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EVOLUTION OF THE SCELOPORINE LIZARDS (IGUANIDAE)

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ABSTRACT.— Phylogenetic relationships among Sceloporine genera are briefly discussed. Species relationships within the genus *Sceloporus* are analyzed, and evolutionary lines of descent are proposed.

The genus *Sceloporus* is composed of three monophyletic groups: Group I, the most primitive, probably developed from *Sator*-like ancestral stock in Miocene times. This group speciated from stock similar to *Sceloporus gadoviae* in southern Mexico to *S. merriami* in the North and contains 7 species in 3 species groups. We propose that these species be included in the genus *Lysoptychus* Cope. Group II arose from Group I and evolved from centrally located *Sceloporus pictus* in all directions throughout Mexico. This intermediate group contains approximately 19 species in 5 species groups. Group III also arose from the primitive stock of Group I and radiated from several desert refugia created by Pleistocene glaciation. Evolution of this group in Mexico was generally from north to south with *Sceloporus malachiticus* extending as far south as Panama. This group contains approximately 33 species in 5 species groups.

In a previous paper (Larsen and Tanner, 1974) we presented our analysis of the species in the lizard genus *Sceloporus*. Numerical statistical methods were used to analyze the species in the genus *Sceloporus* using cranial osteology, external meristic and numeric characters, karyology, display behavior, and geographic distribution. A new classification for the genus was proposed with three major branches or groups. Group I contained 7 species in 3 species groups. Group II contained approximately 19 species in 5 species groups. Group III contained approximately 33 species in 5 species groups. This classification was supported by the cluster analysis of several different sets of data. Cranial osteology, zoogeography, behavior, and karyology were shown to be taxonomically significant as numeric characters. Stepwise discriminate analysis showed that this classification of the species of *Sceloporus* into 3 major groups and 13 species groups was significant at the .999 confidence level.

The purpose of this paper is to present our views on the evolution of the species in the genus *Sceloporus*. We also propose a phylogeny of closely related (Scelop-

orine) genera. We are grateful for the assistance of H. M. Smith, C. C. Carpenter, W. P. Hall, and the following persons at Brigham Young University: A. L. Allen, F. L. Anderson, J. R. Murphy, M. S. Peterson, J. K. Rigby, N. M. Smith, D. A. White, and S. L. Wood.

INTERGENERIC PHYLOGENY

In 1828 Weigmann described several genera, including *Sceloporus* (*S. torquatus*). He distinguished *Sceloporus* from the South American *Tropidurus* mainly on the basis of femoral pores (*Scelo*=thigh, *porus*=pore). In 1852 Baird and Girard described the genus *Uta* (*U. stansburiana*) which is distinguished from the smaller species of *Sceloporus* by its gular fold and granular dorsal scales. In 1854 Hallowell erected the genus *Urosaurus* (*U. graciosus*), which is similar to *Uta* but has several rows of enlarged, carinate, imbricate vertebrae or paravertebrae. Two years later Duméril (1856) described the genus *Phymatolepis* (*Urosaurus bicarinatus*) on the basis of enlarged paravertebrae. In 1859 Baird placed Hallowell's genus *Urosaurus* in synonymy with *Uta*, and in

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1864 Cope did the same with Duméril's *Phymatolepis*. Boulenger (1885) raised Cope's *Uta thalassina* to generic status (*Petrosaurus*), but Cope (1900) rejected this proposal and made *Petrosaurus* a third synonym of *Uta*. In 1888 Cope erected the genus *Lysoptychus* (*L. lateralis*=*Sceloporus couchi*) on the basis of a single specimen that appeared to have a well-developed gular fold. Subsequent investigation (Stejneger, 1904) showed the "gular fold" to be an artifact of preparation on a single specimen which "was preserved in such a manner as to make a fold across the neck, which formed the basis for the erection of the genus" (Smith, 1939, p. 242). Dickerson (1919) described the genus *Sator* (*S. grandaevus*) which has persisted despite *Sator*'s close similarity to *Uta*, *Urosaurus* and *Sceloporus*. In 1942 Mittleman resurrected the genera *Urosaurus* and *Petrosaurus*. He also erected the genus *Streptosaurus* based on *Uta mearnsi*, which is most similar to *Petrosaurus*. He proposed that *Uta*, *Urosaurus*, and *Sator* all arose independently from *Sceloporus*. He placed *Phrynosoma* with the above genera in a distinct group. Smith (1946) moved *Sauromalus* and *Dipsosaurus* to more primitive positions but otherwise retained Mittleman's arrangement. Savage (1958) placed *Streptosaurus* in synonymy with *Petrosaurus*. He separated *Uta* from *Urosaurus* mainly on the basis of sternal and costal morphology. He placed *Uta* and *Petrosaurus* with the sand lizards (*Holbrookia*, *Uma*, and *Callisaurus*), leaving *Sceloporus*, *Sa-*

tor, and *Urosaurus* together. Etheridge (1964) rejected Savage's wide separation of *Uta* and *Urosaurus*, and placed *Uta*, *Urosaurus*, *Sator*, and *Sceloporus* on one side and *Uma*, *Holbrookia*, and *Callisaurus* on the other. Primitive to both groups was *Petrosaurus*. A sand lizard resurrected by Clarke (1965) was Troschel's (1852) genus *Cophosaurus* (*C. texanus*, previously *Holbrookia texana*).

Presch (1969) rejected Etheridge's removal of *Phrynosoma* from the sceloporines and placed *Phrynosoma* with the sand lizards as a primitive member of that group. On the basis of scleral ossicles, Presch (1970) indicated that *Petrosaurus* is a primitive member of the *Sceloporus* branch. Ballinger and Tinkle (1972) proposed an early separation of the *Uta* and *Petrosaurus* stock from the ancestor of *Urosaurus*, *Sator*, and *Sceloporus*.

Several characters suggest further modification of the above arrangement. Our proposed phylogeny of sceloporine genera is illustrated in Figure 1. *Urosaurus* shows a tendency for enlarged scales near the midline of the dorsum. This trend is further developed in *Sator*, which has enlarged dorsals and granular laterals. The migration of enlarged scales around the sides of the body and the increase in scale size and degree of imbrication, mucronation, and carination is a general trend along the chain of genera from *Petrosaurus* to *Sceloporus*. The new phylogeny is also supported by the gradual decrease in development of the gular fold, which is completely lost in all species of *Sceloporus* in Group III. Most of the species in Group I have what Smith (1939) called a rudimentary gular fold. Some of the species in Group II show a less pronounced tendency to develop a gular fold, and Group III lacks it completely. The gradual loss of the gular fold in the *Sceloporus* complex is more probable than a loss (from *Petrosaurus* to *Sceloporus*) and subsequent redevelopment (from *Sceloporus* to *Uta*, *Urosaurus*, or *Sator*). This reversal of the phylogeny resolves a question raised by Smith (1946:178): "It is a curious fact that all genera that have sprung from *Sceloporus* have developed a gular fold—including *Sator*, a Baja California genus. The tendency to develop this fold appears to be restricted to the primitive groups of *Sceloporus* . . . and these are the groups from which *Uta*,

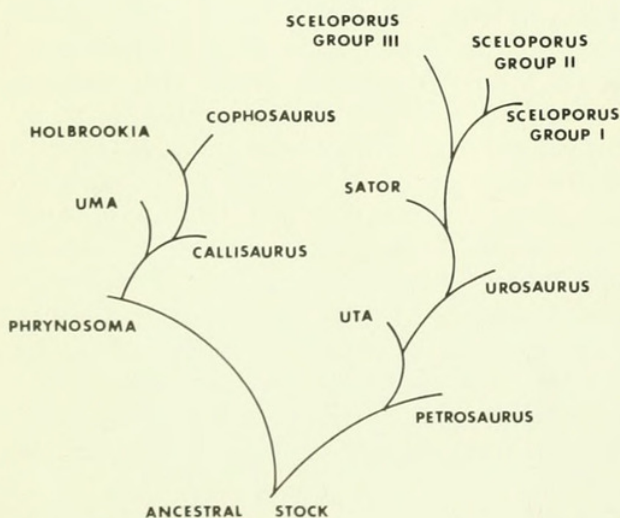


Fig. 1. Phylogeny of sceloporine genera and the three major groups in *Sceloporus*.

Urosaurus, and *Sator* independently appear to have been derived."

Although Smith pointed to this problem, he nevertheless accepted Mittleman's arrangement of the sceloporine genera. More recently, Smith (per comm.): has agreed that *Sceloporus* may be derived with respect to *Uta*, *Urosaurus*, and *Sator*. This position has also been suggested by Hall (pers. comm.): "Inspection of the structure of the femoral pores and their surrounding scales, and the development of mucronation and carination of the body scales, to mention but two sets of characters in various primitive *Sceloporus* and in other sceloporine genera, will suggest that *Sceloporus* is derived even in respect to *Uta* and *Urosaurus*."

We suggest the following conclusions with regard to the new phylogeny and published data on hip ratios of displaying males (Purdue and Carpenter, 1972a, 1972b). The hip ratio (vertical hip movement to vertical eye movement) increased from *Petrosaurus* (0.68) to *Uta* (average 0.74) to *Urosaurus* (average 1.06). After the transition from *Sator* (no published data on hip ratios) to *Sceloporus*, the trend reversed and hip ratios decreased from an average of 1.21 in Group I to 0.66 in Group II to 0.34 in Group III (averages computed from Purdue and Carpenter, 1972b).

Etheridge (1964) illustrated clavicles and scapulocoracoids of 8 sceloporine genera (excluding *Phrynosoma*). If his drawings are superimposed on the new phylogeny (Fig. 2), two trends are apparent: (1) a gradual development of the scapular fenestra (top groove) from *Petrosaurus* to *Sceloporus* Group III, and (2) an increase in size of the clavicular hook. If *Urosaurus* and *Uta* were derived from *Sceloporus*, the scapular fenestra would have developed and then disappeared from *Petrosaurus* to *Sceloporus* to *Uta*. This improbable reversal is similar to the problem with the gular fold. We are persuaded that the new phylogeny is more probable.

INTRAGENERIC PHYLOGENY

The first phylogenetic schemes for the genus *Sceloporus* were proposed by Smith (1934, 1937a, 1937b, 1938, 1939). Other workers have recently modified the phylogeny on the basis of karyology (Cole,

1970, 1971a, 1971b; Hall, 1971, 1973), and behavior (Bussjaeger, 1971).

Larsen and Tanner (1974) redefined relationships among the species in the genus *Sceloporus*. We used Ward's cluster analysis (Wishart, 1968) to cluster 55 species on the basis of external characters, cranial osteology, karyology, behavior, and zoogeography (Fig. 3). We then used step-wise discriminate analysis (Dixon 1967) and found that the arrangement of groups and subgroups is significant at the .999 level of confidence (Table 1).

Although Ward's cluster analysis provides a phenetic dendrogram, it does not give any indication as to which branch of a cluster is derived and which is primitive. In 1939 Smith said, "The most primitive form of this group is undoubtedly *lunaei* which is closely related to *formosus malachiticus*" (p. 60). In other words, *lunaei* is the most primitive form

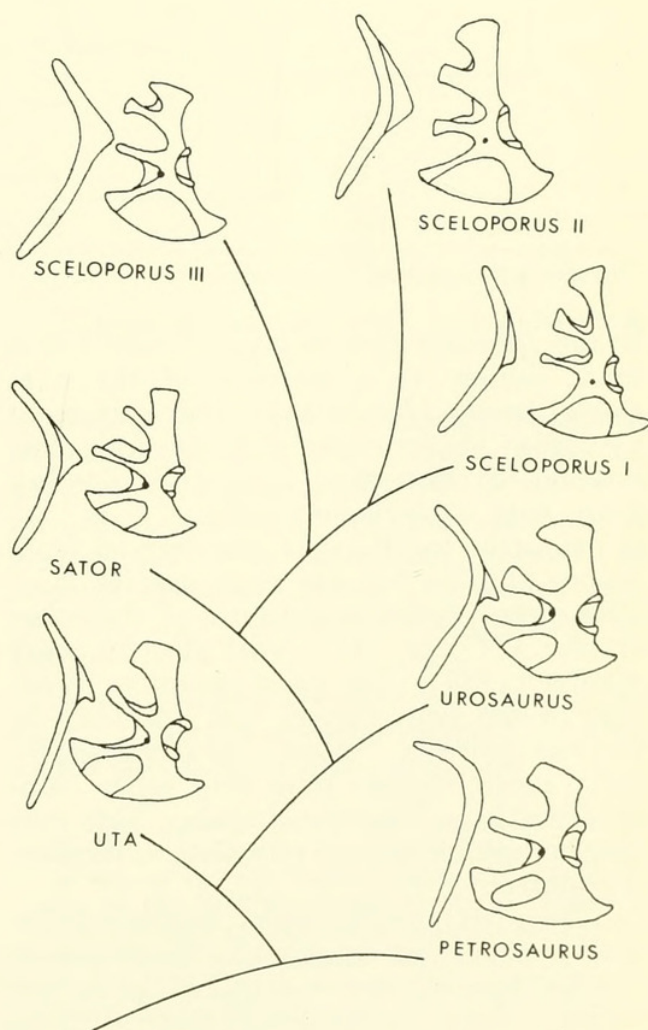


Fig. 2. Clavicles and scapulocoracoids of several sceloporines. All illustrations except *Sceloporus* I, *Sceloporus* II, and *Sceloporus* III are from Etheridge (1964).

TABLE 1.—Groups and subgroups in the genus *Sceloporus*

Group I (7 spp.)	Group II (20 spp.)	Group III (33 spp.)
Subgroup A (1 spp.) gadoviae	Subgroup A (7 spp.) grammicus	Subgroup A (9 spp.) spinosus
Subgroup B (2 spp.) couchi	pictus	orcutti
merriami	megalepidurus	clarki
Subgroup C (4 spp.) maculosus	cryptus	melanorhinus
parvus	shannonorum*	magister
jalapae	heterolepis	olivaceus
ochoterenae	asper	cautus
	Subgroup B (2 spp.) pyrocephalus	horridus
	nelsoni	edwardtaylori
	Subgroup C (3 spp.) scalaris	Subgroup B (7 spp.) formosus
	goldmani*	lunaei
	aeneus	malachiticus
	Subgroup D (4 spp.) siniferus	Subgroup C (5 spp.) undulatus
	carinatus	virgatus
	utiformis	woodi
	squamosus	occidentalis
	Subgroup E (4 spp.) variabilis	graciosus
	cozumelae	Subgroup D (4 spp.) jarrovi
	teapensis	lineolateralis
	chrysostictus	ornatus
		dugesi
		Subgroup E (8 spp.) torquatus
		cyanogenys
		bulleri
		insignis*
		macdougalli
		mucronatus
		serrifer
		poinsetti

*Species not examined in this study.

in the *spinosus* species group because it is most similar to a member of the next closest group (*formosus*). This statement by Smith is consistent with the following method of converting a phenetic dendrogram into a phylogeny (Fig. 4): If "A" is primitive to "B" it is less derived from (more similar to) the stem species "G." The more primitive member of the other cluster ("C" or "D") will also be more similar to "G." The more primitive members of the two clusters will therefore be phylogenetically "closer" and phenotypically more similar than any other combination from the two clusters. This rule can be applied objectively with a similarity matrix.

When all possible pairs between adjacent clusters are compared, the two most similar species are considered primitive within their respective clusters. This technique will convert a dendrogram into a phylogeny.

Ward's cluster analysis and the above phylogeny technique were repeated sever-

al times using external and osteological characters, distribution, karyology, behavior, and combinations of the above. (See Larsen and Tanner, 1974, for a presentation of results.) The differences among results were resolved subjectively to produce a composite phylogeny (Fig. 5). This procedure is based on several assumptions which are admittedly vulnerable. To restrict the scope of our study it was assumed that the alpha taxonomy is complete and correct. That is, it was assumed that all species of *Sceloporus* are now named and correctly defined in the literature. Of course, this assumption may be incorrect. But the purpose of our study is to produce a general overview and not a detailed taxonomic review. The details near the ends of branches are therefore tentative and subject to future review.

In spite of the large number of characters considered (over 80), these results are also subject to errors due to parallelism, convergence, varying rates of diver-

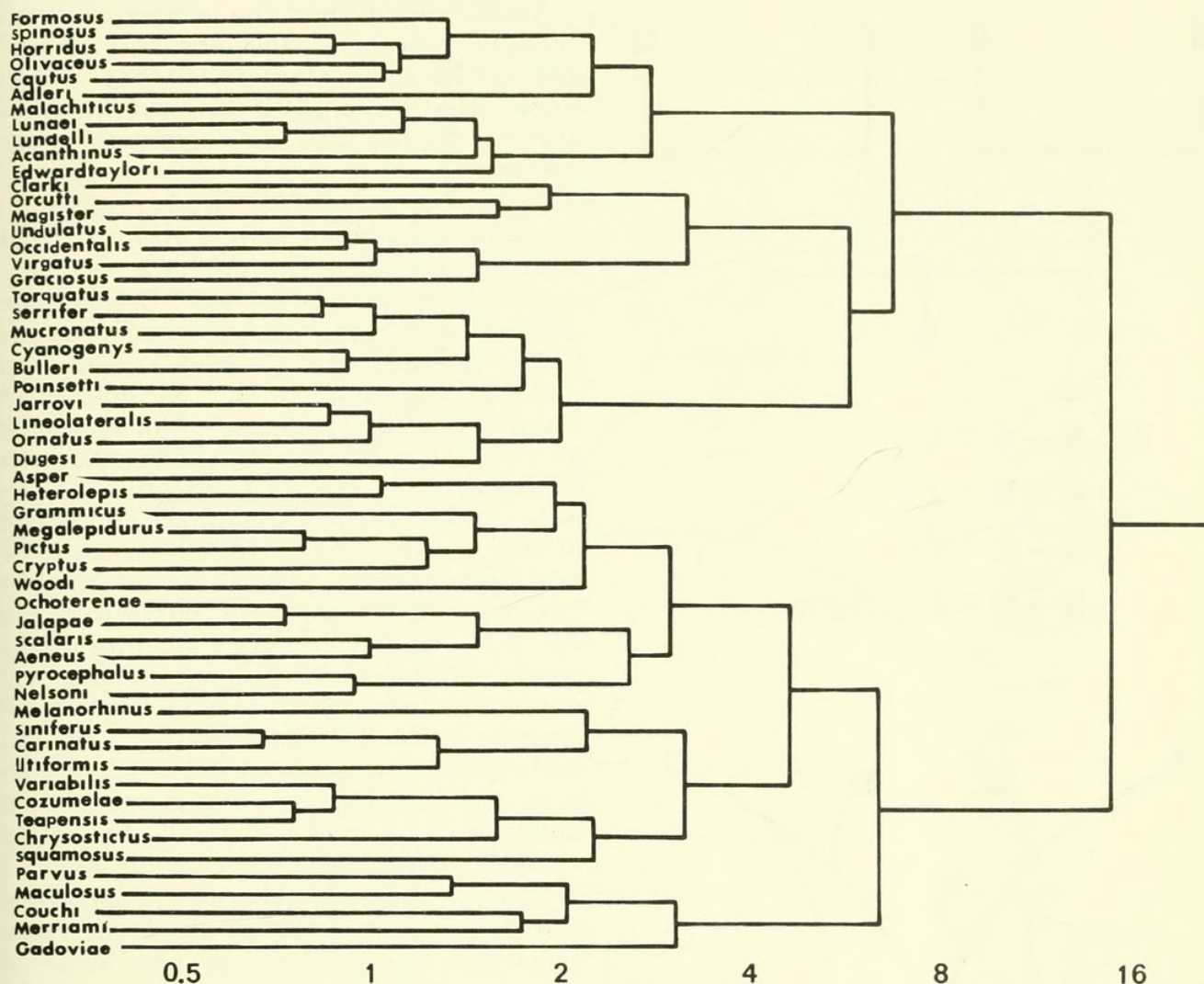


Fig. 3. Dendrogram generated by Ward's cluster analysis of external, skull, and distribution characters (82 characters).

gence, pleiotrophy, and other cases in which the phenotype is not a direct manifestation of the genotype. All phylogenetic conclusions are subject to these limitations, and the systematist can do little more than acknowledge the circumstantial nature of his evidence.

We propose that *Sceloporus* is derived from *Uta* through *Urosaurus* and *Sator* (see above). Smith (1938) suggested that the connection between these genera is from *Urosaurus ornatus* to *Sceloporus couchi*. Smith included *couchi* in the *variabilis* species group.

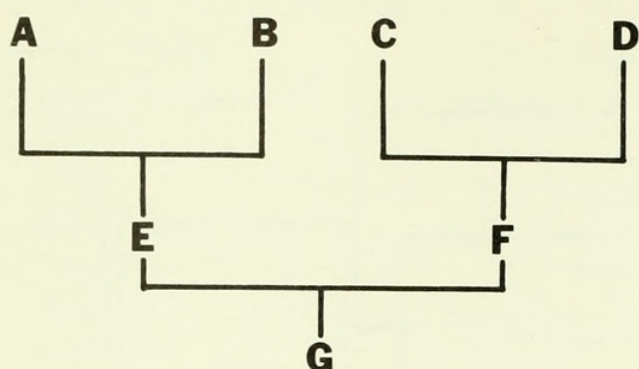
Figure 6 shows the arrangement of species in Smith's *variabilis*, *maculosus*, and *merriami* groups according to Smith (1939, Fig. 42) and the new phylogeny. Four of these species (*couchi*, *parvus*, *maculosus*, and *merriami*) are transferred to Group I. Smith may have allowed for this by placing these four species on one side of his tree next to *Uta*. If *Uta* (*Uta*,

Urosaurus, and *Sator*) is considered primitive to *Sceloporus*, then Smith's evidence supports our conclusion that Group I is primitive to the other two groups in *Sceloporus*. The remaining species in Smith's *variabilis* group (*variabilis*, *cozumelae*, and *teapensis*) are placed in Group II.

Smith (1939:239) allowed for the removal of *parvus* and *couchi* from the *variabilis* group with this statement:

That *parvus* and *couchi* are only distantly related to the remainder of the group is shown by the widely different character of the ventral coloration in the males, smooth head scales, larger number of femoral pores, and general habitus. . . . It is my belief that this section approaches more closely the ancestral stock of *Uta* than the other species of the *variabilis* group.

Smith (p. 239) also associated *merriami* with *Uta*: "It would appear that *merriami* is closely related to *Uta*, and that *Uta*



IF $A - C = 1$
 $A - D = 2$
 $B - C = 2$
 $B - D = 3$ THEN...

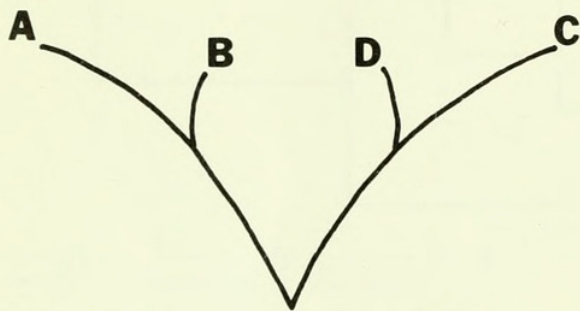


Fig. 4. Phylogeny theory. If the phenetic distance between "A" and "C" is less than that between any other pair, then "A" and "C" are primitive members in clusters "E" and "F."

arose from the forms now extinct which closed the present gap between *couchi* and *merriami*." Note that our new arrangement places *merriami* and *couchi* together.

Another divergence from Smith's phylogenetic tree is the addition of *chrysostictus* to the *variabilis* group. Smith (p. 239) supports this inclusion (and the close proximity of the *siniferus* group): "Another group closely related to the *variabilis* section is the *siniferus* series, which closely approaches the *variabilis* group through *cupreus*. . . . The *chrysostictus* group is also closely related."

Thus it can be seen that Smith allowed for the possibility of removing *parvus* and *couchi* and adding *chrysostictus*, which changes his *variabilis* group into the new *variabilis* group.

Smith stated that the *siniferus* group "closely approaches the *variabilis* group" and yet his illustration (1939, Fig. 3) has these groups separated by several other groups. In the new phylogeny they are adjacent.

Figure 7 compares Smith's arrangement of his *chrysostictus*, *utiformis* and *siniferus* groups with the new arrangement of the same species. Besides the placing of *chrysostictus* in the *variabilis* group (which has already been explained), the only major difference in Figure 4 is the removal of *ochoterenae* to place it in Group I. (The inclusion of *utiformis* in the *siniferus* group is minor). Smith listed 11 diagnostic characters of the *siniferus* group. In three cases he said "except *ochoterenae*" and in another "except *ochoterenae* and *cupreus*." He (p. 301) said, "Postanals tending to be poorly developed (except *ochoterenae* and *cupreus*); two postrostrals (except *ochoterenae*, without postrostrals); . . . ventral scales pointed or, at least not notched (except *ochoterenae* in which they are notched) . . . males without distinctive ventral coloration (except *ochoterenae*)."

If size is discounted, then *ochoterenae* is different in 4 of the 10 diagnostic characters for the *siniferus* group. *S. ochoterenae* also has more femoral pores than any other species in Smith's *siniferus* group. Smith's conclusions, therefore, would not be seriously challenged if *ochoterenae* were removed from the *siniferus* group and placed in Group I next to *jalapae*. In fact, when describing *ochoterenae*, Smith (p. 309) said, "three or four scales on anterior border of ear, not so large as in *jalapae*." So apparently he was comparing these two species.

Smith included *jalapae* in his *scalaris* group, which is otherwise identical to the new *scalaris* group (Fig. 5). Removing *jalapae* from the *scalaris* group to place it in the primitive Group I is supported by the following statement by Smith (p. 331):

The only species doubtfully included in this group is *jalapae*, which differs from the remaining forms in having lateral scales in distinctly oblique rows, and in lacking postrostrals [as does *ochoterenae*]. . . .

S. jalapae is clearly the most primitive member of the group. *S. scalaris*, *aeneus* and *goldmani* are clearly more closely related to each other than any one of these is to *jalapae*.

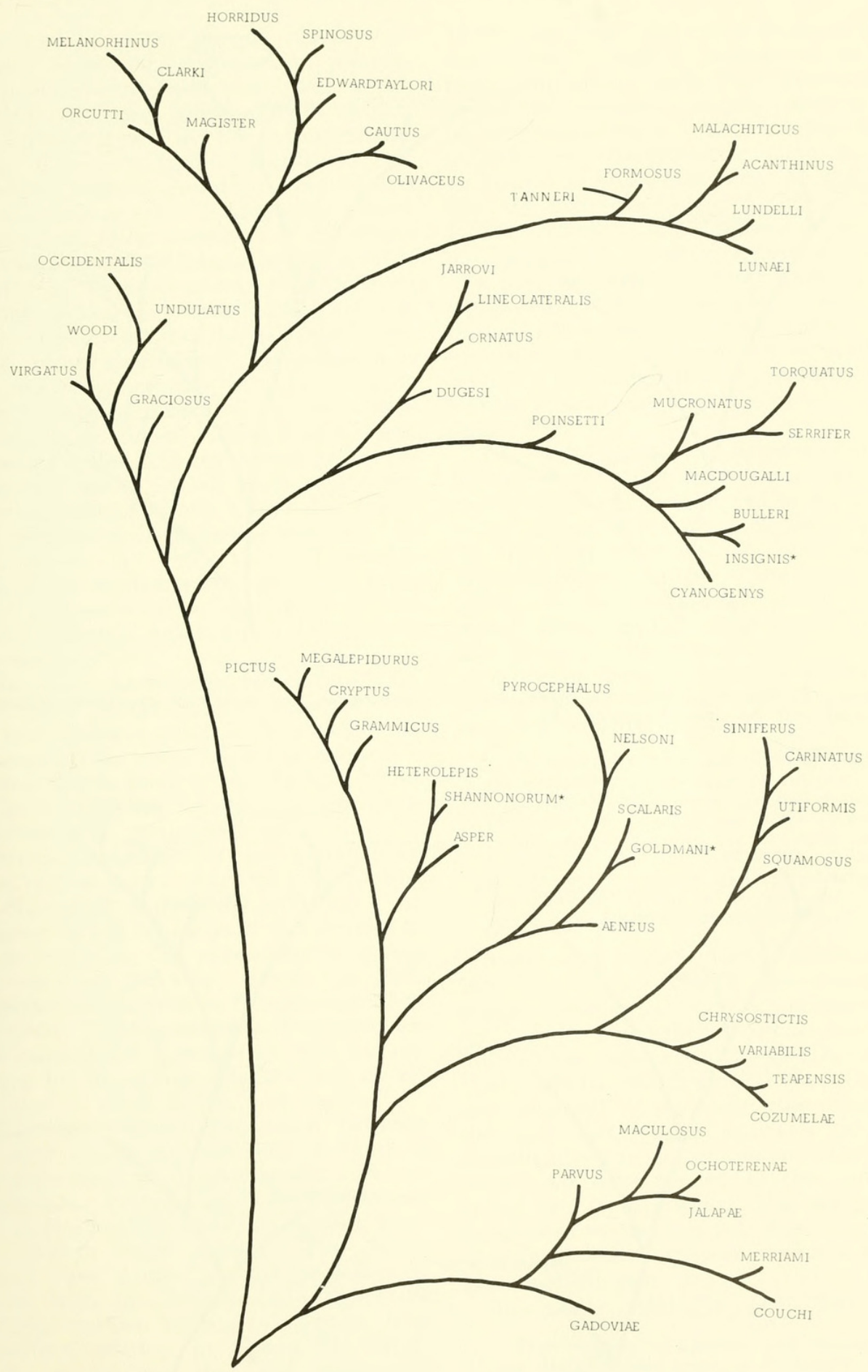


Fig. 5. Proposed phylogeny for the genus *Sceloporus*. (* = species not examined.)

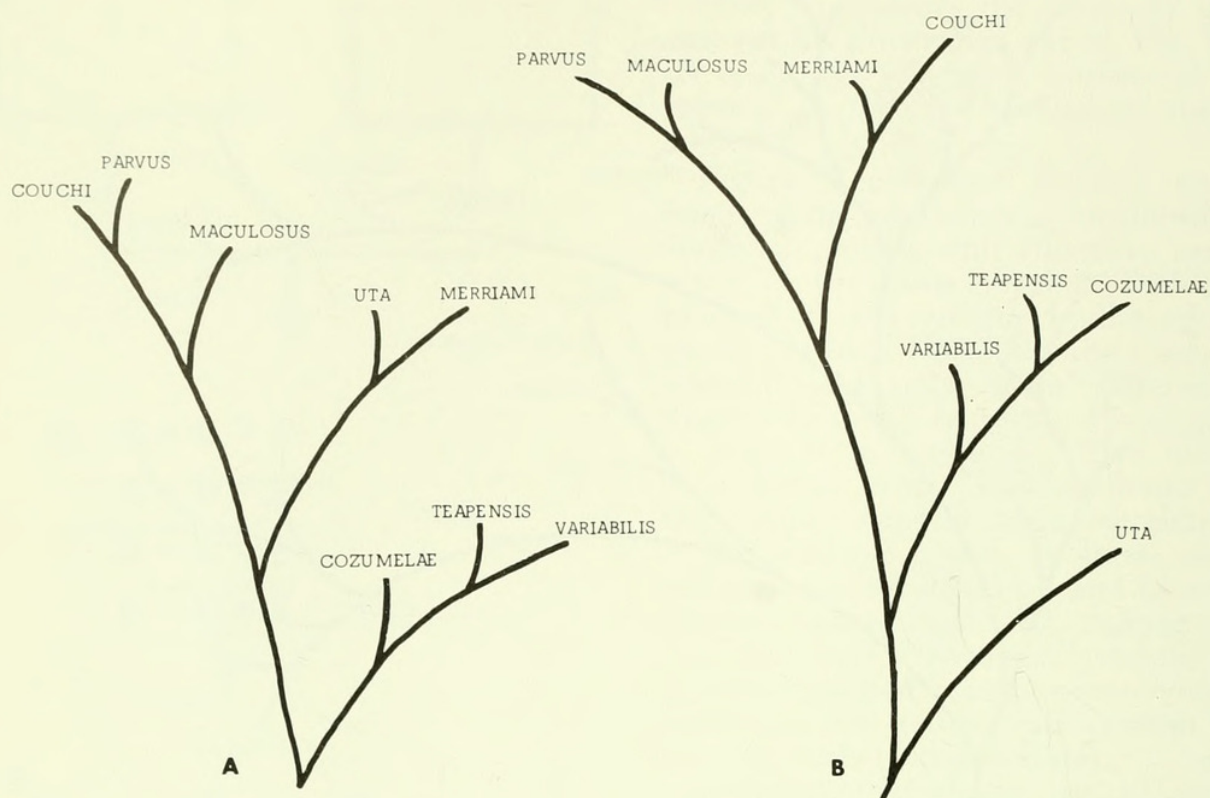


Fig. 6. Phylogeny of Smith's (1939) *variabilis*, *maculosus*, and *merriami* groups according to Smith (A) and the new phylogeny (B).

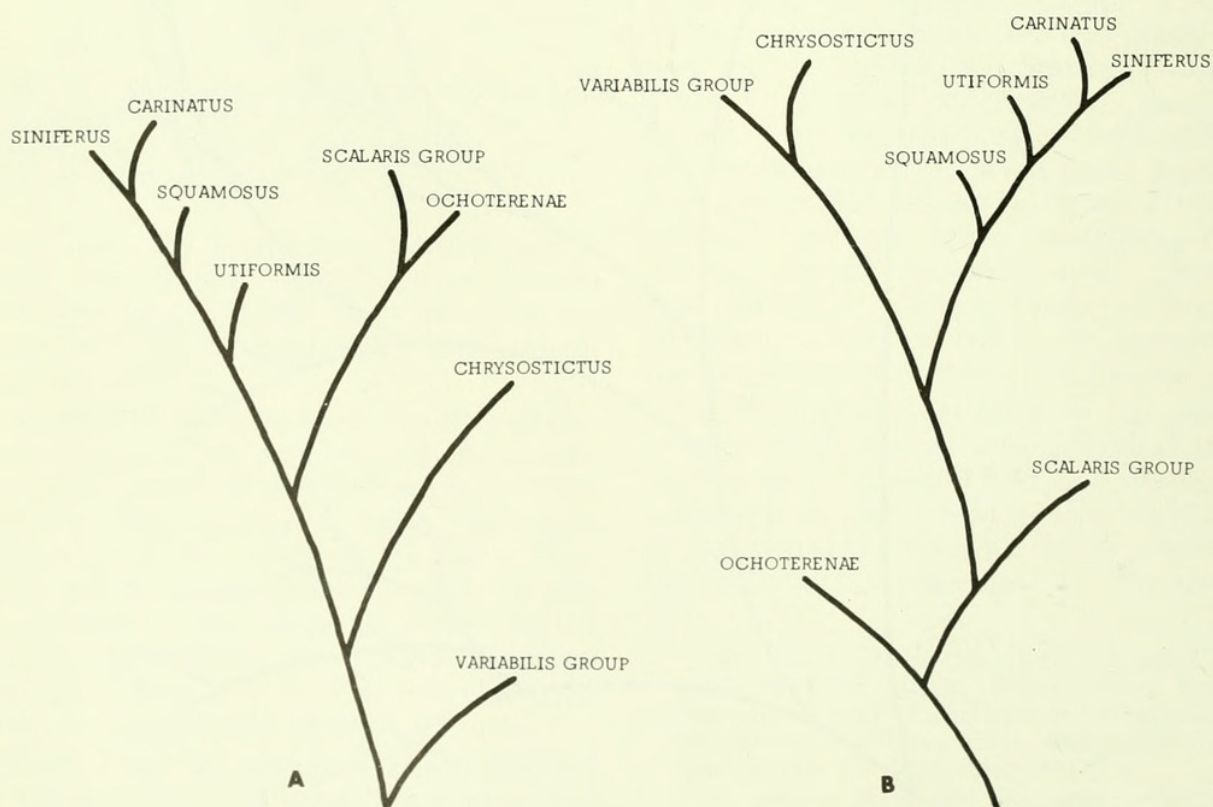


Fig. 7. Phylogeny of Smith's (1939) *chrysostictus*, *utiformis*, and *siniferus* groups according to Smith (A) and the new phylogeny (B).

Group I includes: *parvus*, *couchi*, *maculosus*, *merriami*, *ochoterenae*, *jalapae*, and *gadoviae*, the most primitive. Smith (p. 362) included *gadoviae* with *nelsoni* and *pyrocephalus* in the *pyrocephalus* group. But once again he outlined reasons why *gadoviae* could be removed and placed in Group I. "*S. gadoviae* differs widely from other members of the group in having very small dorsal scales, a large number of femoral pores, a postfemoral dermal pocket, very small scales on posterior surface of the thighs, and many other minor characters." *S. gadoviae* is also the only member of this group to have a vestigial gular fold as mentioned by Smith (p. 374): "scales immediately preceding gular fold region somewhat reduced in size." All of these characters are diagnostic of Group I, and this primitive placement is therefore natural. In fact, Smith (p. 363) said, "I assume *gadoviae* to be nearest the primitive type, as it retains certain characters of the *variabilis* group, from which I believe it was derived."

The main character on which Smith (p. 363) based his inclusion of *gadoviae* with the *pyrocephalus* group is the strong compression of the tail: "That the group is a natural one is more or less assured by its compact range and by the common character of the compressed tail, which is otherwise unknown in the genus." In view of the many characters supporting the placement of *gadoviae* in Group I, we propose that a compressed tail developed twice: once in the *pyrocephalus* group, and once in *gadoviae*. Smith (p. 363) gave further support to this placement of *gadoviae*: "The assumption that *gadoviae* is a remnant of a primitive stock is supported by its secretive habits and its restriction to a somewhat arid region."

The most serious difference between the new phylogeny and that of Smith is the placement of the *grammicus* and *megalepidurus* groups. In both phylogenies the species are arranged in a similar manner within these groups. But Smith placed these groups next to the *formosus* group with the large-scaled, large-sized species, and we have moved them to a primitive position in Group II. However, we propose that the *grammicus* group (we have combined Smith's *grammicus* and *heterolepis* groups) is the most primitive in Group II. In fact, Smith

(1938:552) said "the *microlepidurus* [our *grammicus*] group is assumed to be the most primitive of these [the large-scaled, large-sized species], largely because of its very small scales." This greater separation between the *grammicus* and *formosus* groups is further justified by the fact that the diploid number of chromosomes is 22 (derived) in the *formosus* group and 32 (primitive) in the *grammicus* group. We propose, therefore, that some of the similarities between *grammicus* and *formosus* (coloration, dorsal-scale count, ovoviviparity, and preference for an arboreal habitat) are a result of convergence as is true of *gadoviae* and the *pyrocephalus* group.

The only remaining difference from Smith's *formosus* group is his inclusion of *asper*, which we have moved to the *grammicus* group. This move is justified by the fact that *asper* has 32 chromosomes, as do the other members of the *grammicus* group. If the *grammicus* group is removed from Smith's large-scaled, large-sized branch, the remaining species are the same as those included in Group III. This grouping (the omission of *grammicus*) was allowed by Smith (1938:552):

The relatively small size of the species of the *undulatus* group must be assumed as a parallel development rather than a direct inheritance of the small size of the ancestor in the *variabilis* group, for the close relationship of the *spinosus* and *undulatus* groups cannot logically be disputed, nor is the close relationship of the *spinosus*, *torquatus* and *formosus* groups doubtful."

Smith and Taylor (1950) included the following species within the *undulatus* group: *undulatus*, *cautus*, *occidentalis*, and *woodi*. Since then, *virgatus* has been raised from subspecific to specific status (Cole, 1963). Smith (1939) placed *graciosus* adjacent to the *undulatus* group, so the only discrepancy between the two classifications is the placement of *cautus*, which we have moved to the *spinosus* group next to *olivaceus*. This movement is justified by the fact that there is a zone of intergradation between *cautus* and *olivaceus* (Hall, pers. comm.).

Bussjaeger (1971:151) remarked:

The relation of *cautus* and *olivaceus* and the *undulatus* group of *Sceloporus* has been questioned. Hall's data indicated that these two species were the same and limited data on their displays indicate that they are similar. If one accepts that they are syn-

onyms, then *olivaceus* (*cautus*) would be the connecting link between the *spinosus* and *undulatus* groups.

However, rather than use these forms as a link between species groups, we have placed them together in the *spinosus* group.

Smith (1938:554) indicated that the *torquatus* group consisted of 2 subgroups: "It appears that soon after the separation of the *torquatus* stock from the other groups of *Sceloporus*, there was a separation into two divisions, one of which exhibited a tendency to develop small scales, the other large scales." We have recognized the small-scaled division as the *jarrovi* group.

Figure 8 shows the phylogeny of the *jarrovi* group according to Smith (1938, Fig. 4) and the new arrangement. Although he placed *lineolateralis* further away from *jarrovi* in his diagram, Smith (p. 556) did say, "*S. jarrovi* appears to be most closely related to *lineolateralis*. From this species, or its ancestors, the remaining species of the small-scaled division have obviously been derived."

Figure 9 shows the phylogeny of the *torquatus* group according to Smith (1938,

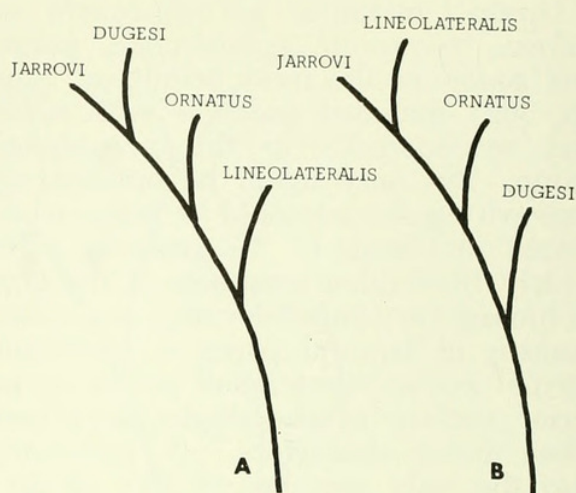


Fig. 8. Phylogeny of *jarrovi* group according to Smith (1938) (A) and the new phylogeny (B).

Figs. 3-4) and the new arrangement. There seems to be little similarity here, except that *torquatus* is derived from *serrifer*, and *poinsetti* is derived from *cyanogenys* in both trees. Smith (1938: 555) raised a question about the ancestral position of *serrifer*:

S. serrifer appears to be the oldest of the large-scaled species. The postulation that this species, which is one of the larger ones

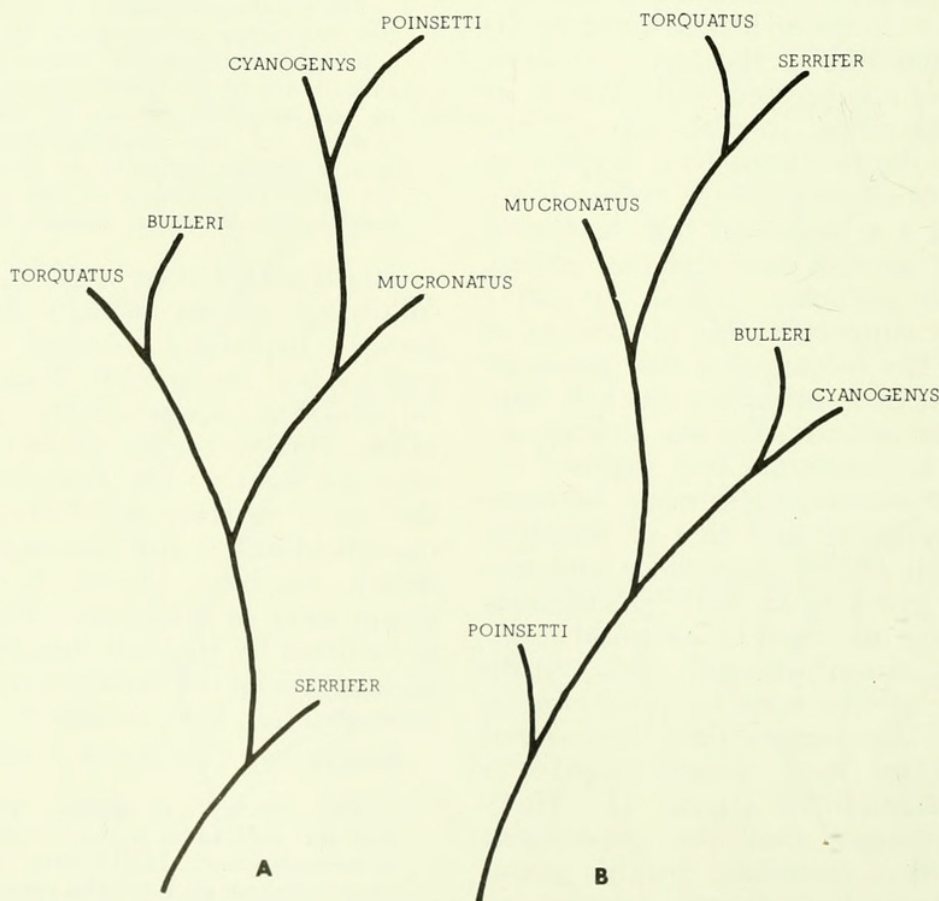


Fig. 9. Phylogeny of *torquatus* group according to Smith (1938) (A) and the new phylogeny (B).

of the genus, and one having large scales, is nearest to the ancestral type of the large-scaled division of the *torquatus* group may appear to be contradictory to the postulation that *Sceloporus* is derived from small species with small scales. However, my assumption seems to be justified by the fact that *serrifer* occupies a southern position on the periphery of the geographical area now occupied by the *torquatus* group.

The reason for this paradox is that Smith assumed speciation in Group III was from south to north. The data in 1938 strongly supported this conclusion. Obviously, Smith did not believe that a peripheral location is necessarily primitive, because on the next page (556) he said, "*S. mucronatus* appears to be the nearest to the ancestral type of these three species (*cyanogenys*, *poinsetti* and *omiltemanus*) despite the fact that it has larger scales than they. I so conclude because of its centralized geographical position with relation to the area occupied by the other three forms."

So the basic problems can be solved, and the trend is indeed from small to large size and small to large scales if this group was developed from north to south rather than south to north. Smith indicated a northward development from *serrifer* to *torquatus* to *mucronatus* to *cyanogenys*, and our phylogeny indicates a southward development from *cyanogenys* to *mucronatus* to *serrifer* to *torquatus*. An ancestral placement of *cyanogenys* is further supported by Smith (1939:209): "Species of this group are as a rule confined to rocky habitats. So far as I am aware, only *cyanogenys* tends to live on or near the ground." Thus, the new phylogeny indicates a trend in this group from small-sized, small-scaled ground dwellers to large-sized, large-scaled rock dwellers. With this reversal in direction, the remaining differences between the two phylogenies in Figure 9 are negligible and the trends within this group fit the overall phylogeny of the genus.

In the genus *Sceloporus*, the *spinosus* group has been the object of more systematic study than any other. No less than four different phylogenetic trees have been proposed by Smith, Bussjaeger, Cole, and Hall. The confusion is further compounded by the fact that the *spinosus* group is the largest in number of species and subspecies. The four phylogenetic trees and our conclusions are presented in Figure 10. Smith (1939) included *acanthinus*, *lunaei*, and *lundelli* with this group. In 1950, he and Taylor moved *acanthinus*

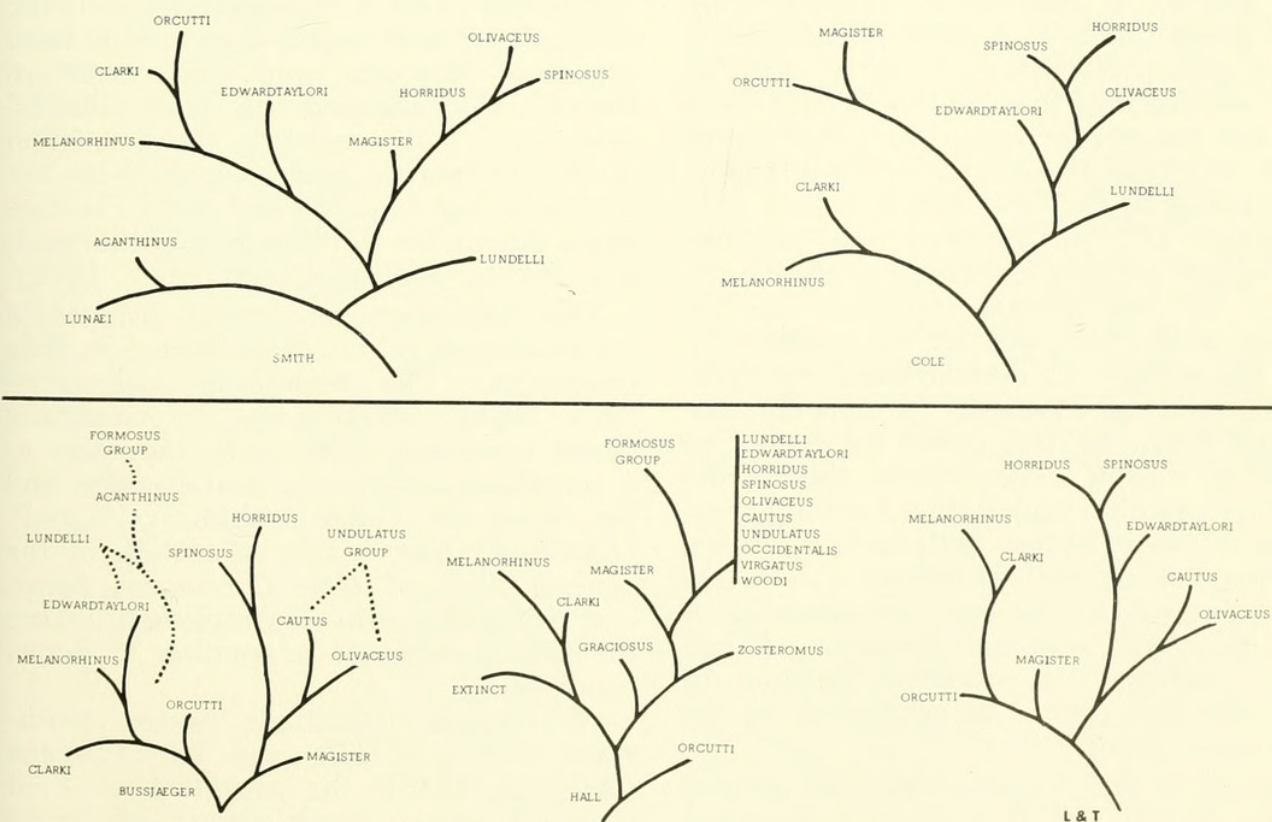


Fig. 10. Phylogeny of *spinosus* group according to Smith (1939), Cole (1970), Bussjaeger (1971), Hall (pers. comm. 1973), and the new phylogeny (L and T).

and *lunaei* into the *formosus* group. However, in 1939 Smith (p. 60) said, "The most primitive form of the group is undoubtedly *lunaei*, which is closely related to *formosus malachiticus*. *S. acanthinus* is a near relative of *lunaei*, as is also *lundelli*." It should therefore be acceptable to remove *lundelli* from the *spinosus* group and place it in the *formosus* group next to *lunaei* as we have done.

Behavioral data also support this arrangement. Bussjaeger (1971:136) observed:

The display-action-patterns of *lundelli gaigei* of the *spinosus* group and *asper*, *acanthinus acanthinus* and *a. lunaei* of the *formosus* group were quite similar with peaked single units and multiple units. *Sceloporus asper* and *lundelli* seemed to share more elements.

In his conclusions, Bussjaeger (p. 151) anticipated the new position of *S. lundelli*:

The status of *lundelli* is questionable. . . . Its display-action-pattern was between *acanthinus* and *orcutti*; but the pattern was based on only one female. More data are needed to establish this species relationship. At present it should be left in the *spinosus* group, although it appears to be closer to the *formosus* group.

Cole's (1970) phylogenetic tree would not allow the removal of *lundelli* from this group unless *melanorhinus* and *clarki* were placed elsewhere. Cole (p. 39, Fig. 17) showed how four centric fusions could change the *melanorhinus-clarki* karyotype into the typical pattern for this group. According to Cole's assumption that only fusions (i.e., no fissions) are possible, *melanorhinus* and *clarki* are primitive not only for this group, but also for the genus *Sceloporus*, and for the entire family Iguanidae! As demonstrated by Webster, Hall, and Williams (1972), chromosomal evolution can occur by fission as well as fusion. We believe this is the only acceptable explanation for the karyotype in *melanorhinus* and *clarki*. If fission is accepted as well as fusion, Cole's data provide support for our arrangement of *orcutti*, *clarki*, and *melanorhinus*. (They also confirm the primitive position of *lundelli* and permit its placement in the *formosus* group.)

If *clarki* and *melanorhinus* are derived from *orcutti* and if *lundelli* is removed from the group, then the only difference between Cole's tree and ours is a minor

shift in the position of *edwardtaylori*. The single remaining difference between Smith's tree and ours is the placement of *edwardtaylori*. The close relationship of *edwardtaylori* to *spinosus* and *horridus* has been proposed by Cole and also by Hall. The justification is that the species clustering on one side (*olivaceus*, *cautus*, *edwardtaylori*, *spinosus*, and *horridus*) all have 22 chromosomes, whereas *orcutti* has 34, *magister* has 26, and *clarki* and *melanorhinus* each have 40.

ZOOGEOGRAPHY

The phylogeny of the genus *Sceloporus* can be considered with its present geographical distribution to produce a theoretical history of events in the speciation in this genus. We conclude that the ancestral sceloporine was a tropical or subtropical lizard (as Smith reasoned) with a distribution somewhat matching the subtropical conditions of western America before the Madro-Tertiary revolution (Ballinger and Tinkle (1972:63). This distribution was not restricted to southern Mexico, where Smith proposed the beginning of *Sceloporus* evolution, but covered a vast area in the western United States extending as far north as Canada.

Milstead (1960:76) said, "Formation of the western deserts is presumed to have begun in Miocene times and continued through Pliocene and into early Pleistocene times." Accordingly, the derivation of the Sceloporine genera could have occurred in late Miocene and early Pliocene times during the development of the western deserts (Ballinger and Tinkle, 1972).

The formation of deserts trapped a mesic-adapted relict (*Petrosaurus*) in Baja California. The remaining sceloporine stock began adapting to the oncoming desert conditions with such characters as a lengthened, sinuous nasal passage and the behavior called "shimmy burial" (Stebbins, 1944). The separation of the generic lines of *Uta*, *Urosaurus*, *Sator*, and *Sceloporus* was accomplished during the initial stages of adaptation to desert conditions.

As tropical conditions moved southward during middle and late Pliocene (Axelrod, 1948), the ancestral stock of Group I moved south almost as far as the Isthmus of Tehuantepec. Some populations did not migrate, but remained and

adapted to more xeric conditions (Group III). The mountains of central and southern Mexico provided a barrier that separated the western Group I and eastern Group II populations. A relict genus (*Sator*) was isolated in Baja California at this time (Fig. 11). The subsequent development of Groups I and II was a matter of adaptive radiation and centrifugal speciation (Brown, 1957).

Figure 12 shows the routes of speciation in Group I. The eastern branch extended from *gadoviae* (in southern Michoacan, Guerrero, Morelos, southern Puebla, and northwestern Oaxaca) northward across the Oaxaca Upland, the Neovolcanic Plateau and into the Sierra Madre Oriental to *parvus* (in Nuevo Leon, southeastern Coahuila, San Luis Potosi, and Hidalgo). Speciation continued northward along the Sierra Madre Oriental to *couchi* (Nuevo Leon, eastern Coahuila, and southern Texas) and *merriami* (northern Coahuila and adjacent Texas). (Locality information in this discussion is from Smith and Taylor, 1950. Topographical terminology is from Raisz, 1964.)

The second branch of Group I extended from *parvus* to *jalapae* (Veracruz, Puebla, and Oaxaca). This radiation then moved across the Mixtec Upland (along the northern border of Oaxaca) and northward along the western flank of the Sierra Madre del Sur (through Guerrero, Michoacan, Colima, and Jalisco) and



Fig. 12. Speciation in Group I.

further northward along the western flank of the Sierra Madre Occidental (through Nayarit and Sinaloa and into Durango). The Durango populations became *maculosus*, and most of the pathway is now occupied by *ochoterenae*.

Figure 13 shows the initial radiation from the ancestral stock of Group II. This ancestral stock is now represented by *pictus* (in central Puebla and central western Veracruz). The first radiation involved four species in four directions: *aeneus* to the north, *pyrocephalus* to the west, *siniferus* to the south, and *cozumelae* to the east.

Subsequent radiation from these centers is shown in Figure 14. *Sceloporus aeneus* (Puebla, Veracruz, Oaxaca, Hidalgo, Morelos, Mexico, Guanajuato, Michoacan, and Jalisco) produced *scalaris* (in Durango, Guanajuato, Hidalgo, Jalisco, Mexico, Michoacan, Puebla, and Zacatecas). *S. pyrocephalus* (Guerrero, Michoacan, and Colima) produced *nelsoni* (in Chihuahua, Jalisco, Sinaloa, and Nayarit).

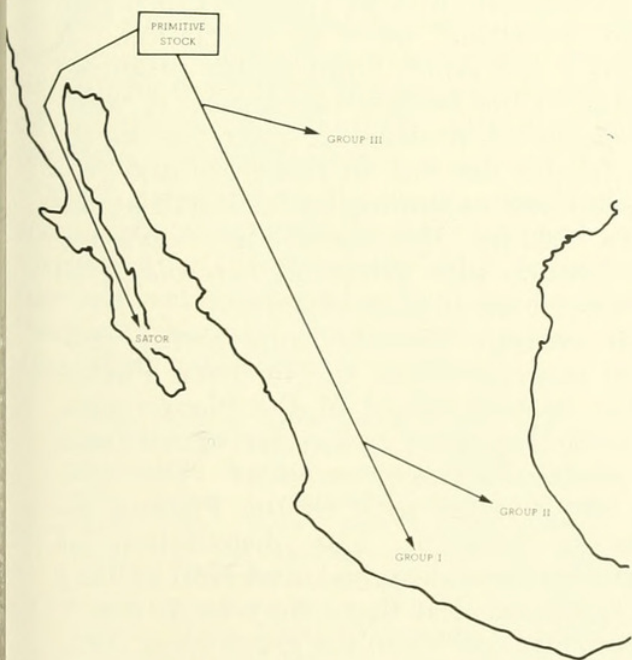


Fig. 11. Isolation of early *Sceloporus* stocks in response to desert formation in middle Pliocene.



Fig. 13. Early radiation in Group II.

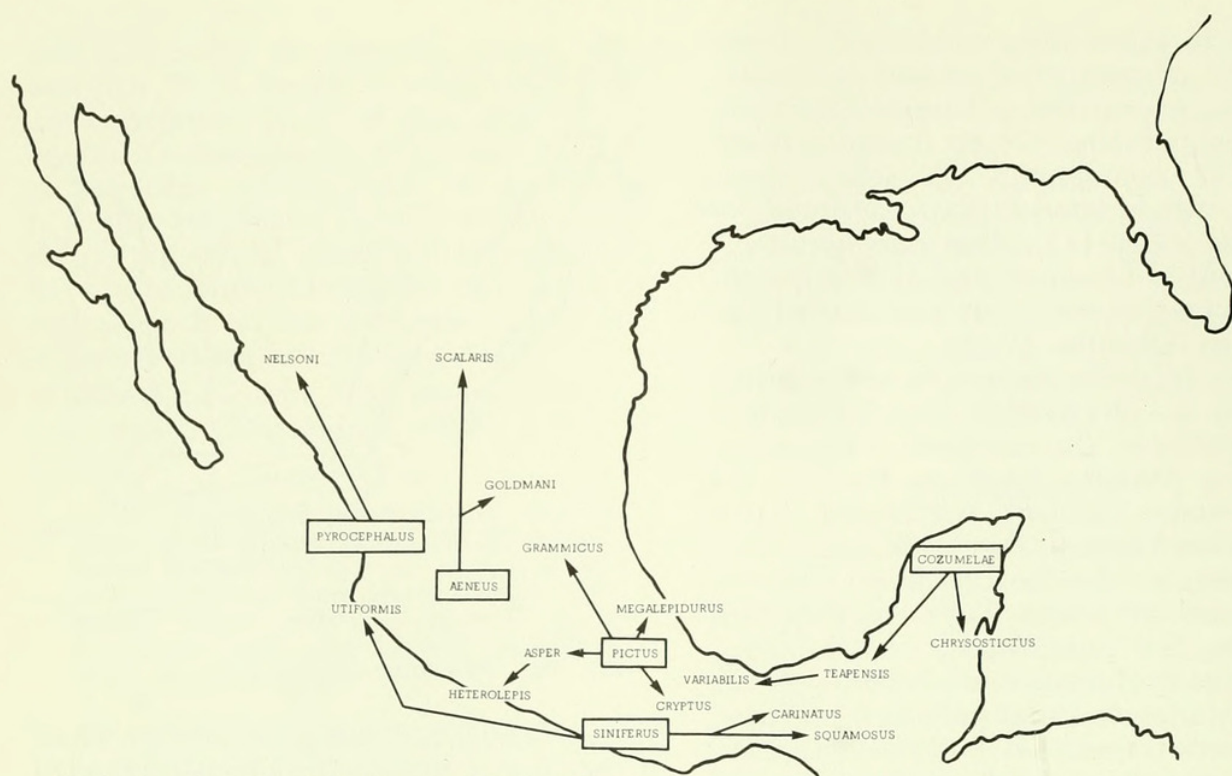


Fig. 14. Second radiation in Group II.

These two species occupy most of the western flank of the Sierra Madre Occidental. According to Hall, the separation of *nelsoni* and *pyrocephalus* occurs along a river in Nayarit (the Rio Grande de Santiago). Concerning this river, Hall (pers. comm., 1973; see also Hall, 1973: 115-125) said:

Evidence from the fresh water fish fauna in the Rio Grande de Santiago (Salvador Contreras B., pers. comm.) suggests that at one time this major river drained the greater part of the Mexican Plateau. Even now it is the outlet for Lake Chapala and the entire Rio Lerma extending east as far as the western border of the Distrito Federal. Although rivers usually are not very effective natural barriers, the steep gradient of this river as it falls off the Plateau and the comparative narrowness of the coastal plain probably would have made it an extremely effective barrier during the Pleistocene pluvial times, which would have provided ample opportunity for the splitting of the proto-*nelsoni* into two stocks.

The southern speciation produced *siniferus* (in Oaxaca, Chiapas, and Guerrero), *carinatus* (in Chiapas), *squamosus* (along the Pacific slopes from Chiapas to Costa Rica), and *utiformis* (to the north along the Pacific slopes of Michoacan, Colima, Jalisco, Nayarit, and Sinaloa). The eastern branch to *cozumelae* (in the northern peninsular states of Yucatan and Quintana Roo) produced *chrysostictus* (in the entire Yucatan Peninsula), *teapensis*

(in southern Veracruz, Tabasco, Campeche, Quintana Roo, northern Guatemala, and British Honduras), and *variabilis* (which has developed subspecies along the Gulf Coast plain from south-central Texas, through Nuevo Leon, Tamaulipas, San Luis Potosi, Queretaro, Hidalgo, Tlaxcala, Puebla, and Veracruz, across the Isthmus of Tehuantepec, through Oaxaca and Chiapas, and into western Guatemala).

The central stock of Group II also produced a second wave of speciation. A southern speciation from *pictus* produced *cryptus* in the Oaxaca highlands. A western speciation resulted in *asper* (in the Sierra Madre del Sur in Guerrero and Michoacan and extending as far north as the Sierra Madre Occidental in Nayarit). This branch also produced *heterolepis* in the coastal mountains of Jalisco.

An eastern branch from *pictus* produced *megalepidurus* in Northern Puebla on the eastern slopes of the Neovolcanic Plateau. The most recent derivation from the *pictus* stock is *grammicus*. This species has invaded most of the Plateau regions in Mexico. The distribution of *grammicus* is widespread, and Hall (1971) has suggested that there may be as many as 6 cryptic species in the *grammicus* complex. Further discussion of this species must therefore be deferred until the alpha taxonomy is more complete.

Speciation in Group III was more complex and probably more recent than in the others. Other workers have suggested that considerable speciation resulted from repeated glaciation in Pleistocene times (Savage, 1960; Ballinger and Tinkle, 1972). Each glacial period forced desert species into southern refugia from which they later speciated through adaptive radiation and centrifugal speciation.

Group III remained originally in the north and adapted to the xeric conditions of the southwest during middle and late Pliocene, as did *Uta* and *Urosaurus*. Subsequent Pleistocene glaciation forced the desert-adapted populations into southern refugia with massive northern extinctions. The five refugia south of 30° latitude include Baja California, the Sonoran Desert, the Mexican Plateau, the Gulf Coastal Plain, and Florida. Barriers include the Gulf of California, the Sierra Madre Occidental, the Sierra Madre Oriental, and the Gulf of Mexico. Ballinger and Tinkle (1972) discussed the first three refugia in considerable detail with reference to the evolution of *Uta*.

After each glacial period, the isolated populations expanded in all directions from their refugia. (A worldwide increase in rainfall would restrict the midlatitude deserts from both sides. A subsequent decrease in rainfall would cause a movement of xeric conditions both northward and southward from a small latitudinal band.) Each southerly movement was preserved as the species adapted to subtropical conditions, but the northerly radiations would be eliminated during the next glacial period (southern rains could be tolerated better than northern snows).

Each invasion to the south required a secondary adaptation to the ancestral environment. This explains why *formosus* has not yet lost a behavioral trait called "shimmy burial." Hall (pers. comm.; see also Hall 1973:99-102) said:

One gathers from Cole's (1970) discussion that he uncritically accepts Smith's (1939) idea that the arboreal, tropical *formosus* group is primitive in the genus. Smith (pers. comm.) believed, not unreasonably on the limited information then available, that the closest primitive relatives of *sceloporus* were the South American tropidurines (from which Weigmann separated *Sceloporus*), and that its close xeric adapted relatives (i.e. "*Uta*" = *Petrosaurus*, *Urosaurus*, and *Uta*) were derived from within the radiation of *Sceloporus*. The

work of Savage (1958), Etheridge (1964), and Presch (1969) tends to refute this idea. . . .

Furthermore, it is interesting to note that the behavioral trait of 'shimmy burial' . . . is also found in most other Sceloporines. . . .

From this analysis, it would seem that all sceloporines above *Petrosaurus* at least primitively know how to use loose sand for escape and sleeping cover. It seems unlikely that this behavior would evolve in a supposedly primitive form like *formosus*, which lives in mountain rain forests where the lizards would rarely or never encounter a suitable substrate for shimmy burial. Its presence in this species probably indicates only that *formosus* has only very recently entered the rain forest habitat. On the other hand, shimmy burial would be selectively valuable to a species inhabiting dry plains or deserts where loose sand might frequently be the only cover available for escape or sleeping.

This quotation explains why Smith (1939) and Cole (1970) proposed phylogenies from south to north. We propose a reversal of these phylogenies, which means that most trends in Group III are from the north and that the Group III forms moved southward and adapted to a climate similar to the one in which the ancestors lived.

The smaller size and greater isolation of Baja California have limited the genetic potential of its populations. This has allowed continental species to move north from the Sonoran Desert and enter the peninsula to trap southern relicts (see Savage, 1960).

Another possible explanation for relict species in Baja California is the separation and westward drift of the peninsula in Miocene-Pliocene times. Concerning this movement, Moore and Buffington (p. 1241) said, "Therefore, from about 4 to 10 million years ago, during late Miocene and Pliocene times, a proto-Gulf of California existed. . . . The present cycle of spreading began about 4 million years ago."

Tanner (1966:191) stated that this same event could apply to the night snakes:

Thus the distribution of *Eridiphus* stock may have reached southern Baja California by a shorter route before the present Gulf of California was formed. Assuming this to be correct, *Eridiphus* is a relic of a once more widespread group of snakes in Western Mexico.

Hall (1973) has suggested that such a mechanism is responsible for speciation

in Baja California and that the Cape region was isolated from the rest of the peninsula as well as the mainland during an intermediate stage.

The first glacial advance divided *Sceloporus* into four refugia: an *orcutti* stock in Baja California, a *formosus* stock in the Sonoran Desert, a *virgatus* stock on the Mexican Plateau and a *cyanogenys* stock on the Gulf Coastal Plain. Subsequent postglacial speciation is illustrated in Figure 15.

The *virgatus* stock expanded northward and as far eastward as Florida. It also expanded westward into the Sierra Madre Occidental. Most of the expansion from this stock was reduced to refugia during a second glacial advance. The second glacial advance was less severe than the first (Ballinger and Tinkle, 1972:63) and a population survived in Florida (*woodi*). The main *virgatus* stock was again confined to the Mexican Plateau, but some of the mountain populations moved west into the Sonoran refuge. This isolation produced *graciosus*.

The subsequent northward migration of *graciosus* and the northern speciation of *undulatus* and *occidentalis* from *virgatus* is shown in Figure 16.

The *orcutti* stock, which was confined

to the Baja California refuge during the first glaciation, emerged with sufficient adaptive specialization to displace the *formosus* stock as far south as Guerrero. The displacement of a mainland population by a restricted peninsular population is explained by the assumption that *formosus* descended from the part of the *Sceloporus* stem that had been adapting to the mountain habitat between the central plains and the western deserts. As the Pacific slopes became more and more arid following glacial retreat, the desert-adapted *orcutti* stock displaced the mountain-adapted *formosus* stock.

From the Pacific slopes in Guerrero, the *formosus* stock speciated southward, producing *formosus* (with subspecies in Guerrero and the central uplands of Oaxaca), *malachiticus* (along the Pacific slopes from Chiapas to Panama), *lunaei* (in the uplands of central Guatemala), *lundelli* (in the central regions of the Yucatan Peninsula), and *tanneri* in Oaxaca (Smith and Larsen, 1975).

Farther north along the Pacific Coast, the *orcutti* stock produced *clarki* (from central Arizona, through the center of Sonora and down the Pacific Coast of Sinaloa to Nayarit) and *melanorhinus* (along the Pacific slopes from Nayarit

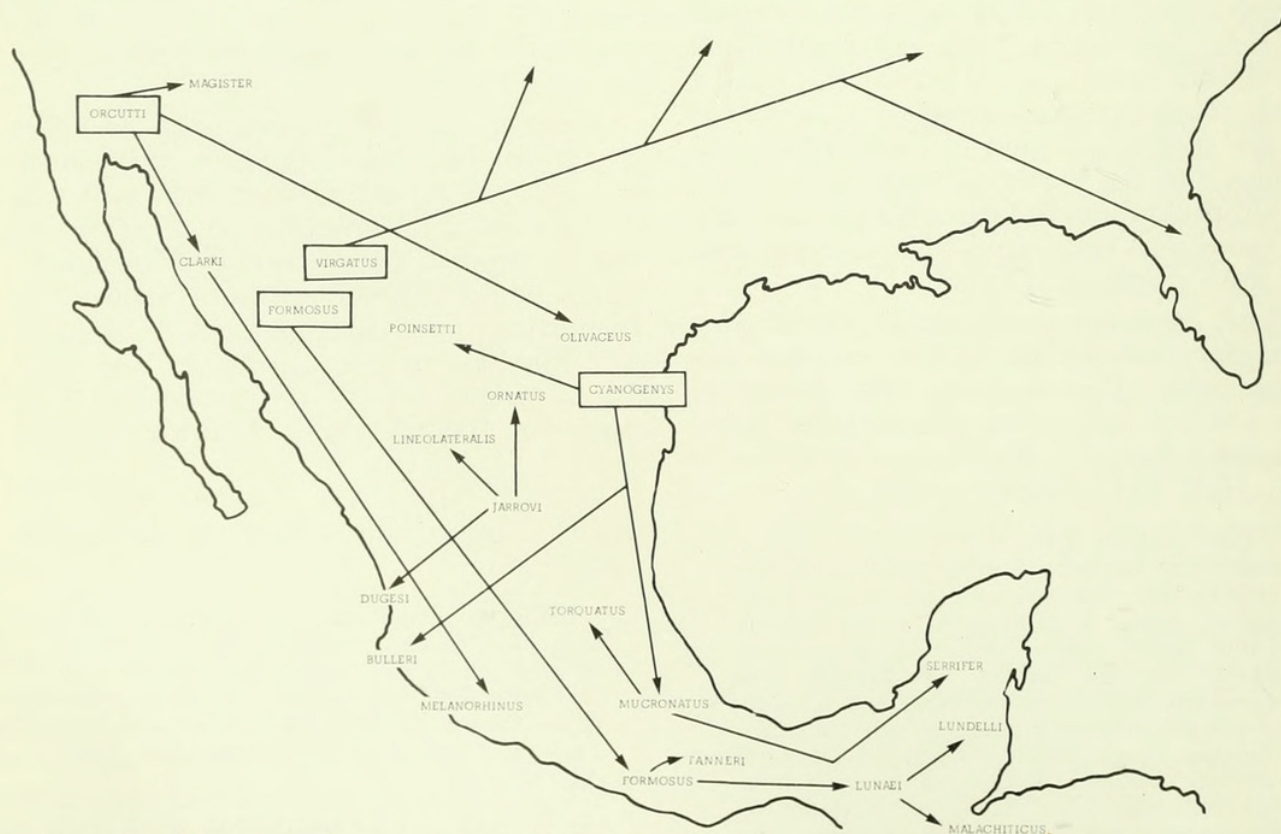


Fig. 15. Early radiation in Group III.

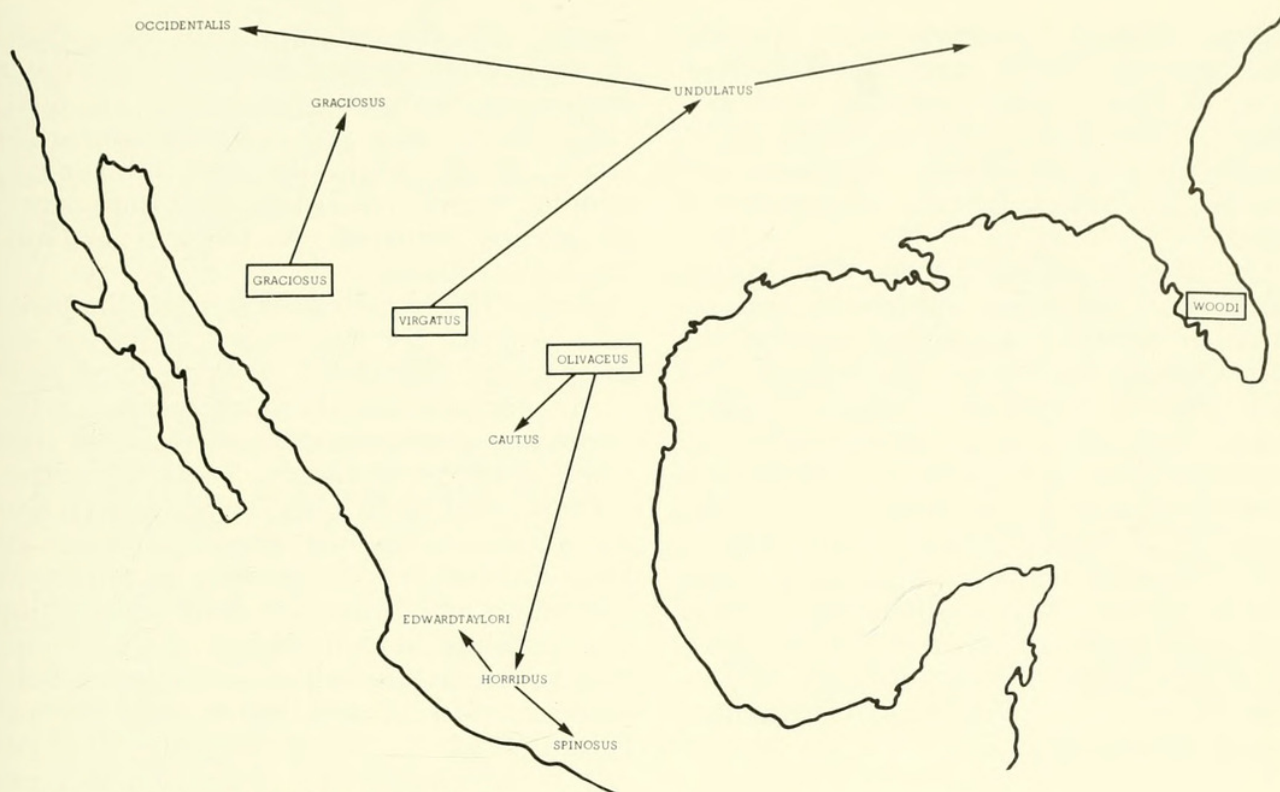


Fig. 16. Second radiation in Group III.

through Jalisco, Colima, Michoacan, Guerrero, and Oaxaca to Chiapas). Hall's comments about the separation of *nelsoni* and *pyrocephalus* along the Rio Grande de Santiago are also appropriate for *clarki* and *melanorhinus*. Apparently this river was a geographic barrier for two groups speciating in opposite directions.

Another branch from the *orcutti* stock produced the *magister* complex. The subsequent subspeciation of *magister* according to Phelan and Brattstrom (1955) was from central California southward into Baja California and southeastward into Arizona and New Mexico. However, *orcutti* has 34 chromosomes, *magister zosteromus* (and all other peninsular subspecies of *magister*) has 30, and *m. magister* has 26. This supports Hall's phylogeny with early speciation in Baja California and subsequent emergence of two stems (*orcutti* and *magister*).

A third and final branch from the *orcutti* stock moved eastward through the interglacial deserts of Arizona, New Mexico, and Texas. This branch (*olivaceus*) became trapped in the Gulf Coastal Plain refuge during the second glacial period (Fig. 15). Speciation proceeded from *olivaceus* (central Texas, Tamaulipas, Nuevo Leon, and adjacent states) southward across the Central Meseta to *spinosus* (occupying the entire Neovolcanic Plateau

from Puebla and Veracruz on the east to the tip of Durango on the west), *horridus* (with subspecies along the entire southern flank of the distribution of *spinosus*), and *edwardtaylori* (in Oaxaca) (Fig. 16).

A secondary speciation from *olivaceus* (to *cautus*) has been questioned by Hall (because of intergrades), but he (pers. comm., 1973) did make this observation:

Most interestingly there seems to be almost no question that *cautus* and *olivaceus* intergrade south and west of Monterrey (Nuevo Leon) with gene flow occurring presently through the dry valleys and passes. There might be an absolute classic circle of subspecies whose terminal populations are fully sympatric.

The last major speciation within *Sceloporus* started with *cyanogenys* in the Gulf Coastal Plain refuge (Fig. 15). The first branch produced *jarrovi* (in the northern plateaus and adjacent escarpments from Arizona on the northwest to Veracruz on the southeast), which in turn produced *ornatus* (in the ranges of southern Coahuila), *lineolateralis* (restricted to the mountains of eastern Durango), and *dugesii* (with subspecies in the mountains of Guanajuato, Michoacan, Colima, Jalisco, and Nayarit.)

The second branch from *cyanogenys* moved westward to produce *poinsetti* (which occupies most of the northern

Plateau through southern New Mexico, southwestern Texas, and the Mexican states of Chihuahua, Coahuila, and Durango). The third branch extended across Mexico in a southwesterly direction and resulted in *bulleri* (in the mountains of Jalisco).

The final radiation from the *cyano-genys* stock extended southward and resulted in *serrifer* (occupying most of the Gulf Coastal Plain in Tamaulipas, San Luis Potosi, Veracruz, Tabasco, Campeche, and Yucatan), *mucronatus* (a mountain form in the Oaxaca Upland and other mountains in the state of Guerrero, Veracruz, Puebla, Mexico, and Hidalgo), and *torquatus* (which inhabits a large area in central Mexico, including parts of Hidalgo, Veracruz, Mexico, Distrito Federal, Puebla, Morelos, Guanajuato, Michoacan, Nuevo Leon, Jalisco, San Luis Potosi, and Zacatecas).

CONCLUSIONS

When presenting his arrangement, Smith (1939) said, "Material from certain areas is still lacking, and more direct evidence of relationships is frequently to be desired. The conclusions now presented are accordingly tentative." Smith's statement may still apply. Problem areas include Baja California and the *grammicus* complex. Also several new species and subspecies are being considered by various workers. New kinds of data are now being researched (microdermatoglyphics, for example). However, a point has been reached at which different sets of data reinforce similar conclusions. With over 80 characters, the new groups and subgroups are distinct at the .999 level of confidence (Larsen and Tanner, 1974). With such a high level of confidence, we conclude that Figure 5 is a natural arrangement of species and that future adjustments may be minor.

When phylogeny and zoogeography are considered simultaneously, several trends are evident in the evolution of *Sceloporus*: (1) the size altered from small to large; (2) the scales, once small, smooth, and granular, changed, becoming large, carinate, mucronate, and imbricate; (3) initial movement and speciation was from north to south, and several secondary radiations were from southern centers northward and from northern centers south-

ward; (4) the geography of Baja California created several relicts; (5) habitat preference changed from ground to rocks, cliffs, and trees; and (6) the ancestral stock, which originally was subtropical, adapted to arid conditions, and then several groups returned to tropical or subtropical climates.

Cope (1900) called *Sceloporus* the *piece de résistance* for the theory of derivation of species. This genus seem to show such principles as parallelism, convergence, divergence, genetic drift, geographical barriers, adaptive radiation, centrifugal speciation, and waif and relict population development. In fact, the cape region of Baja California may provide examples of speciation by continental drift. *Sceloporus* also exhibits a high degree of chromosomal variation, including examples of Robertsonian fission and fusion, and several formulae for sex determination. This genus is extremely well suited for illustration and discussion of evolutionary theory.

We conclude that *Sceloporus* has recently speciated in an explosive manner. Because of this rapid adaptive radiation, it is difficult to determine phylogenetic relationships with classical techniques.

We are persuaded, however, that the genus *Sceloporus* does contain three distinct monophyletic groups. Group I is distinct from the other two groups in having (1) a postfemoral dermal pocket and less than 7 ventrals between the femoral pore series or (2) (if the postfemoral dermal pocket is absent) a vestigial gular fold and no postrostrals. The rest of the species in the genus *Sceloporus* lack either a postfemoral dermal pocket or a vestigial gular fold. If they lack the vestigial gular fold, postrostrals are present and there are more than 8 ventrals between the femoral pore series. In considering the systematics of the entire complex, we believe that it is now feasible to recognize for Group I (Table 1) the Cope (1888) monotypic generic designation of *Lysoptychus* (*L. lateralis*=*Sceloporus couchi* Baird, 1858).

We have not by our methods been able to arrive at a satisfactory taxonomic division of Groups II and III, even though these groups become separable and distinct by use of multivariate analysis. We believe that Groups II and III represent a large assemblage of species that have evolved more recently but that although the characters between the groups are

showing indications of evolutionary separation, they have not reached a point of distinction that permits the development of a workable taxonomic key. We therefore choose at this time to retain them in the genus *Sceloporus*.

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