous soft anatomy.*—Five characters involving variation in soft anatomy (excluding coloration and squamation) were coded. Etheridge and de Queiroz (1988) and Paull et al. (1976) discussed the presence of nasal valves as a synapomorphy of all phrynosomatids exclusive of *Petrosaurus*, but Frost and Etheridge (1989) questioned the level of universality to which the character applied. I have dissected the nasal regions of representatives of all eight phrynosomatid terminal taxa used in this analysis and of a *Crotaphytus*. The only noticeable variation in the degree of development of these valves observed was between sand lizards (with well-developed nasal valves) and the other taxa. Fanghella et al. (1975) and de Queiroz (1989) discussed several features of the throat and shoulder musculature that varied within the *Sceloporus* group. In my dissections of the throat and shoulder musculature of individuals of *Uta*, *Urosaurus*, and *Sceloporus* I found these characters either to be continuously variable or invariant (at least within the *Sceloporus* group). Etheridge and de Queiroz (1988) listed five myological synapomorphies for the *Phrynosoma*-sand lizards clade that were not included in this analysis. These synapomorphies were based on data from unpublished studies and were not included because I lacked information on the distribution of the character states in other phrynosomatids and the outgroups.

- 34. Femoral pores—1: (0) rows widely separated medially; (1) closely approximated medially, usually separated by four or fewer scales.
- 35. Femoral pores—2: (0) continuous row, median pores all in contact; (1) femoral pore row discontinuous, some median pores separated by small scales. The femoral pore row is continuous in *Holbrookia* and *Cophosaurus*, but the sand lizard clade was optimized a priori as having the derived state.
- 36. Gular fold (Etheridge and de Queiroz, 1988; Frost and Etheridge,

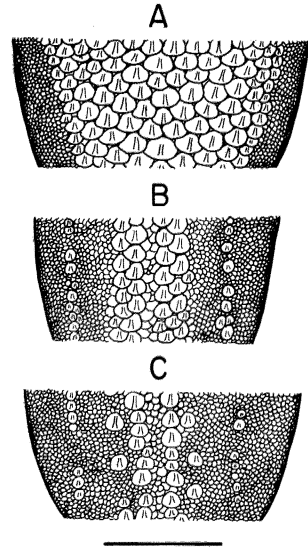


Fig. 11. Dorsal scales of (A) *Sceloporus merriami* KU 128839 (character 33.0); (B) *Urosaurus ornatus* KU 73108 (character 33.1); (C) *Urosaurus bicarinatus* KU 80734 (character 33.1). Scale equals 5 mm.

- 1989): (0) present and uninterrupted; (1) interrupted medially or absent. Unpolarized.
- 37. Dorsal shank muscle innervation (Jullien and Renous-Lécure, 1972; Etheridge and de Queiroz, 1988; Frost and Etheridge, 1989): (0) from interosseous nerve; (1) from peroneal nerve. I have not rechecked the distribution of this character.
- 38. Retractor lateralis anterior (Arnold, 1984; Etheridge and de Queiroz, 1988; Frost and Etheridge, 1989): (0) anterior fibers not reflected outward or posteriorly; (1) anterior fibers reflected outward or posteriorly. Based on data in Arnold (1984) for the following phrynosomatid taxa: *Callisaurus draconoides*, *Cophosaurus texanus*, *Holbrookia maculata*, *Petrosaurus thalassinus*, *Phrynosoma orbiculare*, *Sceloporus torquatus*, *Uma notata*, and *Uta stansburiana*.

*Coloration.*

- 39. Ventral coloration—1 (Etheridge and de Queiroz, 1988; Frost and Etheridge, 1989): (0) blue belly patches absent; (1) blue belly patches present in males (fused in some taxa to form solid blue wash on venter). The belly patches in male *Petrosaurus mearnsi* and *Sator angustus* are tentatively considered to be homologous to those in *Sceloporus* and *Urosaurus*.
- 40. Ventral coloration—2 (Etheridge and de Queiroz, 1988; Frost and Etheridge, 1989): (0) ventrolateral stripes or axillary spot absent; (1) dark axillary spot; (2) dark ventrolateral stripe(s) present. I considered the dark axillary spot of *Uta* to be more likely homologous to the dark ventrolateral stripe(s) or spot(s) of sand lizards than to the blue belly patches of other phrynosomatids. The concomitant presence of a dark ventrolateral stripe(s) in all sand lizards with the absence of blue belly patches in some (e.g., *Uma*) and the differences in sexual dimorphism (blue belly patches in males only, black axillary spot and ventrolateral stripes in both sexes) suggest the independence of these characters. I suspect that these dark spots and stripes may represent modifications of the black collar characteristic of many iguanian species.
- 41. Red female breeding coloration (de Queiroz, 1989; Frost and Etheridge, 1989): (0) absent or unreported; (1) present. From data summarized by the authors cited above. Stebbins (1985) reported red female breeding coloration in both species of *Petrosaurus*, and the genus was, therefore, coded as having the derived state. I observed reddish coloration on the throats of preserved female *Sator angustus* and coded the genus as having both states.

*Karyology.*

- 42. Diploid chromosome number (Etheridge and de Queiroz, 1988; Paull et al., 1976): (0) 36 (12 macrochromosomes plus 24 micro-

chromosomes); (1) 34 (12 macrochromosomes plus 22 microchromosomes); (2) 46 (24 macrochromosomes plus 22 microchromosomes). From data summarized by Paull et al. (1976) and Sites et al. (1992).

#### Behavior.

43. "Shimmy" burial behavior (Paull et al., 1976; Etheridge and de Queiroz, 1988; Frost and Etheridge, 1989): (0) absent or not reported; (1) present. From data summarized by the authors cited above. I have not considered the presence of "shimmy" burial behavior to be plesiomorphic within tropidurids because it is absent in *Leiocephalus* according to Paull et al. (1976) and has not been reported in any other tropidurid except one species of *Tropidurus* (Frost and Etheridge, 1989). I, therefore, differ from Frost and Etheridge (1989) in considering "shimmy" burial behavior to be unequivocally derived within Phrynosomatidae.
44. Push-up display pattern in males (Purdue and Carpenter, 1972): (0) mean hip ratio (vertical hip movement divided by vertical eye movement) 0.1–0.4; (1) mean hip ratio 1.0–2.0. From data presented by the authors above for one species of *Petrosaurus*, five species of *Uta*, five species of *Urosaurus*, and 22 species of *Sceloporus*. Both character states as well as intermediate ratios were reported for the species of *Sceloporus* surveyed, so the genus was coded as polymorphic. Larsen and Tanner (1975) discussed hip ratios as a character in their analysis but incorrectly gave Purdue and Carpenter's (1972) values for shoulder ratios. Unpolarized.
45. Ecology: (0) not regularly arboreal; (1) partially to strictly arboreal. From data summarized by Savage (1958), Guillette et al. (1980), Stebbins (1985), and Etheridge and de Queiroz (1988).

## APPENDIX II. APOMORPHY LISTS

Apomorphies supporting the cladogram in Figure 2 under ACCT-RAN and DELTRAN optimization routines are given. See Appendix I for description of character states.

Internode A.—ACCT-RAN: 2.1, 4.1, 15.1, 23.0, 37.1, 42.1, 43.1. DELTRAN: 37.1, 42.1.

Internode B.—ACCT-RAN: 6.1, 7.1, 8.1, 10.1, 11.1, 27.1, 28.1, 29.2, 35.1, 38.1. DELTRAN: 2.1, 6.1, 7.1, 8.1, 10.1, 27.1, 28.1, 29.2, 35.1, 38.1, 43.1.

Internode C.—ACCT-RAN: 18.1, 20.1, 26.2. DELTRAN: 4.1, 15.1, 18.1, 20.1, 23.0, 26.2.

Internode D.—ACCT-RAN: 14.1, 21.1, 25.1, 31.1. DELTRAN: 21.1, 25.1, 31.1, 43.1.

Internode E.—ACCT-RAN: 11.1, 13.1, 37.0, 39.1, 44.1, 45.1. DELTRAN: 11.1, 13.1, 14.1, 37.0, 39.1, 44.1.

Internode F.—ACCT-RAN and DELTRAN: 30.1, 36.1.

Internode G.—ACCT-RAN: 15.0, 23.1, 26.1, 34.1, 45.0. DELTRAN: 23.1.

Sand lizards.—ACCT-RAN: 15.0, 40.2, 41.1. DELTRAN: 4.1, 11.1, 40.2, 41.1.

*Phrynosoma*.—ACCT-RAN: 4.0, 5.1, 11.2, 12.2, 31.2. DELTRAN: 5.1, 11.2, 12.2, 15.1, 31.2.

*Petrosaurus*.—ACCT-RAN: 2.0, 9.1, 12.1, 16.1, 17.1, 24.1, 41.1, 43.0. DELTRAN: 9.1, 12.1, 16.1, 17.1, 24.1, 41.1.

*Uta*.—ACCT-RAN: 29.1, 40.1. DELTRAN: 2.1, 29.1, 40.1.

*Urosaurus*.—ACCT-RAN: 1.1, 22.1, 23.2, 33.1. DELTRAN: 1.1, 22.1, 23.2, 33.1, 45.1.

*Sator*.—ACCT-RAN: 2.0, 3.1, 4.0, 5.1, 19.1. DELTRAN: 3.1, 4.0, 5.1, 19.1, 45.1.

*Sceloporus merriami*.—ACCT-RAN: 42.2. DELTRAN: 2.1, 15.0, 34.1, 42.2.

*Sceloporus* (excluding *S. merriami*): ACCT-RAN: 32.1. DELTRAN: 26.1, 32.1.

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## LITERATURE CITED

- ARNOLD, E. N. 1984. Variation in the cloacal and hemipenial muscles of lizards and its bearing on their relationships, p. 57–85. *In*: The structure, development, and evolution of reptiles. M. J. Ferguson (ed.). Symp. Zool. Soc. London, England.
- BALLINGER, R. E., AND D. W. TINKLE. 1972. Systematics and evolution of the genus *Uta* (Sauria: Iguanidae). Misc. Pub. Mus. Zool. Univ. Michigan 145: 1–83.
- DE QUEIROZ, K. 1982. The scleral ossicles of the sceloporine iguanids: a reexamination with comments on their phylogenetic significance. *Herpetologica* 38:302–311.
- . 1989. Morphological and biochemical evolution in the sand lizards. Unpubl. Ph.D. diss., Univ. of California, Berkeley.
- DINGKURK, G., AND L. D. UHLER. 1977. Enzyme clearing of alcian blue stained whole small vertebrates for demonstration of cartilage. *Stain Technol.* 52:229–232.
- ETHERIDGE, R. 1964. The skeletal morphology and systematic relationships of sceloporine lizards. *Copeia* 1964:610–631.
- , AND K. DE QUEIROZ. 1988. A phylogeny of Iguanidae, p. 283–368. *In*: Phylogenetic relationships of lizard families: essays commemorating Charles L. Camp. R. Estes and G. Pregill (eds.). Stanford Univ. Press, Palo Alto, California.
- FANGHELLA, C., D. F. AVERY, AND W. W. TANNER. 1975. *Urosaurus* and its phylogenetic relationships to *Uta* as determined by osteology and myology (Reptilia: Iguanidae). *Great Basin Nat.* 35:245–268.
- FARRIS, J. S. 1970. Methods for computing Wagner trees. *Syst. Zool.* 19:83–92.
- FITCH, W. M. 1971. Toward defining the course of evolution: minimal change for a specific tree topology. *Ibid.* 20:406–416.
- FROST, D. R., AND R. ETHERIDGE. 1989. A phylogenetic analysis and taxonomy of iguanian lizards. Misc. Pub. Univ. Kansas 81:1–65.
- GUILLETTE, L. J., R. E. JONES, K. T. FITZGERALD, AND H. M. SMITH. 1980. Evolution of viviparity in the lizard genus *Sceloporus*. *Herpetologica* 36:201–215.
- JULLIEN, R., AND S. RENOUS-LÈCURU. 1972. Variations du trajet du nerf ulnaire (ulnaris) et de l'innervations des muscles dorsaux de la jambe chez les lacertiliens (reptiles: squamates): valeur systématique et application phylogénétique. *Bull. Mus. Natl. Hist. Nat., Zool.* 23:207–246.
- KLUGE, A. G., AND J. S. FARRIS. 1969. Quantitative phyletics and the evolution of anurans. *Syst. Zool.* 18:1–32.

- LARSEN, K. R., AND W. W. TANNER. 1975. Evolution of the sceloporine lizards. *Great Basin Nat.* 35:1–20.
- LEVITON, A. E., R. H. GIBBS, JR., E. HEAL, AND C. E. DAWSON. 1985. Standards in herpetology and ichthyology: Part I. Standard symbolic codes for institutional resource collections in herpetology and ichthyology. *Copeia* 1985:802–832.
- MADDISON, W. P. 1989. Reconstructing character evolution on polytomous cladograms. *Cladistics* (1989) 5:365–377.
- , M. J. DONOGHUE, AND D. R. MADDISON. 1984. Outgroup analysis and parsimony. *Syst. Zool.* 33:83–103.
- MONTANUCCI, R. R. 1987. A phylogenetic study of the horned lizards, genus *Phrynosoma*, based on skeletal and external morphology. *Contr. Sci. Nat. Hist. Mus. Los Angeles County* 113:1–26.
- PAULL, D., E. E. WILLIAMS, AND W. P. HALL. 1976. Lizard karyotypes from the Galapagos Islands: chromosomes in phylogeny and evolution. *Breviora* 441:1–31.
- PURDUE, J. R., AND C. C. CARPENTER. 1972. A comparative study of the display motion in the iguanid genera *Sceloporus*, *Uta*, and *Urosaurus*. *Herpetologica* 28:137–141.
- RAU, C. S., AND R. B. LOOMIS. 1977. A new species of *Urosaurus* (Reptilia, Lacertilia, Iguanidae) from Baja California, Mexico. *J. Herpetol.* 11:25–29.
- SAVAGE, J. M. 1958. The iguanid lizard genera *Urosaurus* and *Uta*, with remarks on related groups. *Zoologica* 43:41–54.
- SITES, J. W., J. W. ARCHIE, AND O. F. VILLELA. 1992. A review of phylogenetic hypotheses for the lizard genus *Sceloporus* (Phrynosomatidae): implications for ecological and evolutionary studies. *Bulletin of the American Museum of Natural History* 213:1–110.
- SMITH, H. M. 1946. *Handbook of lizards*. Comstock Publ. Co., Ithaca, New York.
- STEBBINS, R. C. 1985. *A field guide to western reptiles and amphibians*, 2d ed. Houghton Mifflin, Boston, Massachusetts.
- SWOFFORD, D. L., AND W. P. MADDISON. 1987. Reconstructing ancestral character states under Wagner parsimony. *Math. Biosc.* 87:199–229.
- WYLES, J. S., AND G. C. GORMAN. 1978. Close relationship between the lizard genus *Sator* and *Sceloporus utiformis* (Reptilia, Lacertilia, Iguanidae): electrophoretic and immunological evidence. *J. Herpetol.* 12:343–350.
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