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A REVIEW OF PHYLOGENETIC HYPOTHESES FOR LIZARDS OF THE GENUS *SCELOPORUS* (PHRYNOSOMATIDAE): IMPLICATIONS FOR ECOLOGICAL AND EVOLUTIONARY STUDIES

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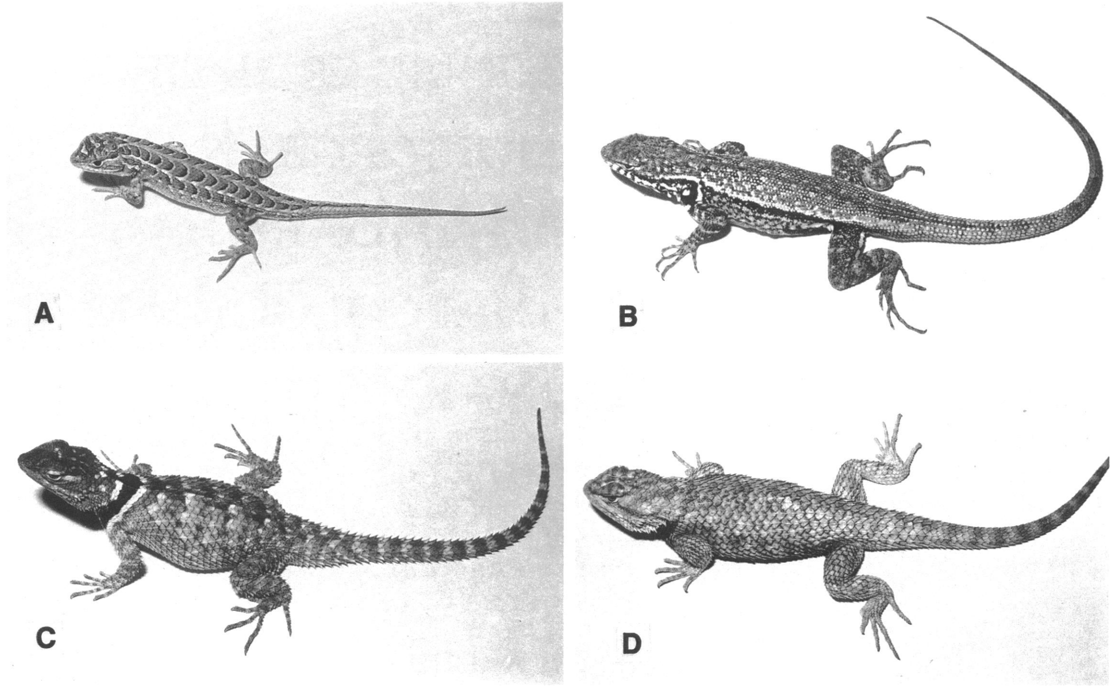

Four species of *Sceloporus*. **A.** *S. goldmani,* female, AMNH 115642, snout-vent length 33 mm. **B.** *S. couchii,* male, AMNH 115645, snout-vent length 60 mm. **C.** *S. cyanogenys* (or *S. serrifer cyanogenys*), female, AMNH 137716, snout-vent length 77 mm. **D.** *S. magister,* male, AMNH 111139, snout-vent length 109 mm.

CONTENTS

ABSTRACT

Species of *Sceloporus* have figured prominently in studies of population, community, and physiological ecology, social behavior, disease transmission, and biogeography, probably in large part because of the broad distribution of the genus in a variety of habitats, its species diversity, and the diurnal and conspicuous habits of most species, which are often locally abundant. Despite these advantages and the prevalence of *Sceloporus* in many research programs in organismal biology, many outstanding systematic and evolutionary problems remain, and the *Sceloporus* radiation has not been rigorously studied from a contemporary phylogenetic perspective. We have undertaken this review with two major objectives: (1) to summarize all information relevant to existing phylogenetic hypotheses for the genus, and make it available in a single document; and (2) to point out some of the ecological and evolutionary questions for which *Sceloporus* is superbly suited for detailed study, within the context of well-corroborated phylogenetic frameworks. With respect to the first objective, we have summarized the major phylogenetic conclusions of Smith, Larsen and Tanner, Cole, and those based on the largely unpublished cytogenetic data sets of W. P. Hall and C. J. Cole. Alternative hypotheses are compared and summarized with regard to major points of congruence and conflict, and we argue that thorough contemporary systematic studies are urgently needed for the entire *Sceloporus* radiation. With respect to the second objective, the *Sceloporus* radiation unequivocally shows three or more independent origins of viviparity, possibly five independently derived heteromorphic sex-chromosome systems, and perhaps six examples of independent secondary loss of sexual dimorphism in color pattern, regardless of which of the existing phylogenetic hypotheses most closely reflects the real evolutionary history. Different radiations within the genus also continue to offer challenging problems in historical biogeography, speciation, macroevolution, hybrid zone dynamics, taxonomy at the species level, population biology, physiological ecology, and comparative ethology. The genus also offers additional potential in relatively unexplored areas such as mate choice/sexual selection, the roles of regional gene duplication in genome evolution; and co-speciation/co-adaptation of host-parasite systems. This potential, particularly great because of the species diversity of the genus, is discussed within the context of comparative biology and phylogenetic inference.

RESUMEN

Las especies del género *Sceloporus* han figurado prominentemente en las investigaciones de ecología de poblaciones, comunidades, fisiología ecológica, comportamiento social, transmisión de enfermedades y biogeografía; probablemente debido, en gran parte, a la distribución tan amplia del género en una gran variedad de hábitats, la riqueza del mismo y los hábitos diurnos y conspicuos de la mayoría de las especies las cuales frecuentemente son muy abundantes localmente. No obstante estas ventajas y el predominio de *Sceloporus* en muchos programas de investigación en biología organísmica, muchos problemas sistemáticos y evolutivos sobresalientes persisten y la mayoría de las radiaciones dentro del género no han sido estudiadas rigurosamente desde una perspectiva filogenética contemporánea. Hemos hecho este trabajo con base de dos objetivos principales: (1) resumir la información pertinente de todas las hipótesis filogenéticas para el género y hacerla disponible en un solo documento, y (2) señalar algunas de las interrogantes ecológicas y evolutivas para las cuales el género *Sceloporus* sería un objeto de estudio ideal dentro de un marco de teorías filogenéticas bien corroboradas. Con respecto al primer objetivo, hemos resumido las conclusiones filogenéticas más importantes de Smith, Larsen y Tanner, Cole y aquellas basadas sobre los datos citogenéticos inéditos de W. P. Hall y C. J. Cole. Hipótesis alternativas son comparadas y resumidas con relación a los puntos mas importantes de congruencia y conflicto, se sugiere que estudios en sistemática contemporánea se requieren urgentemente para practicamente toda la radiación dentro del género. La radiación de *Sceloporus* muestra, inequivocamente, por los menos tres orígenes independientes de la viviparidad, posiblemente cinco orígenes independientes de sistemas heteromórficos derivados de cromosomas sexuales y posiblemente seis ejemplos de pérdida independiente de caracteres sexuales secundarios, como pérdida del patrón de coloración; independientemente de cual sea la hipótesis filogenética que refleja la genealogía más cercana. Diferentes radiaciones dentro del género también continúan ofreciendo incógnitas desafiantes en biogeografía histórica, especiación y macroevolución, dinámica de las zonas híbridas de intercambio, taxonomía a nivel de especie, biología de poblaciones, ecología fisiológica y etología comparada. También ofrece problemas interesantes en áreas relativemente inexploradas tales como selección de la pareja/selección sexual, y coespeciación/coadaptación en sistemas de huésped-parásito. Este potencial, particularmente grande debido a la riqueza de especies dentro del género, se discute dentro del contexto de la biología comparativa y la inferencia filogenética.

INTRODUCTION

Ever since herpetology became recognizable as a distinct subdiscipline of North American natural history, members of the genus *Sceloporus* have been an element of major interest. This genus has figured prominently in reptilian studies of, among other things, population, community, and physiological ecology; social behavior; disease transmission (see contributions in Milstead, 1967; Huey et al., 1983); homing behavior (Ellis-Quinn and Simon, 1991) and biogeography (Smith, 1941; Morafka, 1977; Murphy, 1983a, 1983b). In one recent review of methods for field population studies of reptiles, Dunham et al. (1988a) listed 398 citations, of which 97 (24% of the total) dealt with lizards. Of these 97 lizard papers, 28 dealt exclusively or largely with one or more species of *Sceloporus* (29% of the lizard citations) while 11 lizard papers (12%) dealt exclusively or largely with another prominent New World lizard radiation, that of *Anolis*. Similarly revealing totals are found in another review by Dunham et al. (1988b) of life history patterns in squamate reptiles. One hundred and sixty three lizard papers are cited from a total of 255 references (64%), and of the lizard papers, 25 dealt with *Sceloporus* and 10 with *Anolis* (15 and 6% respectively).

The prominence of *Sceloporus* in these kinds of studies is undoubtedly due to at least three factors. First, the genus is extremely widely distributed in North America, with representatives ranging from the Pacific northwestern section of the United States and extreme southern British Columbia, Canada, across most of the continental United States (Smith, 1946), then south through all of Mexico and much of Central America into Costa Rica and extreme western Panama (Savage, 1982; Kourani et al., 1970; see fig. 1). Second, the genus is extremely diverse in terms of number of species and in their morphological, ecological, ethological, and physiological adaptations. Although the exact number of distinct species within *Sceloporus* is uncertain (see below), its monophyly is reasonably well established (if *Sator* is included, see Etheridge and de Queiroz, 1988; also Frost and Etheridge, 1989; but see Wiens, 1992, for an alternative arrangement) and the total number of species is likely to be at least 69 by very conservative estimates (Paull et al., 1976; Hall, 1980). Finally, many species are locally common to abundant, diurnal, very conspicuous, and relatively easy to collect. These characteristics make them very suitable for all kinds of field investigations. As H. M. Smith pointed out in his 1939 monograph of this genus, "Attractive problems in species formation and geographical distribution are presented, and their solution is brought within reach by the fact that these lizards are frequently abundant and relatively easy to observe and collect" (p. 9).

Despite these advantages and the widespread use of many species of *Sceloporus* in a variety of biological studies, there are many outstanding systematic and evolutionary problems within the genus, and much of its vast radiation has not been studied from a contemporary phylogenetic perspective. In an earlier paper, Smith (1936 [1938]) emphasized some of these concerns: "Studies of this nature must of a necessity be somewhat incomplete, because of the inadequacy of available material, the lack of more direct evidence of relationships, and the lack of absolute knowledge of the methods of speciation." We will likely never have either completely adequate material or absolute knowledge of the details of speciation events for most organisms, but *Sceloporus* nevertheless offers a superb resource for developing well-corroborated phylogenetic hypotheses within which to frame additional questions relevant to evolution, ecology, behavior, physiology, genetics, or biogeography. Students of comparative physiology, ethology, and community ecology are now calling for a reunification of phylogenetic systematics with each of these disciplines (Huey, 1987;

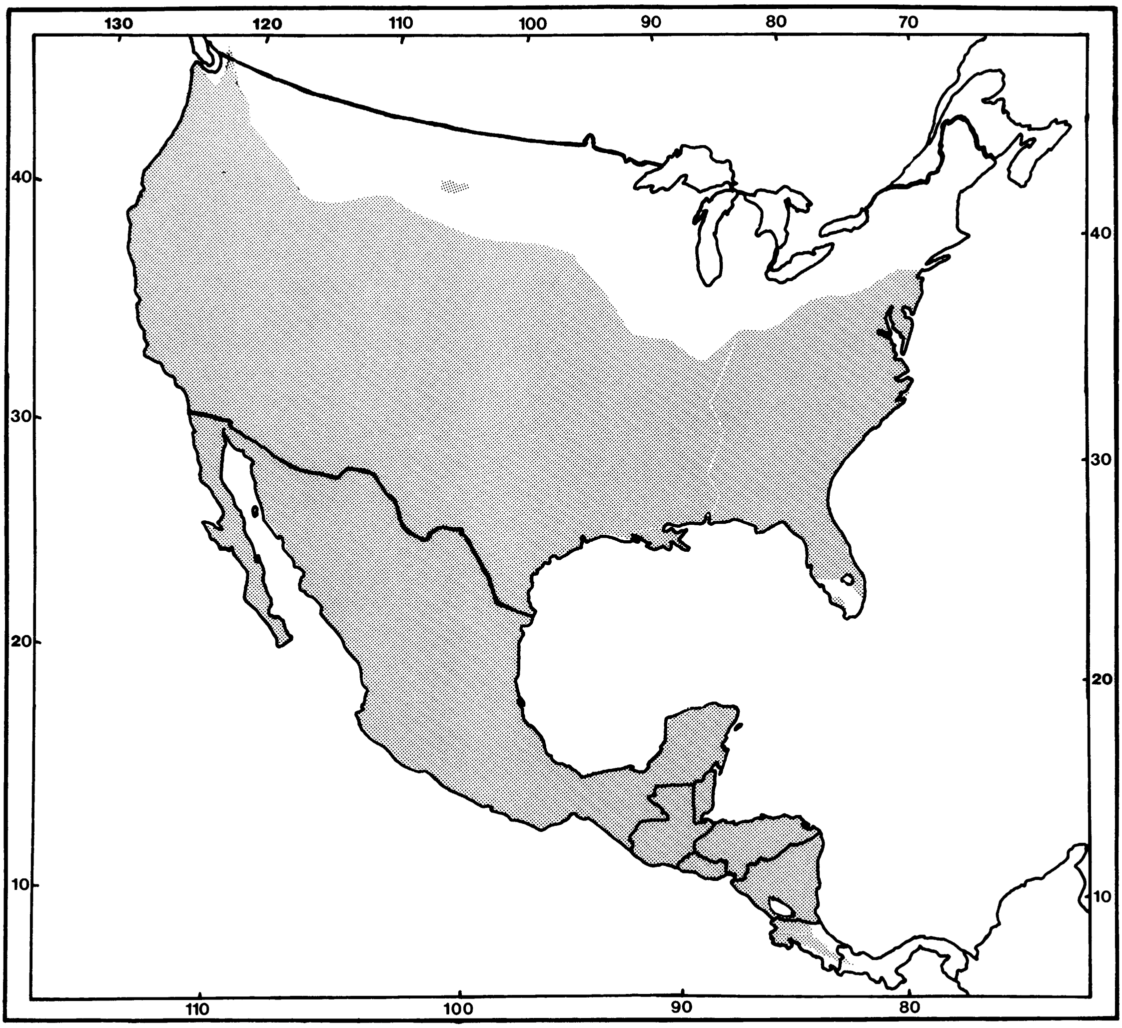

Fig. 1. Distribution of *Sceloporus,* a North American genus.

Ricklefs, 1987, 1989; McLennan et al., 1988; Ferris and Ferris, 1989; Wanntorp et al., 1990; Brooks and McLennan, 1991; Harvey and Pagel, 1991) and workers in more traditional systematically based disciplines are developing productive new ways to use historical information (Lauder, 1981, 1982; Endler, 1982; Dobson, 1985; Wiley and Mayden, 1985; Greene, 1986; Huey and Bennet, 1987; Sessions and Larson, 1987; Strauss, 1987; Wake and Larson, 1987; Coddington, 1988; Mayden, 1988; Pearson et al., 1988; Carpenter, 1989; Donoghue, 1989; Lynch, 1989; Losos, 1990a, 1990b, 1990c, 1990d; Maddison, 1990; McLennan, 1991). Within the framework of these and other recent efforts at broader syntheses of historical biology with a host of other comparative evolutionary questions (Felsenstein, 1985; O'Hara, 1988; Pagel and Harvey, 1988; Bell, 1989; Maddison, 1989; Ridley, 1989; Gittleman and Kot, 1990; Ronquist and Nylin, 1990; Lynch, 1991; Maddison and Slatkin, 1991; Martins and Garland, 1991; Harvey and Purvis, 1991), we have undertaken this review with two main objectives.

First, we wished to summarize all information relevant to existing phylogenetic hypotheses of the genus *Sceloporus* and make it available in a single document. This is important because three separate efforts have been made to analyze the systematics of the entire genus. Each is based on different data sets and different methodologies. There are substantial areas of both concordance and disagreement among the three available phylogenies. This is also crucial because one of the existing data sets is largely unpublished. We refer to the extensive chromosomally based phylogenetic schemes in the Ph.D. thesis and an unpublished manuscript by W. P. Hall (1973 and 1977, respectively). We present Hall's data and hypotheses here because we consider them of such significance that they should be published. One of us (JWS) has made extensive but unsuccessful attempts to locate and correspond with Hall for the past several years, and apparently similar attempts at correspondence by Dr. E. E. Williams, Hall's thesis advisor at Harvard, have also been unsuccessful. This review will therefore both recognize Hall's important contributions, and make his chromosomally based phylogenetic hypotheses available as alternatives to the previously published schemes.

Second, we point out some of the many kinds of ecological and evolutionary questions that can be profitably studied in *Sceloporus,* given a strongly corroborated phylogenetic framework. For example, three or more radiations within the genus appear to have independently evolved viviparity, several species have independently evolved different structural classes of morphologically distinct sex chromosomes, and several species have independently lost sexual dimorphism in color pattern. The genus also continues to offer a great deal to students in population biology/ecology, physiological ecology, comparative ethology, chromosomal evolution and speciation, hybrid zone dynamics, species-level taxonomy, and biogeography; it also offers possibilities in relatively unexplored areas such as mate choice/sexual selection, regional duplication of single-copy gene loci, and/or the cospeciation/coadaptation of host-parasite systems.

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THE SMITH PHYLOGENY

INTRODUCTION

Smith (1939) provided an extensive treatment of almost all species and subspecies of *Sceloporus* recognized at the time, and an evaluation of the relationships and composition of all species groups. Smith had previously published small papers dealing with specific groups of *Sceloporus* (1936, 1937a, 1937b, 1938), but his 1939 monograph explicitly summarized all systematically relevant information on type localities, distribution, geographic variation in meristic and qualitative characters, body size and proportions, coloration, sexual dimorphism, and habits and habitats for all 95 Mexican/Central American taxa he recognized. Smith segregated these into 15 species groups "of approximately equivalent morphological value," and presented a phylogenetic hypothesis of their relationships (fig. 3, p. 28 of Smith, 1939). This was followed by a dichotomous key, while the rest of the monograph was devoted to a detailed treatment of all taxa comprising each of the groups, and hypotheses of relationships of the species within each group. A later treatment (Smith and Taylor, 1950) recognized those same 15 species groups, but some were changed in composition because of taxonomic rearrangements and emendations. Smith and Taylor (1950) recognized a total of 104 species and subspecies of *Sceloporus,* with 89 named taxa in 52 species occurring in Mexico.

Many new species have since been described on the basis of morphological criteria, representing both discoveries of new taxa and the elevation of subspecies to full species. Similarly, several revisions have included some previously recognized species as subspecies of widespread polytypic forms. The evidence in favor of either position is often equivocal. We have usually opted to consider these taxa as species, but have emphasized the uncertainty of many proposals, and presented the information strictly in the form of testable hypotheses. We have not treated subspecies except where these have been considered to be species by some authors.

We present in figures 2 and 3 an amended version of Smith's (1939) original "phylogenetic hypothesis" of relationships among the 15 species groups, with each group showing subsequently described species and other modifications to be discussed below. We emphasize that Smith may not have used the term phylogenetic in the same context in which it is used today, and that his figure 3 (p. 28 of the 1939 monograph) is inconsistent with many of the species phylogenies presented elsewhere in his monograph. For example, the topology of Smith's figure 3 depicts a sister-group relationship for the *grammicus* and *megalepidurus* groups, with both of these being the sister group of the *formosus* group (see also our fig. 3). However, Smith's more detailed phylogeny for the *formosus* group (fig. 4, p. 33 of Smith, 1939; our fig. 5A) depicts a genealogy in which two species of the *formosus* group are more closely related to members of other species groups than they are to any of the other species in the *formosus* group. In other words, his detailed hypothesis interpreted the *formosus* group as paraphyletic, with *S. malachiticus* being the sister taxon of the *spinosus* group, and *S. smaragdinus* sharing a sister-group relationship with the *grammicus–megalepidurus* groups.

Smith's methods were not strictly phylogenetic in the modern sense, and many of his species groups were diagnosed by a combination of apomorphic and plesiomorphic characters. This resulted in his recognition as species groups assemblages of species within which some species were hypothesized to share more recent common ancestors with members of other groups than with those of their own group, as in the example just given. These are the species groups that, in our figures and many of Smith's, now appear to be paraphyletic. Smith probably intended his figure 3 to symbolize some sense of "natural" relationship (we are not certain of what this meant in 1939), and we use figures 2 and 3 here to summarize both the general topology of his figure 3, and the hypothesized contemporary composition of species groups. Smith's specific hypotheses are treated on a group-by-group basis below, but readers should be aware of the aforementioned inconsistencies.

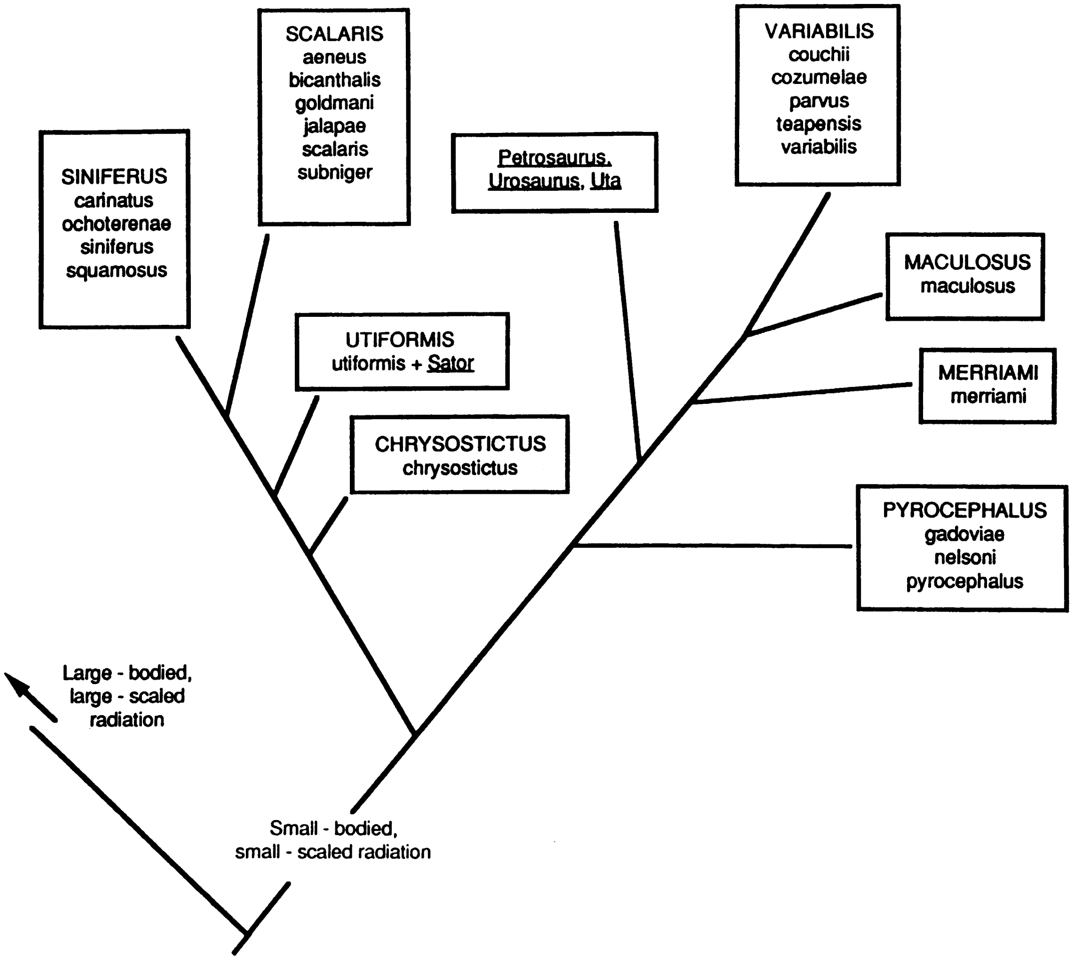


Fig. 2. Species groups (enclosed in squares) and phylogenetic relationships within the small-bodied, small-scaled radiation of *Sceloporus*, as presented by Smith (1939). The composition of several groups has been modified to incorporate taxonomic changes (see text).

Smith hypothesized an early split into two major radiations, the most species-diverse being characterized by generally large-bodied, large-scaled species (fig. 3), and the smaller radiation comprising small-bodied, small-scaled species (fig. 2). The latter group also included the ancestors of *Uta, Urosaurus,* and *Petrosaurus* (all then included in *Uta*), and from a different group, the genus *Sator* (see Dickerson [1919]; Schmidt [1922]; Smith [1936]; Mittleman [1942]). Within the small-bodied, small-scaled radiation, the *scalaris* and *siniferus* groups were proposed to be closely related and derived from the lineage from which the *chrysostictus* and *Sator-utiformis* groups were earlier derivatives. The second radiation within this group included the *pyrocephalus* group as an early offshoot, and the stock including *Uta* and the *merriami, maculosus,* and *variabilis* groups of *Sceloporus.*

Within the large-bodied, large-scaled radiation, Smith (1939: 33) proposed that the *formosus* group was near the ancestral position (fig. 3). He (1939) placed the origin of the *grammicus* group within the *formosus* group (p. 178), and argued that the *megalepidurus* group was most closely related to the *grammicus* group (p. 199). He also placed the *spinosus* group—including its derivatives the *graciosus* and *undulatus* groups—and the *torquatus* (= *poinsetti* in 1939) group as forming

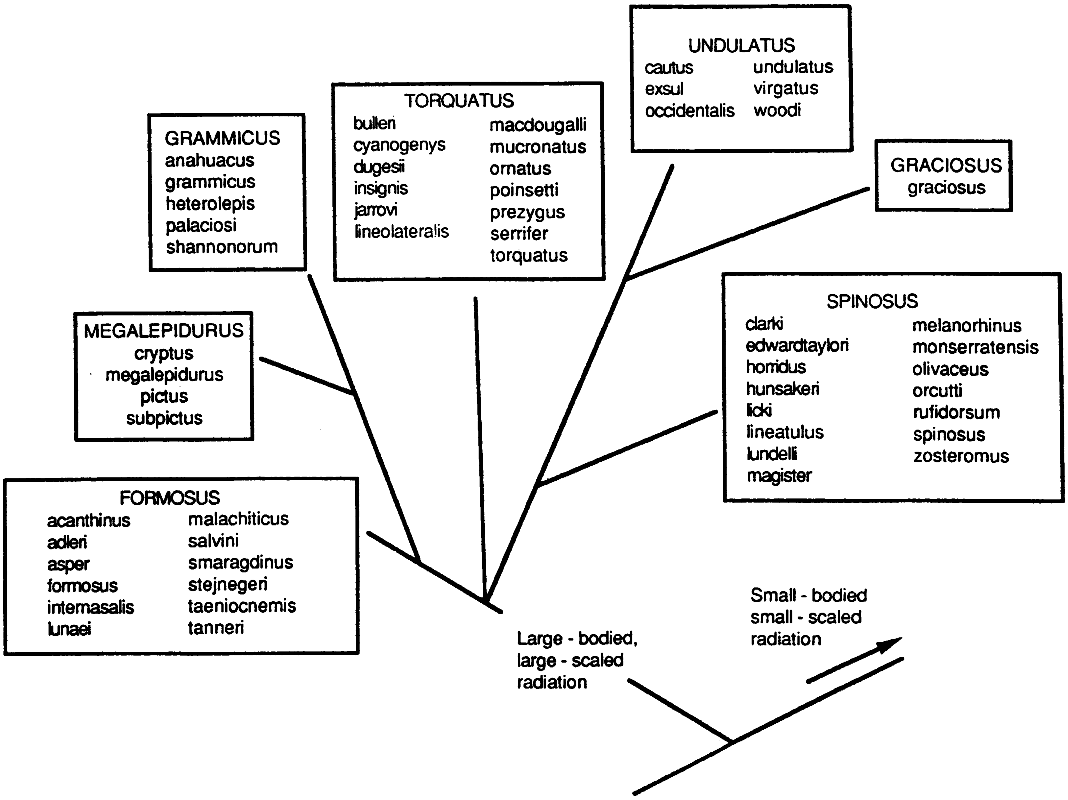


Fig. 3. Species groups and phylogenetic relationships for the large-bodied, large-scaled radiation of *Sceloporus*, as presented by Smith (1939). Again, group compositions have been amended in several cases to accommodate taxonomic changes.

a trichotomy with the *formosus* group (fig. 3). Smith was inconsistent in his statements regarding the origin of the *torquatus* group (compare his figs. 3 and 21), but as pointed out by Hall (1973), if the compositions of Smith's (1939) species groups are accepted, and it is also accepted that the primitive *Sceloporus* was of tropical origin (see Smith, 1946), then the arrangement in which the *spinosus* and *torquatus* groups formed a trichotomy with the *formosus* group is not unreasonable. However, a number of recent studies within the genus *Sceloporus* and of the higher-level relationships of *Sceloporus* and the utiform species (including *Petrosaurus, Urosaurus,* and *Uta*) suggest that some of Smith's phylogenetic hypotheses are inaccurate (Paull et al., 1976; Hall, 1983; Etheridge and de Queiroz, 1988; Frost and Etheridge, 1989; Wiens, 1993), thus requiring a reevaluation of relationships within the genus.

Smith's (1939) monograph originally included descriptions of characteristics diagnostic of most of the 15 species groups of *Sceloporus,* and these were usually accompanied by trees depicting presumed relationships among the species within each polytypic group. We have attempted to summarize each of these statements here, and to update them for all groups in which the composition of species has changed. We begin first with the small-bodied, small-scaled radiation.

SMALL-BODIED, SMALL-SCALED RADIATION

Figure 4A summarizes the relationships proposed for the *maculosus, merriami, pyrocephalus,* and *variabilis* groups, as depicted

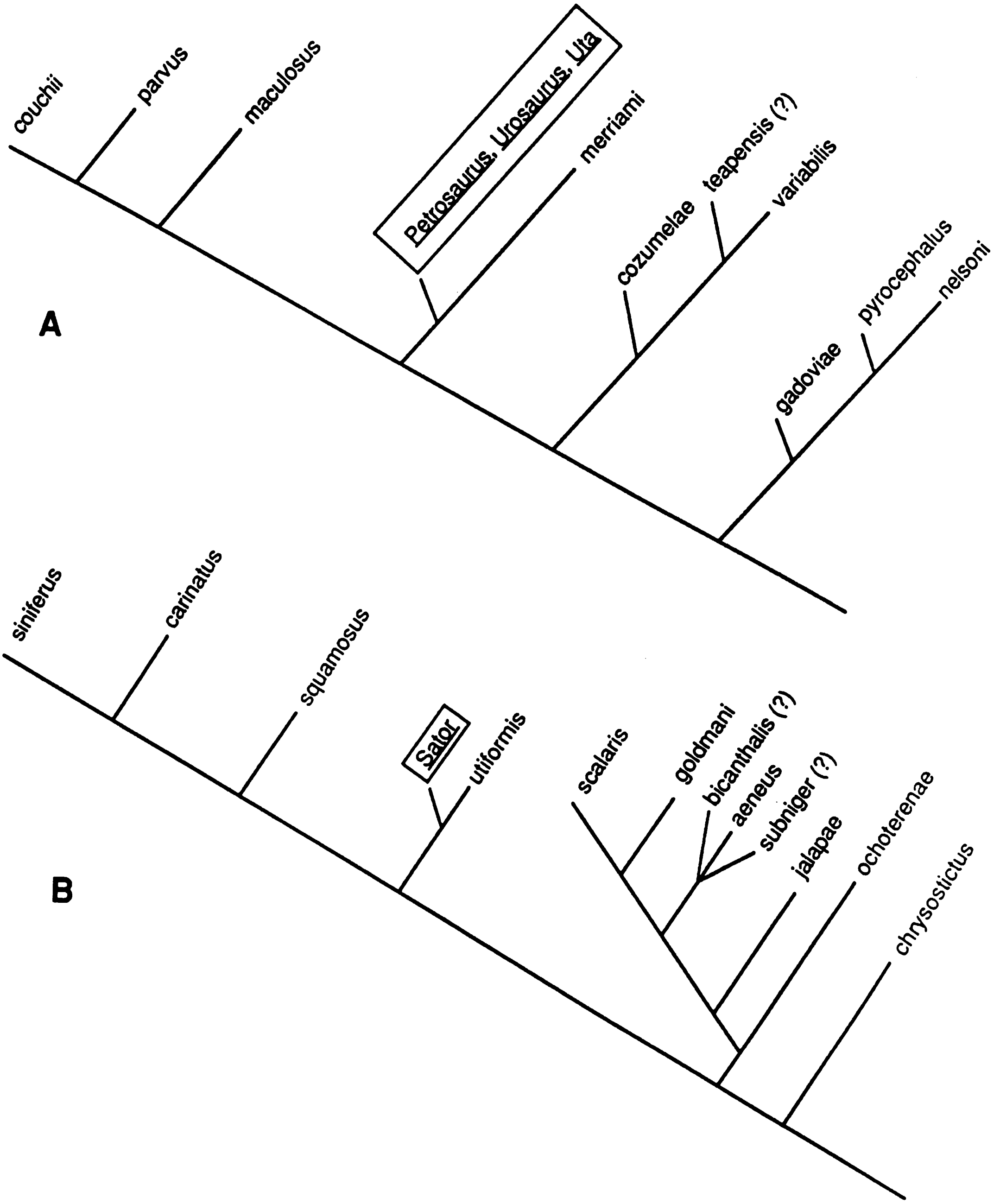


Fig. 4. Interspecific relationships for members of the two major radiations of small-bodied, small-scaled *Sceloporus*, as outlined by Smith (1939). Question marks in this and other trees denote species of uncertain status. **A**, *maculosus, merriami, pyrocephalus,* and *variabilis* groups; **B**, *chrysostictus, scalaris, siniferus,* and *utiformis* groups.

in figures 42 and 58 of Smith (1939). The *variabilis* group was originally postulated to contain five species (*S. couchii, S. cozumelae, S. parvus, S. teapensis,* and *S. variabilis*), and to have two (*S. couchii* and *S. parvus*) which shared a more recent common ancestor with the *maculosus* group than with other members of the *variabilis* group. The *variabilis* group was also postulated to be the sister group of a (*couchii* + *maculosus*) + (*Uta* + *merriami*) group, with *Uta* in this group representing the *Uta-Urosaurus-Petrosaurus* radiation (depicted only as *Uta* in fig. 42 of Smith, 1939: 238). Thus, the *variabilis* group as originally conceived by Smith (1939) is paraphyletic. The *pyrocephalus* group was postulated to be the sister taxon of the *variabilis* radiation (including *S. maculosus, S. merriami,* and *Uta*). All of these species are generally recognized by small to moderate body sizes (50–78 mm snout–vent length), high femoral pore counts, granular or subgranular lateral scales aligned in diagonal or oblique rows, and smooth preanals in both sexes. The three *pyrocephalus* group species also are distinct in sharing a laterally compressed tail, and in the reduction or absence of enlarged postanal scales in males. The *maculosus* and *variabilis* groups and their supposed derivatives share the presence of a well-developed postfemoral dermal pocket, while *S. merriami* typically lacks subnasal scales and shows a rudimentary gular fold.

Within this radiation, there is some morphological evidence against continued recognition of *S. teapensis* as a full species. Cole (1978) first showed that several samples of *S. teapensis* could not be unequivocally separated from parapatric populations of *S. variabilis* on the basis of characters previously described as diagnostic. He suggested the use of a new combination—*S. variabilis teapensis*—to describe these populations at a subspecific level. Cole's findings were verified by a more extensive multivariate statistical study carried out by Sites and Dixon (1982). Smith (1987) disagreed, however, arguing that absence of the subnasal and presence of asymmetrical parietal peritoneal pigmentation in combination are presumably unique in *S. teapensis.* Additional study will be necessary to determine the status of *S. teapensis* as a distinct species.

Figure 4B summarizes hypothesized relationships for the *chrysostictus, scalaris, siniferus,* and *utiformis* groups, as depicted in figure 48 of Smith (1939), but with the following modifications. *Sceloporus cupreus* (*siniferus* group) and *S. bicanthalis* (*scalaris* group) were relegated to subspecies of *S. siniferus* and *S. aeneus,* respectively, by Smith and Taylor (1950), and the status of *S. cupreus* has not been challenged since. *Sceloporus* "*cupreus*" is subsumed by *S. siniferus* in figure 4B for convenience, but since these taxa are allopatric (compare figs. 49 and 50 of Smith, 1939), the hypothesized conspecificity of these populations requires phylogenetic verification.

In other sections of this group, the status of both *S. aeneus* and *S. bicanthalis* has been contested since 1950. Davis and Smith (1953) suggested that *S. a. aeneus* was oviparous, and that *S. a. bicanthalis* was viviparous (on a two-year cycle), and that both should be accorded full species rank on the basis of presumed parity differences. This suggestion has not been followed by most workers (see below), but was reintroduced and supported by Smith and Brandon (1971). The diagnosis of *S. aeneus* was further complicated by the placement of *S. scalaris slevini* into the species *S. aeneus* by Poglayen and Smith (1958), which then raised a question concerning the specific status of *S. scalaris.* Martin (1958) also suggested that there were ecological and morphological reasons for associating *S. scalaris slevini* with *S. aeneus* rather than retaining it in *S. scalaris.* Smith and Hall (1974) proposed the use of parity type for phylogenetic inference in assessing relationships in the *S. aeneus–scalaris* complex, assigned viviparous and oviparous forms to the *aeneus* and *scalaris* complexes, respectively, and named a new taxon, *S. scalaris samcolemani.* These authors rejected the earlier proposal of Davis and Smith (1953) that *S. a. aeneus* was specifically distinct from *S. a. bicanthalis.*

Thomas and Dixon (1976) reevaluated the entire *scalaris* group (as defined by Smith, 1939) from a morphological perspective, and placed *S. scalaris slevini* and *S. scalaris unicanthalis* in the synonymy of *S. scalaris,* but recognized the latter as a distinct monotypic species. These authors also reaffirmed the specific status of *S. goldmani,* and failed to find consistent morphological characters separating *S. aeneus* from *S. bicanthalis.* Thomas and Dixon (1976) therefore recommended continued recognition of a single polytypic species, *S. aeneus,* but acknowledged its reproductive bimodality. Thomas and Dixon (1976) also provisionally removed *S. jalapae* and *S. ochoterenae* from the *scalaris* and *siniferus* groups, respectively, and placed them together in a *jalapae* group.

Detailed studies of the reproductive cycles and anatomy of *S. a. aeneus* and *S. a. bicanthalis* by Guillette (1981, 1982) showed that populations assigned to the former were definitely oviparous but with prolonged egg retention, while the latter were unquestionably viviparous. The former were largely confined to the western portions of the range, while the latter were eastern, and the two parity types were characterized by consistent differences in oviductal and ovarian morphology, and in oviductal vascularity (details in Guillette, 1982). In a later paper, Guillette and Smith (1985) again argued for species-level recognition of these two parity types. They also suggested that *S. aeneus subniger* might be a distinct species, but offered no definitive support for this. In contrast to Thomas and Dixon (1976), Guillette and Smith (1985) showed that differences in either number of canthal scales or reproductive mode could distinguish between *S. aeneus* and *S. bicanthalis* with 100 percent resolution, and that differences in throat coloration and pattern were diagnostic in 90 percent of all cases. They tentatively proposed recognition of a viviparous *bicanthalis* complex containing *S. bicanthalis, S. goldmani,* and *S. subniger,* and relegated the two oviparous species to a closely related but distinct *scalaris* complex (*S. aeneus* and *S. scalaris*). However, Guillette and Smith (1985) acknowledged the tentative nature of this arrangement.

According to Smith's views, the *siniferus* group (including *S. carinatus, S. ochoterenae, S. siniferus,* and *S. squamosus*) is paraphyletic because (1) the *utiformis* group is derived from within it, and (2) the entire *scalaris* group (*S. aeneus, S. goldmani, S. scalaris,* and *S. subniger,* as currently recognized) is the sister group of *S. ochoterenae.* The monotypic *chrysostictus* group is postulated to be the sister group of a group composed of the *siniferus, utiformis,* and *scalaris* groups plus *Sator.* Morphologically, all of these species are small to medium in length (60–70 mm SVL), possess moderate to large dorsal scales (counts range from 28 to 57, depending on the species) relative to most other "small-scaled" species and have preanals keeled in males; and the *siniferus* and *utiformis* groups have relatively long tails.

LARGE-BODIED, LARGE-SCALED RADIATION

We have depicted in figure 5A a highly amalgamated and updated version of Smith's hypothesis for the *formosus* group (fig. 4 of Smith, 1939) within the large-bodied, large-scaled radiation. Smith considered this group to be at or near the basal radiation for the genus, and some components of it were considered directly ancestral to the *grammicus, megalepidurus,* and *spinosus* groups. It is by far the most poorly understood group in the genus, as is obvious from the large polytomy in figure 5A, and many questions remain to be addressed with regard to both species boundaries and intragroup species affinities. Smith (1939) originally considered the group to contain only five species (*S. asper, S. formosus, S. malachiticus, S. salvini,* and *S. smaragdinus*), and considered *S. salvini* to be an early derivative without a close phylogenetic relationship to any other species in either the *formosus* group or the genus. Smith and Taylor (1950) considered the additional species *S. lunaei* (placed in the *spinosus* group in the 1939 monograph), *S. prezygus,* and *S. stejnegeri* as part of this group, and simultaneously relegated *S. salvini* to subspecific status within *S. malachiticus.* There have been numerous other taxonomic rearrangements within this group since 1939. *Sceloporus prezygus* (Smith, 1942) has since been relegated to subspecific status within *S. serrifer* in another group (Stuart, 1970). *Sceloporus internasalis,* originally described as a subspecies of *S. malachiticus* (Smith and Bumzahem, 1955), was considered as a poorly known but distinct species by Stuart (1971). Stuart (1971) also recognized *S. acanthinus* (also part of the *spinosus* group in Smith [1939]), *S. smaragdinus,* and *S. taeniocnemis* as specifically distinct from *S. malachiticus.* He considered *S. lunaei* a close relative of *S. acanthinus,* but did not comment further on species affinities. Both *S. acanthinus* and *S. lunaei* had originally been included by Smith (1939) in the *spinosus* group, but in a subsequent paper, he (1942) formally transferred *S. lunaei* to the

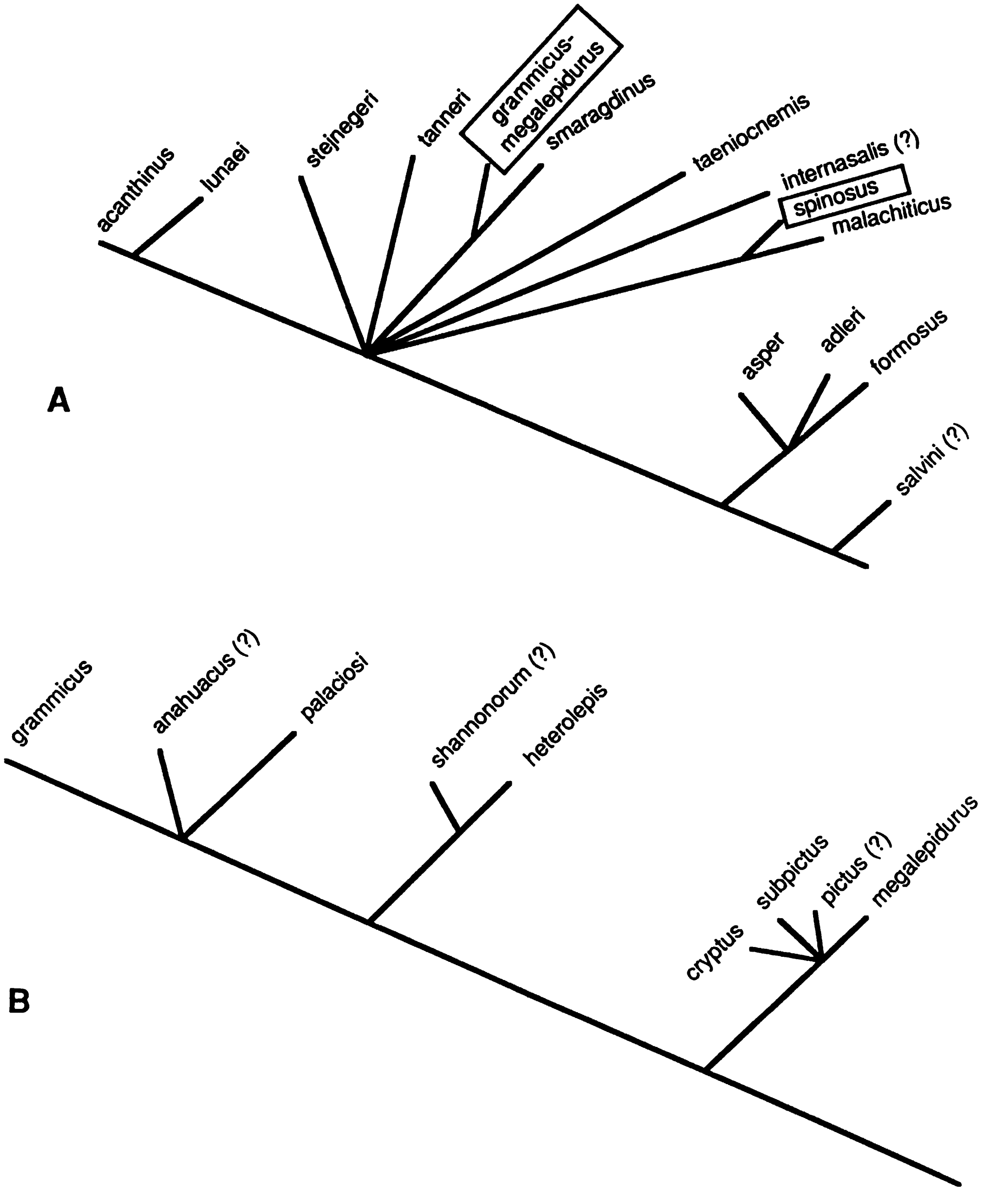


Fig. 5. Modified version of interspecific relationships within the *formosus* (**A**) and *grammicus–megalepidurus* (**B**) radiations of large-bodied, large-scaled *Sceloporus*, as depicted by Smith (1939).

formosus group. No such statement was made for *S. acanthinus*, but in the same paper Smith provided a key to the species of the *formosus* group (1942: 356) in which *S. acanthinus* and *S. salvinii* both appear under the names *S. malachiticus acanthinus* and *S. malachiticus salvinii*; Stuart (1971) later referred to the latter as a full species, *S. salvinii*. Two additional species, *S. adleri* (Smith and Savitsky, 1974) and *S. tanneri* (Smith and Larsen, 1975), have been described from *formosus*-like and *malachiticus*-like populations, respectively. This group is generally characterized by moderate body sizes (81–95 mm SVL), and a prominent black shoulder spot that may extend dorsally to form an unbordered nuchal collar.

Figure 5B depicts a modification of Smith's hypothesis of relationships within and between the *grammicus* and *megalepidurus* groups (fig. 15 of Smith, 1939; the *grammicus* group was then the *microlepidotus* group). Smith postulated a derivation of the *grammicus* group from within the *S. malachiticus* complex, and then a derivation of the *megalepidurus* group from the *grammicus* group (fig. 5A, B). Both Smith (1939) and Smith and Taylor (1950) recognized either two or three species within each of these groups. The *megalepidurus* group originally consisted of *S. megalepidurus* and *S. pictus*. The *grammicus* group comprised *S. grammicus, S. heterolepis,* and *S. microlepidotus,* but Smith and Taylor (1950) relegated the latter to a subspecies of *S. grammicus.* Recently, Smith (1987) resurrected *S. microlepidotus* as a full species, including the subspecies *S. m. disparilis,* but presented no justification. Two new species have been described in the *megalepidurus* group, including *S. subpictus* (Lynch and Smith, 1965) and *S. cryptus* (Smith and Lynch, 1967), and Dasmann and Smith (1974) have relegated *S. pictus* to subspecific status within *S. megalepidurus* on the basis of intergrade populations found by Hall (1973; discussed further below). Langebartel (1959) described *S. shannonorum* as a third species within the *grammicus* group, and allied it with *S. heterolepis.* Webb (1969) challenged this assessment, and considered *S. shannonorum* to be only a race of *S. heterolepis.* Hall (1973) rejected Webb's conclusions, and reaffirmed Langebartel's specific recognition of *S. shannonorum.* The name *S. grammicus* currently applies to an extremely chromosomally polytypic complex of populations which may contain additional species. Two new species were described by Lara-Gongora (1983): *S. anahuacus* was applied to some very localized high-elevation populations of Hall's (1973) "P1" chromosome race (P1 = polymorphic for a centric fission of macrochromosome pair 1), and the name *S. palaciosi* was designated for selected populations of Hall's "F6" race (= fixed for a centric fission of macrochromosome pair 6), which is largely confined to several volcanoes in the vicinity of the Valley of Mexico. Sites et al. (1988) surveyed levels of allozyme divergence among several Central Mexican populations of this complex, including both *S. anahuacus* and *S. palaciosi,* and concluded that the latter was likely a distinct species, and that there was no evidence of intergradation between the two where their ranges were in contact (but see Hall and Selander, 1973).

Morphologically, members of the *grammicus* and *megalepidurus* groups are generally characterized by small to moderate body sizes (48–81 mm SVL) relative to other members of the "large-bodied" radiation, four postrostral scales, lateral scales that are slightly smaller than the dorsals and in oblique rows, smooth preanal scales in both sexes, and enlarged postanal scales in males.

Figure 6A summarizes the hypothesized relationships for species within the *spinosus* group (modified from fig. 7 of Smith, 1939), which Smith considered to be an early derivative from the *formosus* group (specifically *S. formosus malachiticus*). We discussed above Smith's original proposal that included both *S. acanthinus* and *S. lunaei* as members of this group. *Sceloporus licki* was originally recognized as distinct by Van Denburgh (1896), but was considered subspecific to *S. orcutti* by Smith (1939) and Smith and Taylor (1950). Hall and Smith (1979) showed that *S. orcutti licki* of the southern Cape Region of Baja California included two species—the arboreal *S. licki* and the petricolous *S. hunsakeri*—neither of which is a subspecies of *S. orcutti.*

A parallel history characterizes the *S. magister* complex from the Baja California Peninsula (fig. 6A). Van Denburgh (1922) recognized five distinct species, including *S. lineatulus, S. magister, S. monserratensis, S. rufidorsum,* and *S. zosteromus.* Linsdale (1932) considered *S. rufidorsum* and *S. zosteromus* to be subspecies of *S. magister,* and both Smith (1939) and Smith and Taylor (1950) considered *S. monserratensis* and *S. lineatulus* as additional subspecies of *S. magister.* This view has generally been upheld,

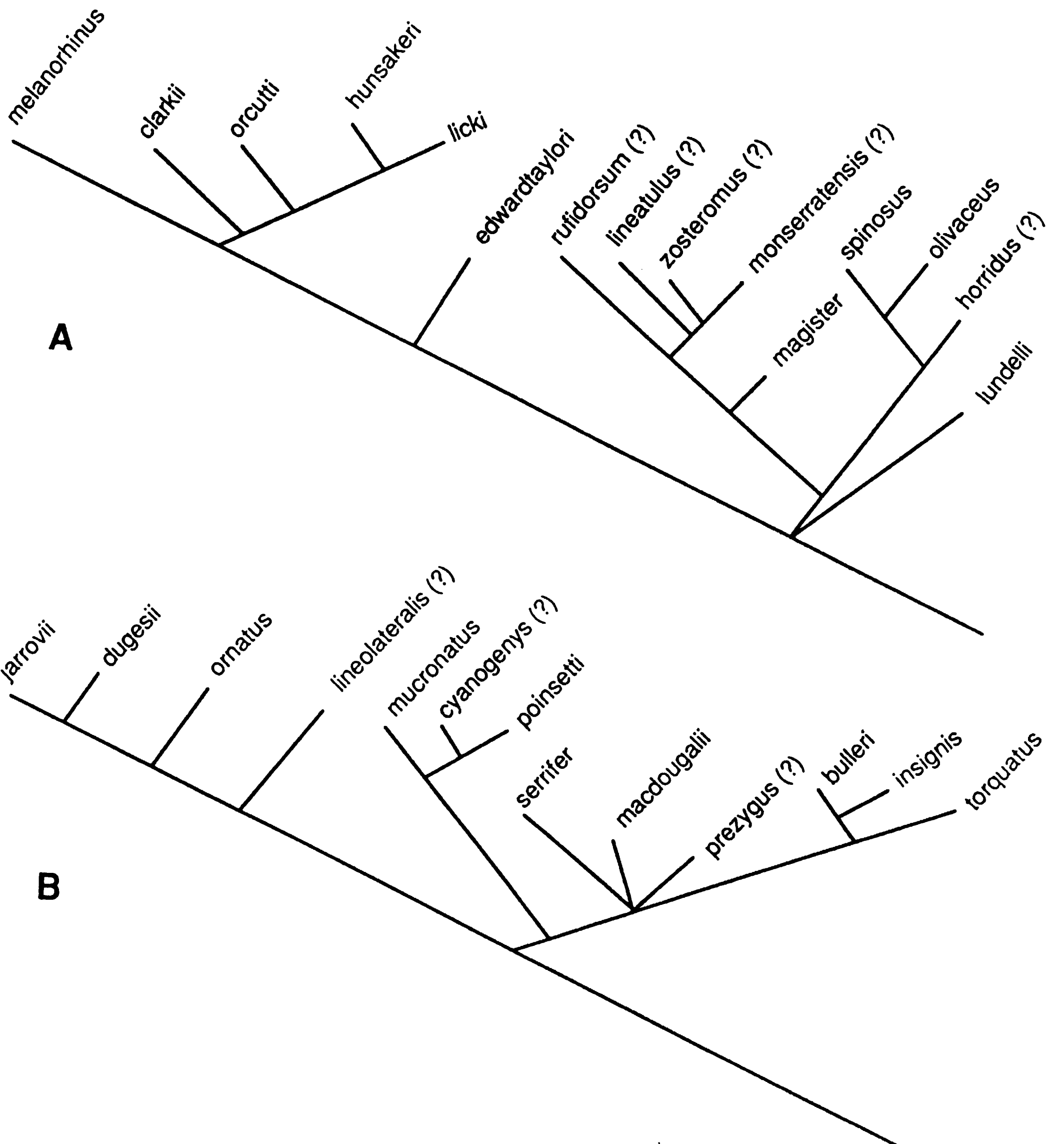


Fig. 6. Modified version of interspecific relationships within the *spinosus* (**A**) and *poinsetti* (**B**) groups of large-bodied, large-scaled *Sceloporus*, as recognized by Smith (1939).

but preliminary electrophoretic studies suggest that all five of the species originally described by Van Denburgh may be valid (Murphy 1983a, 1983b). One other question raised within this complex concerns the specific status of *S. horridus*. In the original revision, Boulenger (1897) regarded it as a subspecies of *S. spinosus*, while Smith (1939) separated the two because of absence of evidence of intergradation in the upper Rio Balsas basin of Oaxaca, where their ranges approach each other. However, Boyer et al. (1982) reported morphological evidence (primarily the number of supraocular scales) for intergradation between *S. horridus* and *S. spinosus* (albeit from a sample not near the zone of contact), and proposed that all races of the former were properly regarded as subspecies of *S. spinosus*. Morphologically, members of the *spinosus* group are generally large as adults (86–140 mm SVL), usually possess a single series of supraoculars that partially contact the median head scales, have relatively large dorsal scales (26–40) that are strongly mucronate, femoral pore series that are widely separated medially, and enlarged postanals in males.

Figure 6B presents hypothesized relationships for species within the *torquatus* group (modified from fig. 21 of Smith, 1939; see also Smith, 1936). Smith (1939: fig. 3) postulated that this group arose from an ancestor common to the *spinosus* group. Taxonomic changes have included the aforementioned reallocation of *S. prezygus* from the *formosus* group to subspecific status within *S. serrifer* (Stuart, 1970), the description of *S. macdougalli* by Smith and Bumzahem (1953), the description of *S. insignis* as distinct from *S. bulleri* by Webb (1967), and the inclusion of *S. lineolateralis* as a subspecies of *S. jarrovi* by Webb and Hensley (1959). More recently, Olson (1987) has reallocated *S. cyanogenys* to a subspecies of *S. serrifer* on the basis of intergrade specimens from southern Tamaulipas. The *torquatus* group species are distinguished chiefly by the relatively large, flattened body and the presence of a prominent black nuchal collar having both anterior and posterior light borders.

The only polytypic group for which an explicit phylogenetic tree has not been published is the *undulatus* group; it was not treated in detail by Smith because most of its range is north of Mexico. Smith (1938) did treat this group separately in an earlier paper but presented no phylogenetic hypothesis, and appeared to have had difficulty defining it on a firm morphological basis. Smith (1939) argued for derivation of the *undulatus* group from within the *spinosus* group, and considered *S. cautus* as a possible link between the two. Smith (1938) recognized *S. cautus, S. undulatus,* and *S. occidentalis* (see p. 16 of Smith, 1938) as distinct species, with *S. undulatus* comprising seven subspecies.

Changes in composition of the *undulatus* group (fig. 3) include: (1) the informal inclusion of *S. woodi* (Smith, 1946), which had been considered a subspecies of *undulatus* by Burt (1935) and Neill (1957), and a semispecies by Jackson (1973a, 1973b); (2) the recognition that *S. virgatus* is not conspecific with *S. undulatus* by Cole (1963); and (3) the description of *S. exsul* by Dixon et al. (1972). The monotypic *graciosus* group was considered by Smith (1939) to be the sister group of the *undulatus* group (fig. 3). A recent proposal by Collins (1991) encourages the recognition of two subspecies of *S. graciosus, S. g. arenicolous* and *S. g. vandenburgianus,* as distinct species.

THE LARSEN AND TANNER HYPOTHESIS

INTRODUCTION

Larsen and Tanner (1974, 1975) analyzed 55 species of *Sceloporus* using numerical-phenetic clustering techniques. The analysis was based on an extensive array of intrinsic and extrinsic characters, including external morphology, cranial osteology, zoogeography, karyology, and display behavior. Larsen and Tanner subsequently interpreted their results in a phylogenetic context, and recognized three major species groups. Two of the three species groups were recognized as belonging to the single genus *Sceloporus,* and the generic name *Lysoptychus* Cope was resurrected to represent the other species group. Figures 7 and 8 depict the relationships among the major groups of species proposed by Larsen and Tanner (1975: fig. 5). As detailed below, several of these groups are the same as or similar to those proposed by Smith (1939). However, Larsen and Tanner (1975) proposed substantial rearrangement and reconstitution of several other groups. Since Smith (1939, 1946) and others (Mittleman, 1942) believed that several other genera, including *Uta, Sator,* and *Urosaurus,* were derived from within the genus *Sceloporus,* and since this hypothesis has been reversed more recently (Savage, 1958; Etheridge, 1964; Presch, 1969), it is not surprising that a substantial rearrangement of groups and realign-

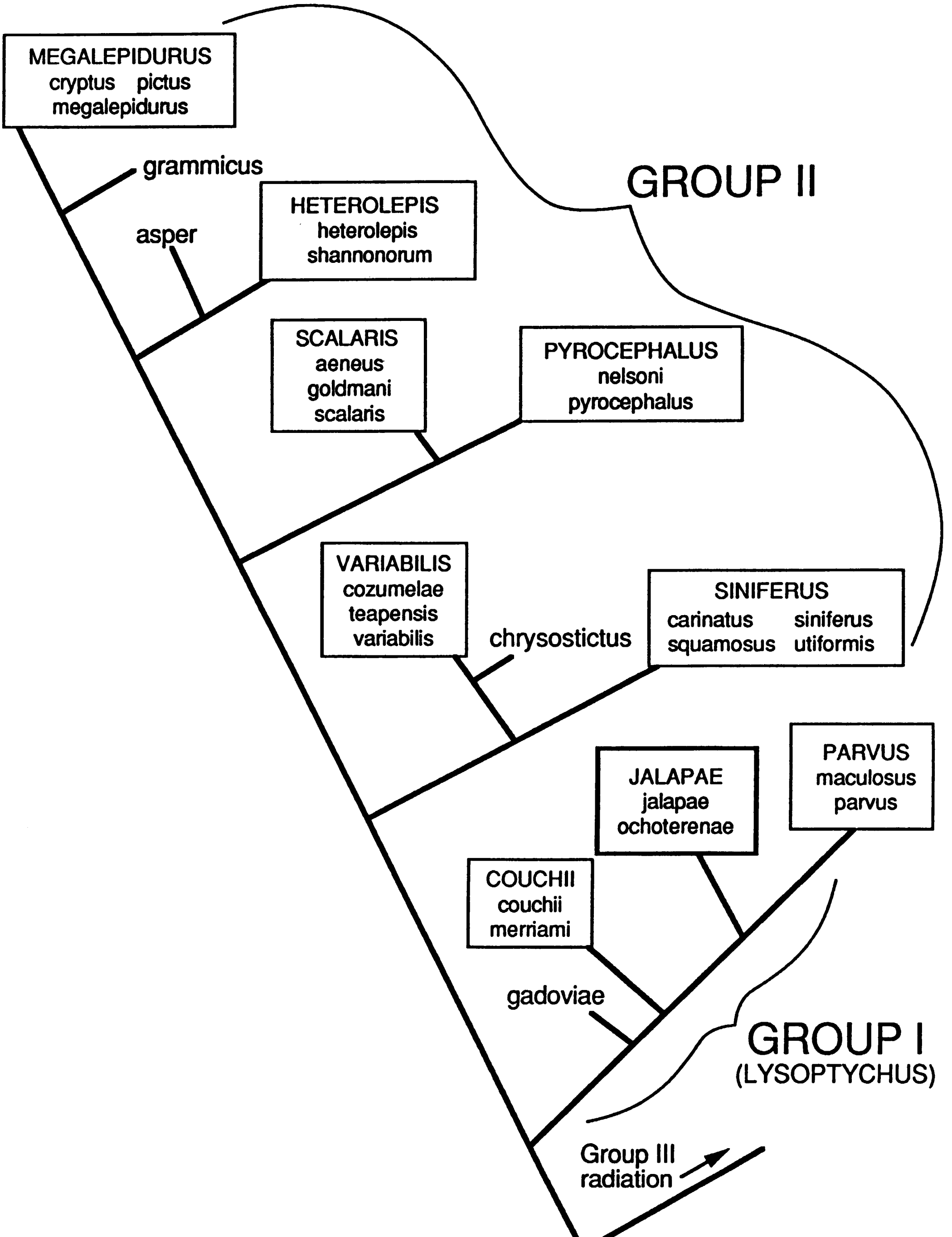


Fig. 7. Species groups and phylogenetic relationships for Group I and Group II radiations of *Sceloporus* as defined by Larsen and Tanner (1975).

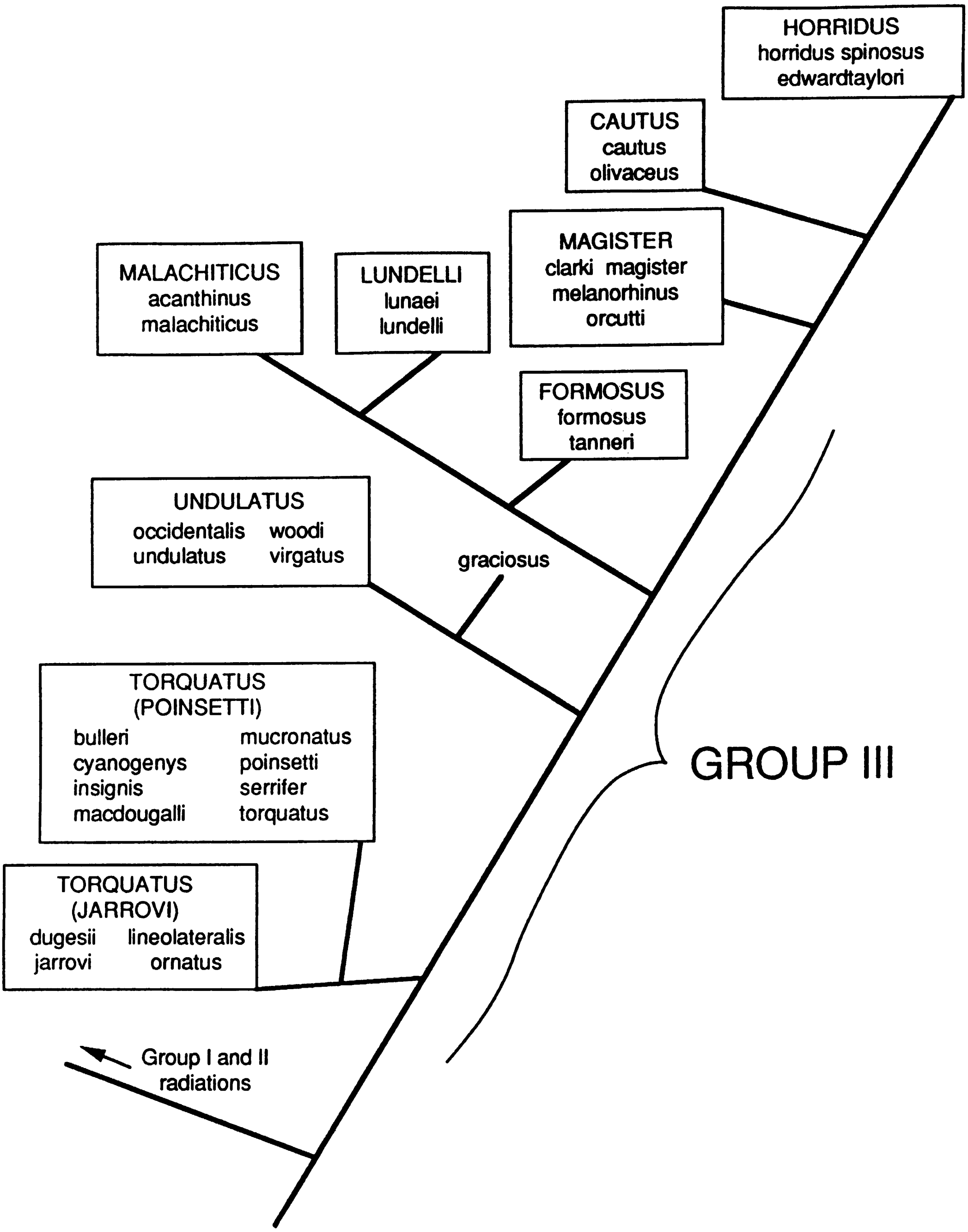


Fig. 8. Species groups and phylogenetic relationships for the Group III radiation of *Sceloporus* as defined by Larsen and Tanner (1975); parentheses denote distinct subgroups of the *torquatus* group.

ment of species within groups has occurred. Smith (1939, 1946) alluded to many problems and possibilities for uncertain relationships within and among the species groups which Larsen and Tanner (1975) used to justify, in part, the extensive rearrangements they

TABLE 1

Cranial Osteological Measurements Taken on *Sceloporus* by Larsen and Tanner (1974, 1975)

A. DORSAL VIEW:

1. Posterior extent of supraoccipital to anterior border of parietal foramen
2. Parietal foramen to suture between nasals
3. Length of suture between nasals
4. Length of premaxilla
5. Posterior tip of suture between frontal and nasal to posterior end of suture between prefrontal and nasal
6. Posterior end of suture between prefrontal and nasal to anterior end of suture between prefrontal and nasal
7. Anterior end of suture between prefrontal and nasal to anterior end of suture between maxillary and nasal
8. Anterior end of suture between maxillary and nasal to anterior end of suture between maxillary and premaxillary
9. Pineal foramen to posterior end of suture between prefrontal and lacrimal
10. Posterior extent of lateral wing of parietal to posterior end of suture between parietal and postorbital
11. Length of postorbital
12. Posterior end of suture between parietal and postorbital to anterior edge of parietal foramen
13. Posterior tip of prefrontal to anterior end of suture between prefrontal and nasal
14. Posterior end of suture between prefrontal and lacrimal to anterior tip of prefrontal
15. Narrowest width of frontal
16. Anterior width of parietal (along suture with postorbital)
17. Lateral side of jugal on transverse line through anterior border of parietal foramen to lateral extent of suture between postorbital and parietal
18. Interfenestral width (on line passing through posterior tip of both postorbitals)
19. Lateral edge of parietal on line passing through posterior tip of both postorbitals to posterior tip of postorbital on same side
20. Anterior end of suture between prefrontal and nasal to posterior end of suture between prefrontal and lacrimal
21. Distance between left and right anterior ends of suture between prefrontal and nasal
22. Internarial width
23. Distance between left and right anterior ends of suture between maxillary and premaxillary

B. VENTRAL VIEW:

24. Posterior tip of occipital condyle to medial corner of tip of basipterygoid process of the basisphenoid
25. Lateral tip of ectopterygoid to anterior tip of premaxilla

TABLE 1—(*Continued*)

26. Medial corner of tip of basipterygoid process to lateral tip of ectopterygoid
27. Posterior corner of lateral side of palatine to lateral limit of suture between palatine and maxilla
28. Posterior tip of quadrate ramus of pterygoid to lateral tip of ectopterygoid
29. Lateral tip of ectopterygoid to medial limit of suture between maxilla and ectopterygoid
30. Distance between lateral tips of ectopterygoid
31. Medial limit of suture between maxilla and ectopterygoid to posterior corner of lateral side of palatine
32. Posterior corner of lateral side of palatine to medial limit of suture between palatine and pterygoid
33. Smallest width of basisphenoid
34. Diagonal distance from lateral tip of ectopterygoid on one side to posterior tip of quadrate ramus of pterygoid on the other side
35. Length between lateral tip of ectopterygoid to posterior tip of quadrate ramus of pterygoid
36. Tangent of the angle between the midline and the extended line which passes through the midpoint on the tip of the basipterygoid process and the midpoint on the most narrow part of the neck of the basipterygoid process

C. LATERAL VIEW:

37. Tip of maxilla to most ventral extent of ectopterygoid projected onto a line from the tip of premaxilla to tip of quadrate ramus of pterygoid
38. Tip of premaxilla to posterior tip of postorbital
39. Most ventral extent of ectopterygoid to tip of quadrate ramus of pterygoid projected onto a line from the tip of premaxilla to tip of quadrate ramus of pterygoid
40. Tip of premaxilla to anterior end of suture between prefrontal and lacrimal
41. Anterior end of suture between prefrontal and lacrimal to posterior tip of prefrontal
42. Posterior tip of prefrontal to anterior end of suture between postfrontal and parietal
43. Anterior end of suture between prefrontal and lacrimal to posterior tip of prefrontal (direct)
44. Posterior tip of prefrontal to most ventral extent of ectopterygoid
45. Anterior end of suture between postfrontal and parietal to tip of quadrate ramus of pterygoid

D. POSTERIOR VIEW:

46. Dorsal ridge of supraoccipital to dorsal edge of foramen magnum
47. Top of parietal at midline to ventral edge of parietal at midline
48. Height of foramen magnum along midline
49. Ventral edge of foramen magnum on midline to ventral edge of condyle

TABLE 1—(*Continued*)

50. Dorsal corner of lateral process of exoccipital to ventral corner of lateral process of exoccipital
51. Distance between right and left dorsal corners of lateral process of exoccipital
52. Distance between right and left ventral corners of basioccipital tubercles
53. Tangent of the angle formed by the dorsal corner of the lateral process of the exoccipital and its intersection with the midline (at right angles) and the ventral corner of the basioccipital tubercle
54. Tangent of the angle formed by the shortest width of the parietal, its intersection with the midline, and the line from that intersection to the dorsal corner of the lateral process of the exoccipital

proposed, and more recently, Cole (1978) returned *Lysoptychus* to the synonymy of *Sceloporus.*

CHARACTERS ANALYZED

Cranial osteology. A total of 40 cranial osteometric characters were included in the analysis. All of these were derived as ratios of 51 original cranial measurements plus three angles between landmarks (table 1). The measurements were obtained from photos taken at fixed angles of the dorsal, ventral, lateral, and posterior surfaces of the skull. Ratios were formed presumably to standardize to a common size factor, although the reason for this is not made clear by Larsen (1973) or Larsen and Tanner (1974). Many of the characters were formed by dividing original measurements by a single common measurement (table 2). This practice has been criticized by Atchley et al. (1974) because it causes correlations between the characters divided by the common variable (particularly when the denominator variable has a high variance). For each species, only a single skull was examined, so no indication of the comparative variability of the measurements could be determined. The character ratios used could be expected to have substantial coefficients of variation.

External morphology. A total of 40 meristic and mensural characters were used in this analysis (table 3). These included most of the diagnostic and key characters used consistently in the analysis of *Sceloporus* systematics in general, and in particular, by Smith (1939).

Karyology and behavior. The only karyological characters used were the number of microchromosomes. These were available for 36 species. Two behavioral characters were used (as reported by Purdue and Carpenter, 1972a, 1972b): (1) the ratio of vertical movement of the shoulder to the vertical movement of the eye; and (2) the ratio of vertical movement of the hip to the vertical movement of the eye in display action patterns. Unfortunately the extensive behavioral repertoires assembled by Carpenter (1978), Purdue and Carpenter (1972a, 1972b), and Bussjaeger (1971) could not be quantified for this analysis.

Geographic distribution. Geographic distribution characters were entered as the approximate longitude and latitude of the geographic center for each species distribution. The proximity of geographic centers of distribution would seem to be useful information on phylogenetic relationships if a linear

TABLE 2

Characters Used by Larsen and Tanner (1974, 1975) in Phenetic Analysis as Ratios of Measured Variables

(The numerical designations for each character refer to measurements described in Table 1)

1.	1/2	11.	15/16	21.	29/30	31.	42/38
2.	3/2	12.	17/16	22.	31/30	32.	43/41
3.	4/2	13.	18/16	23.	32/30	33.	44/45
4.	5/6	14.	19/16	24.	33/30	34.	46/47
5.	7/2	15.	20/21	25.	34/35	35.	48/47
6.	8/2	16.	22/23	26.	5 × 36	36.	49/47
7.	9/2	17.	24/25	27.	37/38	37.	50/47
8.	10/2	18.	26/25	28.	39/38	38.	51/52
9.	11/12	19.	27/25	29.	40/38	39.	5 × 53
10.	13/14	20.	28/25	30.	41/38	40.	5 × 54

TABLE 3

External Characters, Including Measurements, Ratios, and Scale Counts, Used by Larsen and Tanner (1974, 1975) in Phenetic Analyses of *Sceloporus* Relationships

(All measurements were taken in millimeters)

1. Snout–vent length
2. Snout–vent/snout–parietal eye length
3. Humerus (from ventral midline to outside of elbow)/snout–vent
4. Femur (from ventral midline to outside of knee)/snout–vent
5. Outside length of tibia/snout–parietal eye
6. Length of fourth toe/femur length
7. Height-to-width ratio of tail at point one head length from vent
8. Snout–parietal eye
9. Width of head at parietal eye/snout–parietal eye
10. Vertical height of head at parietal eye/snout–parietal eye
11. Width of head anterior to orbit/snout–parietal eye
12. Distance between nares/snout–parietal eye
13. Length of frontal scale(s)/snout–parietal eye
14. Length of frontal scale(s)/smallest width of frontal
15. Largest linear measurement on internasal scale/snout–parietal eye
16. Length of interparietal/width of interparietal (through parietal eye)
17. Width of widest supraocular/snout–parietal eye
18. Width of widest supraocular/length of same
19. Parietal eye to posterior edge of interparietal/length of interparietal
20. Length of median frontonasal/width of median frontonasal
21. Length of median frontonasal/snout–parietal eye
22. Number of dorsals from interparietal to posterior edge of thigh
23. Number of ventrals from anterior edge of shoulders to vent
24. Number of dorsals equal to one head length (between points 2 and 3 head lengths posterior to interparietal)
25. Number of laterals equal to one head length midway between limbs
26. Number of ventrals equal to one head length (between points 2 and 3 head lengths posterior of snout)
27. Number of dorsals equal to ½ head length (counting laterally from midline at a point 2 head lengths from interparietal)
28. Number of ventrals equal to ½ head length (counting laterally from midline at a point 3 head lengths from snout)
29. Total number of femoral pores (both sides)
30. Number of ventrals between medial limits of femoral pore series
31. Number of ventrals from vent to a line connecting femoral pore series

TABLE 3—(*Continued*)

32. Number of caudals equal to one head length (between points 1 and 2 head lengths from vent)
33. Number of supralabials (total both sides and rostral)
34. Number of infralabials (total both sides and mental)
35. Number of sublabials (total both sides and mental)
36. Number of caudals around tail one head length from vent
37. Number of dorsals equal to one interparietal (counting posterior from interparietal)
38. Number of ventrals equal to one interparietal (counting anterior from vent)
39. Number of head shields in contact with interparietal
40. Number of fourth toe lamellae

dispersal model or vicariance model without dispersal were reasonable. Within some subgroups of the genus, e.g., the *nelsoni–pyrocephalus* group, *spinosus,* or *formosus* groups, this may be a reasonable expectation. However, when the entire genus is considered, many of the species and species groups have many more than one subgroup with broadly overlapping distributions. As a result, it is not likely that similarity of geographic centers of distribution can be thought of as useful characters for a phylogenetic analysis.

NUMERICAL METHODOLOGY

Larsen and Tanner used Ward's cluster analysis on a variety of subsets of their entire data set of 85 characters. These included: external morphology alone (57 species); cranial osteology alone (55 species); external morphology plus cranial osteology (55 species); external, skull, and distribution data (55 species); external, skull, distribution and display data (23 species); external, skull, distribution, and chromosomal data (36 species); external, skull, distribution, display, and chromosomal data (18 species); and distribution, display, and chromosomal data (18 species). Given the variety of data sets analyzed and the disparities in numbers of species used for each, we have not attempted to include here (in our figures) taxa of uncertain status or more recently described species. The phylogenetic interpretations of Larsen and Tanner were based on a subjective evaluation of shared subsets in single and combinations of the phenograms.

Subsequent to the cluster analyses, Larsen and Tanner (1975) proposed a novel way of modifying a phenogram to represent a phylogram or pattern of phylogenetic relationships. One of the basic differences between phenograms and cladograms is that the latter are basically two-dimensional representations or summaries of the intertaxon distance relationships, while phenograms are basically one-dimensional representations. This is because all terminal taxa in a phenogram are equidistant from their common ancestor (the implied distances among taxa exhibit ultrametric properties) while in a cladogram the terminal branches may be of different length (the implied distances among taxa exhibit 4-point metric properties). As a result, additional distortion of the original distance array can be expected in phenograms in comparison to cladograms. Larsen and Tanner (1975) attempted to use the original distance values from their analysis to modify their phenograms to better represent the distance values and, hence, the phylogenetic relationships among the taxa. They reasoned as follows: "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." Their conceptualization of more primitive species is obviously anagenetic (versus cladogenetic), implying that species that were early offshoots of a lineage are likely to exhibit little anagenetic change after origin.

RESULTS OF DATA ANALYSIS

Larsen and Tanner's (1975) Group I species (figs. 7 and 9) were placed in the resurrected genus *Lysoptychus* Cope (1888). The proposed group consists of a conglomerate of seven species from six of Smith's (1939) original groups: two species of Smith's *variabilis* group (*S. couchii* and *S. parvus*; see below), *S. merriami* (a monotypic group), *S. maculosus* (also a monotypic group), *S. ochoterenae* (*siniferus* group), *S. jalapae* (*scalaris* group), and *S. gadoviae* (*pyrocephalus* group). The characters that these species have in common, based on the description of Larsen and Tanner (1974, 1975) and Smith (1939), are: very small dorsal scales, a large number of femoral pores, very small scales on the posterior surface of the thighs, rudimentary gular fold (*S. merriami, S. couchii, S. gadoviae*), absence of postrostrals (*S. jalapae, S. ochoterenae,* and *S. maculosus*), and a postfemoral dermal pocket (*S. couchii, S. gadoviae, S. parvus,* and *S. maculosus* [also present in *S. variabilis, S. teapensis,* and *S. cozumelae*]). Smith (1939) noted that *S. merriami* is very similar in all of its diagnostic characters to *S. couchii* and *S. parvus* from his *variabilis* group. This large number of similar external features causes the species to appear together as a distinct group on the phenograms of Larsen and Tanner based on external characters alone as well as the external-plus-cranial osteology characters. They are not so united on the other phenograms, including that derived from cranial osteology alone. The hypothesized phylogenetic relationships of the species within the group corresponds identically to those in the external-plus-cranial osteology phenogram.

The diagnostic characters of *Lysoptychus,* as listed above, are either primitive (symplesiomorphies), or of arguable polarity, shared to a greater or lesser extent with members of the genera *Uta, Sator,* and *Urosaurus.* The species of *Lysoptychus* may form a monophyletic group, as hypothesized by Larsen and Tanner (1975), or they may represent basal members of several of the other species groups within *Sceloporus,* as hypothesized by Smith (1939) who listed *S. jalapae* as the most basal member of the *scalaris* group. *Sceloporus jalapae* has a 2n = 34 chromosome number, the ancestral state, while the other members of the *scalaris* group have 2n = 24. *Sceloporus gadoviae* possesses a postfemoral dermal pocket, common to members of the *variabilis* group as well as remnants of a gular fold, the lack of which is a character uniting species of *Sceloporus* with *Sator.* Several of the species, notably *S. ochoterenae,* were noted for their lack of apomorphic features of the groups in which Smith placed them. Thomas and Dixon (1976) also removed *S. jalapae* and *S. ochoterenae* from the *scalaris* and *siniferus* groups, respectively, and placed them in their own group without suggesting an alignment to other groups. *Sceloporus merriami* and *S.*

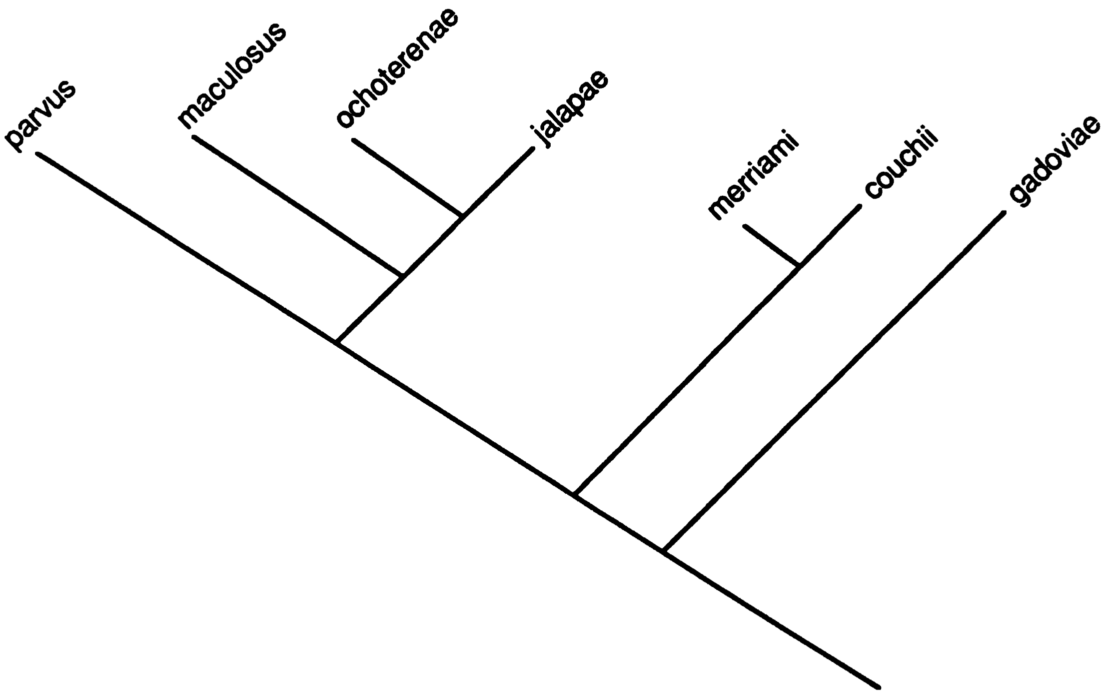


Fig. 9. Modified version of interspecific relationships within the Group I radiation (*Lysoptychus*) of *Sceloporus*, as presented by Larsen and Tanner (1975).

maculosus were two species Smith could not place in other species groups because of their lack of morphological similarities with other species. Hall (1973) also proposed a distinct *jalapae* group containing the four species *S. jalapae, S. ochoterenae, S. parvus,* and *S. gadoviae,* but did not discuss the evidence for diagnosis of this group. In addition, Hall (1973; see below) placed the other species of Larsen and Tanner's *Lysoptychus* as basal members of Smith's small-scaled radiation of *Sceloporus.* He was unable to resolve the relationships of these groups beyond a polytomy with the rest of the small-scaled radiation. Except for *S. merriami* (2n = 46), the species of *Lysoptychus* all possess the presumed plesiomorphic karyotype (2n = 34, see below).

No synapomorphic characters are listed for the genus *Lysoptychus* by Larsen and Tanner (1975). Phenetic methodology might be expected to utilize the symplesiomorphic similarities apparent among members of the group to unite the species. Such similarities do not provide evidence of exclusive common ancestry. The arrangement of the Group I species and the proposed resurrection of the genus *Lysoptychus* for them, which Larsen and Tanner argue form a monophyletic group (1975: 18), would therefore seem to be among the most problematical proposals in the Larsen-Tanner hypothesis. In addition, if these taxa are a monophyletic group, then the genus *Sceloporus,* sensu stricto, is paraphyletic or polyphyletic (depending on the diagnostic characters) according to Larsen and Tanner's hypothesis of relationships (figs. 7, 8). This could only be resolved by: (1) considering the large-scaled (Group III) radiation as *Sceloporus,* as *S. torquatus* is the type species (Smith, 1939: 28), and including the other small-scaled species (Group II) in *Lysoptychus* with Group I; or (2) creating an additional genus for the small-scaled (Group II) radiation, while retaining *Sceloporus* for Group III and retaining *Lysoptychus* for Group I.

The second group of species (Group II, figs. 7 and 10) identified by Larsen and Tanner (1975) includes the remainder of Smith's (1939) small-scaled, small-bodied species not

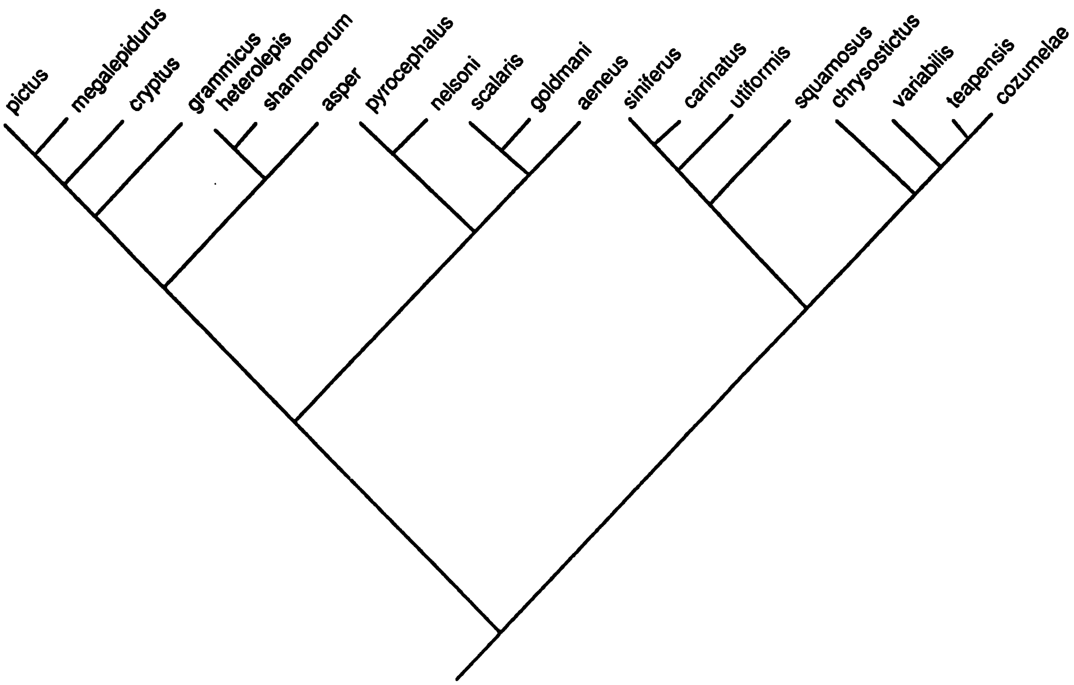


Fig. 10. Modified version of interspecific relationships within the Group II radiation in *Sceloporus*, as presented by Larsen and Tanner (1975).

included in *Lysoptychus* (*pyrocephalus*, *variabilis*, *siniferus*, *scalaris*, *utiformis*, and *chrysostictus* groups) plus two entire groups (*grammicus* and *megalepidurus*) as well as *S. asper* from the *formosus* group that Smith (1939) placed in the large-scaled, large-bodied radiation (fig. 3). The composition and relationships of species both among and within species groups within Group II form another radical part of Larsen and Tanner's overall hypothesis of relationships within the genus, as it deviates extensively from Smith's (1939) original hypothesis.

The new *variabilis* group of Larsen and Tanner contains *S. cozumelae*, *S. teapensis*, and *S. variabilis* from Smith's *variabilis* group species (less *S. couchii* and *S. parvus* which are now placed in Group I) plus *S. chrysostictus*, which Smith placed in the radiation leading to the *siniferus* and *scalaris* groups within the small-scaled, small-bodied radiation. The *variabilis* group plus *S. chrysostictus* is placed as the sister group of the *siniferus* group (figs. 7, 10). Smith's hypothesis of relationships presents the *variabilis* group as being paraphyletic. *Sceloporus variabilis*, *S. teapensis*, and *S. cozumelae* form one distinct radiation, and *S. parvus* and *S. couchii* form a separate radiation (fig. 4A). However, *S. maculosus*, *S. merriami*, and the genera *Petrosaurus*, *Urosaurus*, and *Uta* were postulated by Smith (1939) to be closely related to this second radiation. With the hypotheses that the evolution of the phrynosomatids be reoriented (Presch, 1969; Larsen and Tanner, 1975; Etheridge and de Queiroz, 1988; Frost and Etheridge, 1989), which places *Urosaurus* and *Uta* as the first and second taxonomic outgroups of *Sceloporus*, a complete realignment of species in this pivotal group should not be totally unexpected. One distinct character that Smith used to unite the *variabilis* group was the postfemoral dermal pocket, which is found in all members. This character appears to be plesiomorphic as it is found in *S. gadoviae* and *S. maculosus* (Smith, 1939). Many of the other characters used to unite the *variabilis* group by Smith may also be considered plesiomorphic for the genus as a whole.

As mentioned above, the *siniferus* group (*S. siniferus*, *S. carinatus*, *S. utiformis*, and

S. squamosus) was placed as the sister group of the *variabilis* group by Larsen and Tanner (fig. 10). The contents of this group were unchanged from Smith's hypothesis (fig. 4B). Only a single change of the relationships within the group was suggested. This gives an arrangement in almost perfect agreement with that of Hall (1973; see below).

The second major radiation within Larsen and Tanner's Group II includes one subgroup containing the *scalaris* and *pyrocephalus* groups from Smith's small-scaled, small-bodied radiation, plus a second subgroup containing the *grammicus–heterolepis* and *megalepidurus* groups from Smith's large-scaled, large-bodied radiation (figs. 7, 10). These are all species which, as noted above, are significantly smaller than the other species of the large-bodied radiation. Smith (1939) originally placed the *scalaris* and *pyrocephalus* groups in separate subgroups (fig. 4), but with the reorientation of the relationships of the genus to *Uta* and *Urosaurus*, as with the *variabilis* and *siniferus* sister-group arrangement, a substantial realignment should not be surprising. The *scalaris* group is diagnosed by several synapomorphic chromosomal rearrangements (fusions; $2n = 24$), while the *pyrocephalus* group retains the presumed plesiomorphic karyotype ($2n = 34$, with one fixed pericentric inversion in *S. pyrocephalus*; see below).

The second subgroup within this radiation contains *S. asper* from the *formosus* group, plus the *grammicus–heterolepis* and *megalepidurus* groups from Smith's large-scaled, large-bodied radiation. *Sceloporus asper* and *S. heterolepis* appear repeatedly together on the phenograms obtained by Larsen and Tanner (1974), and are in turn united with members of the *grammicus–megalepidurus* complex on some phenograms. These latter two groups were considered most closely related by Smith (fig. 5B). The removal of *S. asper* from the *formosus* group is justified by Larsen and Tanner by its relatively underived chromosome number ($2n = 32$) as compared to the members of the *formosus* group ($2n = 22$). Similarly, the separation of the *formosus* and *grammicus* radiations was justified by the relatively underived chromosome number of most members of the *grammicus* complex (but see below). *Sceloporus asper* appears together with *S. heterolepis* on the cranial osteology and external morphology-plus-cranial osteology phenograms. The sister-group alignment of the two groups (*S. asper* and *heterolepis* group) in these phenograms is most apparent only when distributional characters are added to the data set. These characters are also useful in defining the Group II clade as a whole. An examination of the species distributions for this group (figs. 20–23) indicates that they are primarily southern species, while many of the Group III species are primarily northern in distribution. As noted below, Hall (1973) removed *S. cryptus* from the *grammicus–heterolepis* complex and placed it in the *formosus* group of the large-scaled radiation.

Most of the species in this subgroup do not meet the criterion of being relatively large-scaled and large-sized as the Smith categorization would suggest. In fact, their relatively small-scaled nature is likely the primary reason for placement with the other small-scaled species in Group II. However, Smith (1939: 33) considered all the species in the *grammicus–heterolepis–megalepidurus* complex to occupy relatively intermediate positions (sequences of derivation) in the large-scaled, large-bodied radiation. The reorientation of the origin of the genus (*Uta* and *Urosaurus* as outgroups) results in the complete separation of this complex into a distinct radiation (Group II) that is the sister group of Group I, rather than the placement of the groups on the trajectory leading to the large-scaled, large-bodied forms (fig. 7). Larsen and Tanner (1975) stated that they considered the *grammicus* group to be the sister group of all other Group II species, although the placement of the species in the phylogeny does not make this apparent. Clearly, relative phylogenetic position is a subjective, anagenetic qualifier in this case as they appear in a relatively derived location on the Group II species phylograms (figs. 7, 10). As mentioned above, Hall (1973) placed *S. cryptus* in the *formosus* group of the large-scaled radiation. Table 4, however, shows that this decision was based on an unknown number of individuals, and such an observation cannot be verified at this time. The

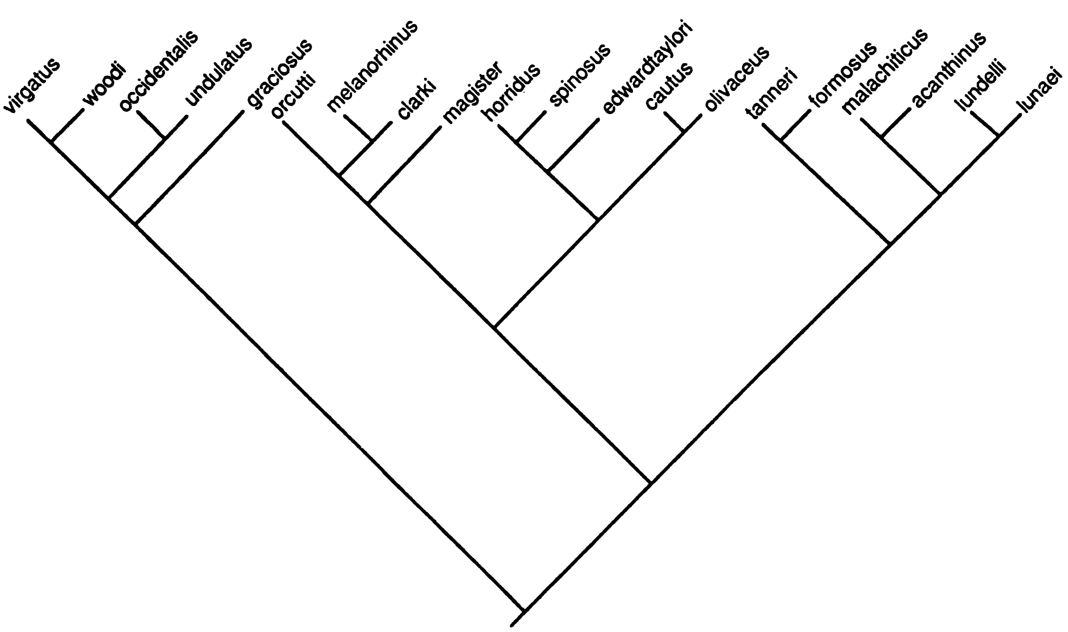


Fig. 11. Modified version of interspecific relationships within and among the *horridus–cautus–magister–malachiticus–lundelli–formosus–undulatus/graciosus* groups of the Group III radiation of *Sceloporus,* as presented by Larsen and Tanner (1975).

placement of *S. cryptus* on the phenograms is extremely tentative.

Larsen and Tanner's Group III species include the *formosus, graciosus, undulatus, spinosus,* and *torquatus* groups, all members of Smith's large-scaled, large-bodied radiation (figs. 8, 11, 12). Each of these groups is depicted as being monophyletic by Larsen and Tanner (1975). The most notable changes that they proposed are realignments of affinities between the groups. Smith depicted the *formosus* group as being paraphyletic, with the *spinosus* (*horridus*) and *grammicus–megalepidurus* groups being derived from *S.* [*f.*] *malachiticus* and *S.* [*f.*] *smaragdinus,* respectively (fig. 5A). Thus, *S. formosus* (as known at that time) was seen by Smith as being a paraphyletic species. Larsen and Tanner removed *S. asper* and the *grammicus–megalepidurus* complex from the large-scaled, large-bodied radiation, and made the *spinosus* group (including the *magister, horridus,* and *cautus* radiations) the sister group of the *formosus* group, thus making the *formosus* group monophyletic (fig. 11). Smith and Taylor (1950) modified Smith's original *formosus* group to include *S. acanthinus* and *S. lunaei* (formerly in the *spinosus* group, as previously discussed). This modification is consistent with the relationships proposed by Larsen and Tanner (fig. 8). Larsen and Tanner (1975) also removed *S. lundelli* from the *spinosus* group and placed it in the *formosus* group (fig. 11). All three of these latter species had been considered early derivatives of the *spi-*

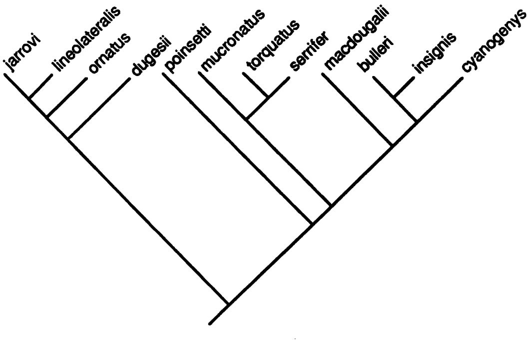


Fig. 12. Modified version of interspecific relationships within the *torquatus* group of the Group III radiation of *Sceloporus,* as presented by Larsen and Tanner (1975).

nosus radiation by Smith (1939). The phenograms presented by Larsen and Tanner (1974) show four of the species (less *S. formosus*) of this complex grouped together (their fig. 14, p. 18). However, these phenograms show little justification for the placement of *S. formosus* with the others in the complex. For all analyses in which it is present, *S. formosus* is grouped together with the members of the *spinosus* or *undulatus* groups. Their analyses indicate that the three groups are very similar and presumably are closely related, but do not provide a consistent indication of relationships. Once *S. acanthinus, S. lunaei,* and *S. lundelli* have been removed from the *spinosus* group, only the placement of *S. edwardtaylori* in the *spinosus* group (removed from the *clarki–orcutti* radiation to the *magister–spinosus* radiation) has been altered by Larsen and Tanner (fig. 11).

The *undulatus* group (*S. undulatus, S. occidentalis, S. virgatus,* and *S. woodi*) of Larsen and Tanner (1975) is identical to that of Smith and Taylor (1950) except for the placement of *S. cautus* as the sister taxon of *S. olivaceus* in the *spinosus* group (fig. 11). Its removal from the *undulatus* group and specific realignment is justified primarily on the basis of behavior data, although *S. cautus* appears frequently on the Larsen-Tanner phenograms with members of the *spinosus* group (1974; figs. 14, 16). *Sceloporus graciosus* appears as the sister group of the *undulatus* group as proposed by Smith (fig. 11).

The *jarrovi* and *torquatus–poinsetti* subtaxa of the *torquatus* group are placed as sister groups by both Larsen and Tanner (1974, 1975) and Smith (1938, 1939), and contain the same species (fig. 12). Within the *jarrovi* complex, there is a difference in the placement of *S. dugesii* and *S. lineolateralis* in their relationship with *S. jarrovi.* Within the *torquatus–poinsetti* complex, the relationships between the hypotheses of Smith and Larsen and Tanner conflict completely (a strict consensus tree between the two has no resolution). Smith (1938, 1939) proposed that *S. serrifer* (the most southerly distributed form) was the earliest derived from the group with *S. poinsetti* (the most northerly distributed form) being the most recently derived and the sister species of *S. cyanogenys.* Larsen and Tanner (1975) proposed that *S. poinsetti* was the earliest derived species and that *S. serrifer* (now the sister taxon of *S. torquatus*) was the most recently derived. This latter arrangement is consistent among their phenograms and is exactly reproduced in the analysis containing distribution data (only *S. mucronatus* is aberrant without these latter data).

ADDITIONAL SPECIES

Larsen and Tanner (1974, 1975) analyzed 55 species of *Sceloporus.* A total of 16 other species were either unavailable for analysis or were undescribed at the time. They are as follows: *S. adleri, S. salvini, S. anahuacus, S. shannonorum, S. subpictus, S. palaciosi, S. prezygus, S. tanneri, S. hunsakeri, S. insignis, S. goldmani, S. macdougalli,* and four former subspecies of *S. magister* (*rufidorsum, lineatulus, zosteromus, monserratensis*). Most of these can be placed reasonably easily into species groups. Larsen and Tanner proposed placement of four of these (*S. tanneri, S. insignis, S. shannonorum,* and *S. goldmani*) although well corroborated hypotheses of relationships within existing species groups had not been proposed for most.

BIOGEOGRAPHIC SCENARIO

Larsen and Tanner (1975) devised a series of scenarios to explain both the distribution and diversity of the species in the genus *Sceloporus* based on their proposed phylogeny. Their scenarios are based extensively on the principle of adaptive radiation and centrifugal speciation (Brown, 1957), accompanied by substantial dispersal and the expected climatic changes brought about by successive Pleistocene glacial events. Although an explanation of species dispersal is necessary because of the extreme complexity of diversity and patterns of distribution, alternative scenarios can be devised incorporating an orientation toward vicariance biogeography that are more consistent with their phylogenetic hypotheses. Below we outline the hypotheses of Larsen and Tanner emphasizing primarily the distributions of the species groups without reiterating the dispersal scenarios.

Group I species (*Lysoptychus*) are distributed in the transverse Sierras of southern Mexico and extend north along the Sierra Madre Oriental and Central Highlands to southern Texas. The earliest inferred speciation event is that of *S. gadoviae* (found primarily in the Rio Balsas basin) from the lineage ancestral to all other species (except *S. ochoterenae*) with more northerly distributions (fig. 25). *Sceloporus merriami* and *S. couchii* are northern species (figs. 21, 22) and their lineage would have been separated by a speciation event from the *parvus–maculosus–jalapae–ochoterenae* group that has a more southerly distribution (figs. 9, 20, 25). A more or less simultaneous splitting of the distribution of this radiation could have given rise to separate *parvus, maculosus,* and *jalapae–ochoterenae* lineages.

Group II subtaxa supposedly arose in central Puebla and western Veracruz with a more or less simultaneous radiation of five separate groups (fig. 7). Within these separate subtaxa, the distributions of species provide plausible agreement with their phylogenetic hypotheses and imply relatively recent diversification. First, the *variabilis–chrysostictus* group species are all found in extreme southeastern Mexico, Yucatan, and Belize (figs. 20, 22, 23). Second, the *siniferus–utiformis* group species are coastal and Pacific slope species of western and southern Mexico, and extend into Central America (*S. squamosus*) (fig. 24). The *scalaris* group is found throughout the Central Plateau of Mexico with *S. goldmani* and *S. aeneus* having restricted ranges somewhat at the periphery of *S. scalaris* (fig. 25). *Sceloporus pyrocephalus* and *S. nelsoni* are distributed parapatrically along the Pacific slope and mountains of western and southern Mexico (fig. 22). *Sceloporus heterolepis, S. shannonorum,* and *S. asper* (figs. 20, 32) have moderately overlapping distributions in the Sierra Madre Occidental from Michoacan to southern Sinaloa (*S. heterolepis* and *S. asper*), and then north through much of montane Sinaloa (*S. shannonorum*). The *grammicus* complex has an extensive range throughout much of central Mexico (fig. 32) while *S. pictus, S. megalepidurus,* and *S. cryptus* all have small distributions in northern Oaxaca (*S. cryptus* and *S. pictus*) and neighboring Puebla, Tlaxcala, and Mexico state (*S. megalepidurus*) (figs. 20, 30).

Group III subtaxa overlap extensively throughout Mexico and Central America not only with Group I and II radiations but also with themselves. The *graciosus–undulatus* group occurs extensively throughout the United States and has only a limited range in Mexico (figs. 21, 28, 29). Larsen and Tanner (1975) proposed that *S. woodi* was an early Pleistocene glacial relict, derived from *S. virgatus* and that the *occidentalis–undulatus* group was independently derived from *S. virgatus.* The *formosus* group is distributed from Guerrero and Veracruz south through most of Central America. Many of the species have very restricted ranges while others are distributed relatively widely (figs. 30, 31). The distributions of the *horridus* group species are largely parapatric but extend from the Isthmus of Tehuantepec (*S. edwardtaylori*) to northern Texas (*S. olivaceus*) (fig. 29). Species in the *magister* group form a geographically linear series from Guatemala (*S. melanorhinus*) through coastal western Mexico (*S. clarki*) into the United States (*S. magister*), and also Baja California (the *magister* complex and *orcutti* complexes) (figs. 20, 24, 27). The two subtaxa of the *torquatus* group overlap extensively throughout most of Mexico, but within each radiation the species are largely parapatric or allopatric (fig. 33). The northernmost species of the large-scaled group is *S. poinsetti,* whose distribution extends into the United States. The three species in the proposed *torquatus* subtaxon occupy much of the Central Plateau of Mexico, while the four species in the *cyanogenys* subtaxon appear as peripheral isolates. In fact, these distributions are among the most difficult to explain in light of the hypothesized relationships. The three species of the *jarrovi* clade, other than *S. jarrovi* itself, have distributions that appear peripheral to *S. jarrovi.*

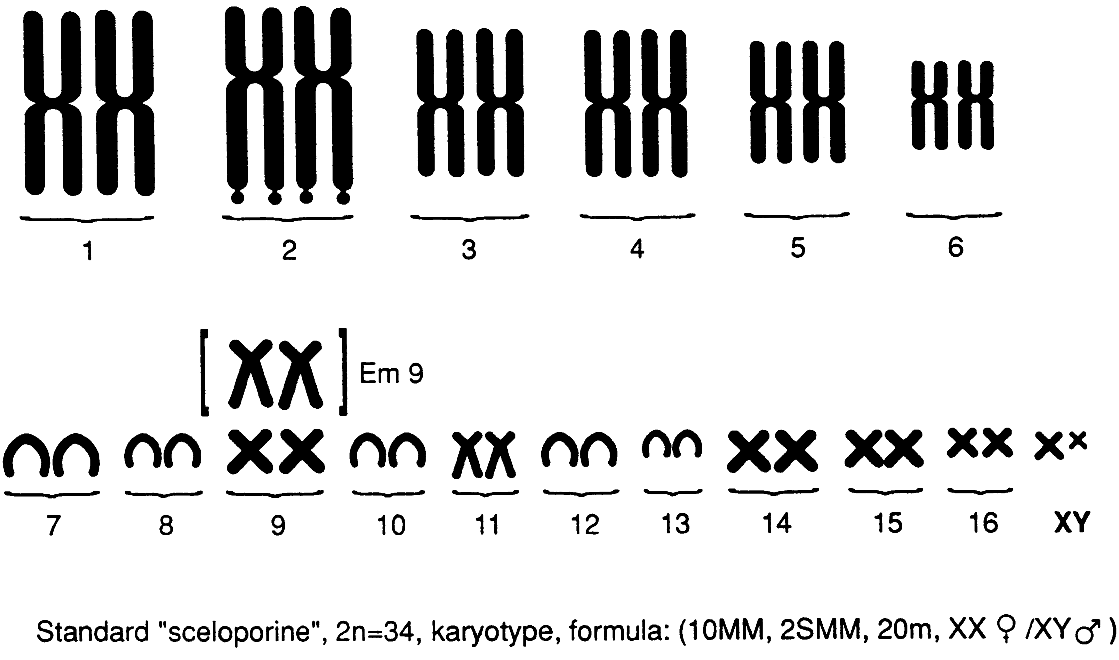


Fig. 13. Standard nondifferentially stained "sceloporine" 2n = 34 karyotype (Paull et al., 1976) consisting of six pairs of biarmed (metacentric or submetacentric) macrochromosomes, 10 pairs of microautosomes, and a sex chromosome system based on XY male heterogamety. See text for details.

CHROMOSOMALLY BASED ALTERNATIVES TO SMITH AND LARSEN-TANNER HYPOTHESES

INTRODUCTION

Before beginning a review of the Cole and Hall data sets, we present a summary of the basic chromosomal characters upon which these two authors have based their hypotheses and conclusions. Figure 13 diagrammatically illustrates what has been called the standard "Sceloporine" karyotype, which represents all genera now included in the family Phrynosomatidae (Frost and Etheridge, 1989). This karyotype consists of six pairs of biarmed macrochromosomes (M) and 11 pairs of microchromosomes (m), and can be briefly summarized as 2n = 34 (12M + 22m). It differs only by the absence of a single pair of microchromosomes from the 2n = 36 (12M + 24m) karyotype that has been hypothesized to be ancestral for the "Iguania" and possibly all lizards (Gorman, 1973; Paull et al., 1976). The 2n = 34 (12M + 22m) karyotype is found in all phrynosomatid genera, and none but *Sceloporus* shows any intrageneric deviation from this pattern (Paull et al., 1976; Hall, 1973, 1977, 1980, 1983). The macrochromosomes are arranged and numbered from the largest to the smallest pair (1 through 6 in fig. 13), and are distinctly separate from the microchromosomes. Most macrochromosome pairs can be identified by a combination of size and morphology with the exception of pairs 3 and 4; these are virtually identical in size and centromere position. Pairs 1 and 2 are similar in size, but pair 1 is slightly submetacentric whereas pair 2 is conspicuously submetacentric, and in good preparations pair 2 frequently exhibits secondary constrictions and small satellites at the termini of the long arms. Pairs 5 (metacentric) and 6 (slightly submetacentric) are conspicuously different in size from each other and from all other macrochromosomes in the complement.

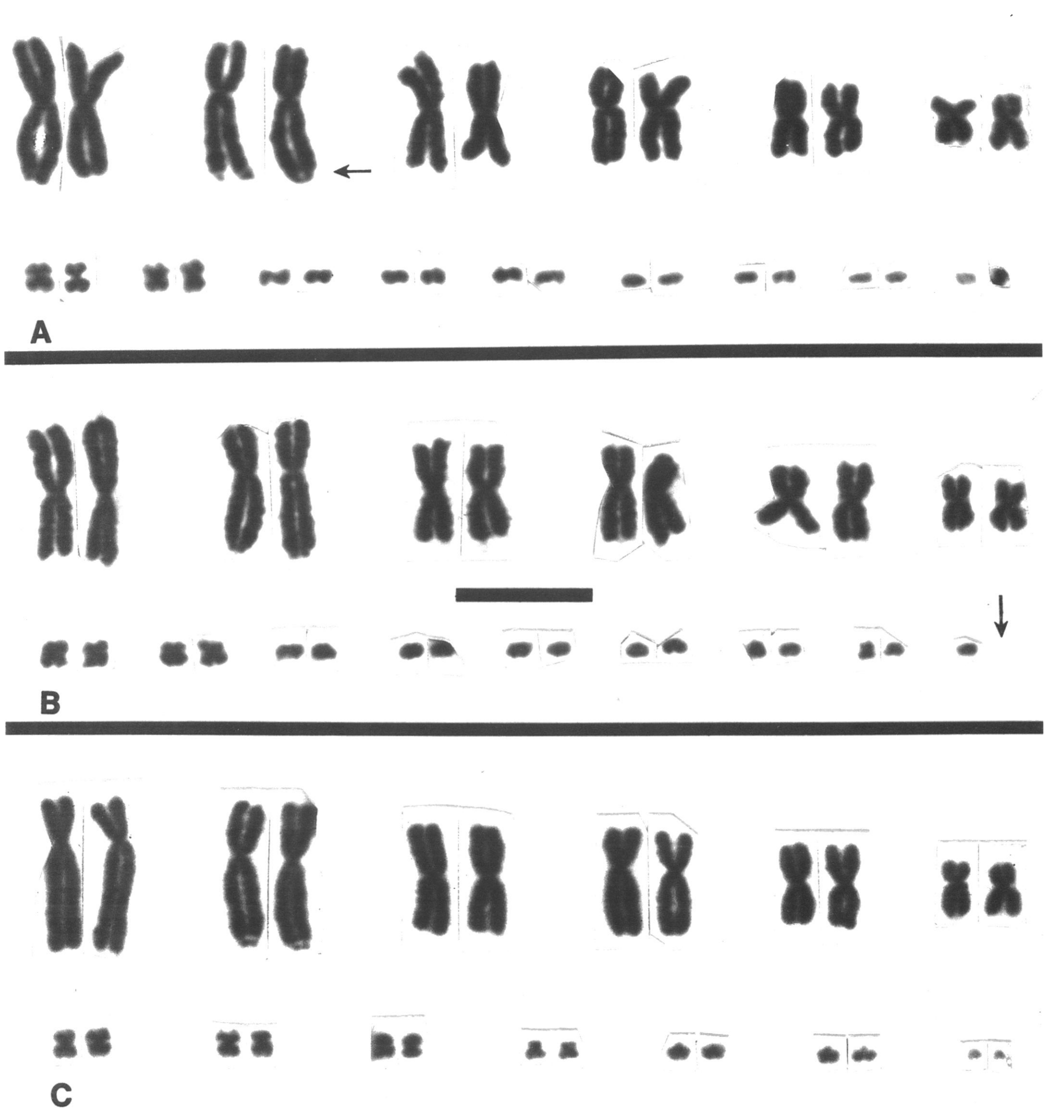


Fig. 14. Karyotypes of two species of *Sceloporus*. **A.** *S. rufidorsum*, female (2n = 30), AMNH 107493, with secondary constrictions at termini of long arm of macrochromosome pair 2 (arrow) typical for most species of *Sceloporus*. **B.** *S. rufidorsum*, male (2n = 29), AMNH 107491, with one microchromosome fewer (arrow) than in females; line represents 10 μm. **C.** *S. magister* (2n = 26), female, UAZ 16233; note that macrochromosome pair 1 is clearly submetacentric.

The microchromosome morphology of this karyotype is less certain because the sizes of the smaller pairs often approach the limits of optical resolution with light microscopes. However, Hall (1973) established a numbering system for his material based on exceptionally clear preparations, and we have also represented this schematically in figure 13, although confirmation awaits further study. The microautosomes include seven pairs of acrocentric, subacrocentric, or metacentric chromosomes, arranged in order of decreasing size from 7 through 13. Normally the morphology of these microchromosomes appears constant, but Hall (1973) identified what he termed the "Em" or "enlarged micro" mutation for microautosome pair 9, in which a few species are either polymorphic or fixed

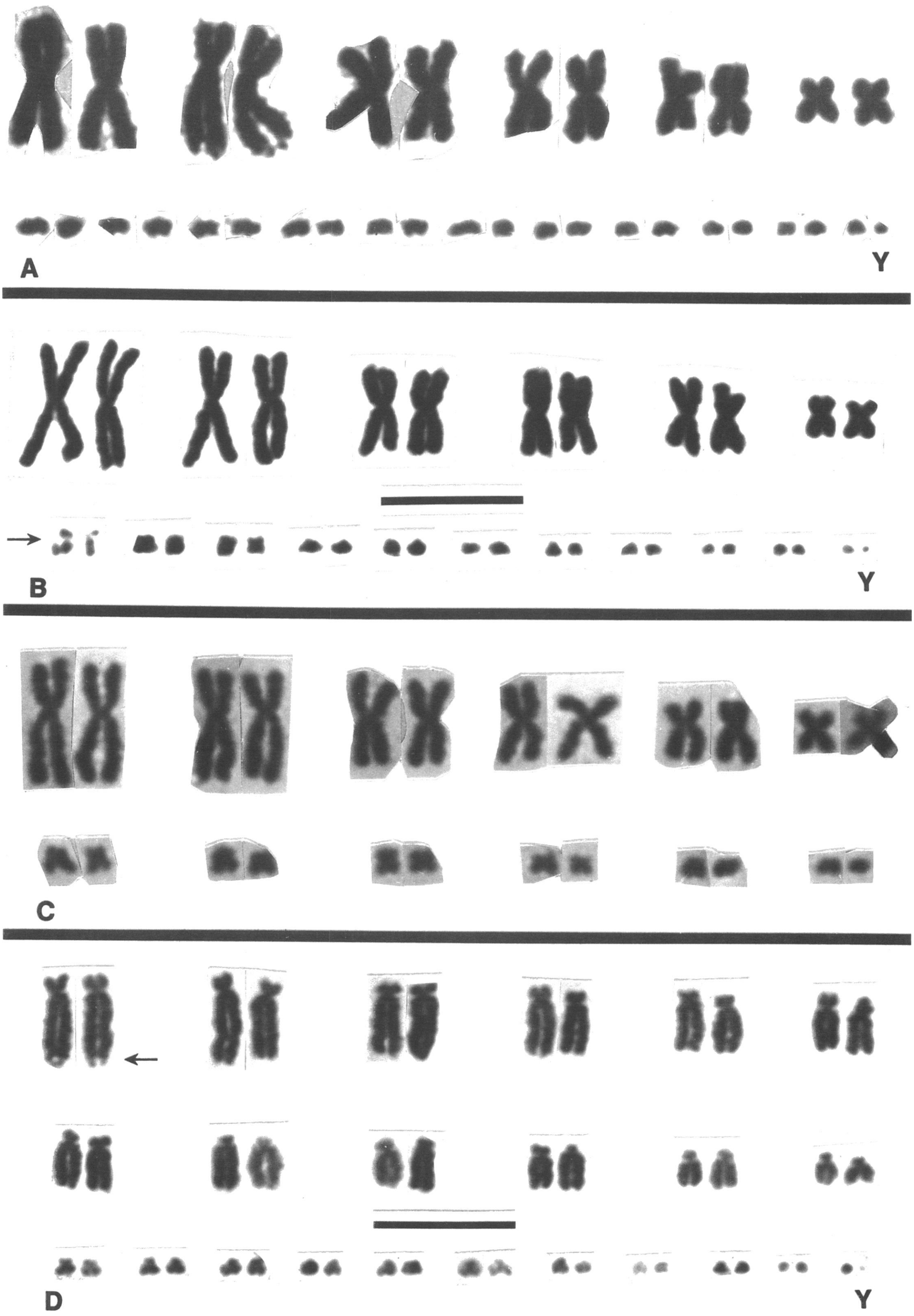
Fig. 15. Karyotypes of three species of *Sceloporus*. **A.** *S. formosus*, male (2n = 22), AMNH 106414; note that pair 7 (arrow) is heteromorphic, with one submetacentric (typical) and one subtelocentric (atypical) element. **B.** *S. adleri*, female (2n = 22), AMNH 136767. **C.** *S. subpictus*, male (2n = 22), AMNH 106534; line represents 10 μm.

for much larger long arms of this pair. In addition to these pairs, three additional pairs of metacentric or submetacentric microautosomes can be arranged in order of decreasing size from 14 through 16. The sex chromosome system is characterized by an XY heteromorphism in which the Y chromosome is small to minute. (This hypothesis must be considered tentative without meiotic data, however, because it is based on the accuracy of pairing the smallest microchromosomal elements.)

Hall (1977) expanded the above-described karyotype formula to include more information about macrochromosome morphology and sex chromosome systems. The hypothetical karyotype in figure 13 can be summarized with the following symbols: upper and lower case M and m refer respectively to macro- and microautosomes; MM designates a metacentric or slightly submetacentric macrochromosome morphology (pairs 1 and 3–6 in fig. 13); SMM refers to a conspicuously submetacentric macrochromosome morphology (pair 2 in fig. 13); and SA or A refer to subacrocentric or acrocentric macrochromosomes, respectively (none shown in fig. 13). A simple sex chromosome system such as the one illustrated in figure 13 would be summarized as XX♀/XY♂. Sex chromosomes are treated in more detail below because several morphologically different systems appear to have evolved independently within *Sceloporus*. The hypothetical karyotype in figure 13 would thus be summarized as: 2n = 34 (10MM,2SMM, 20m,XX♀/XY♂). Modified karyotypes are identified with a modified version of this formula. For example, the karyotype of *S. pyrocephalus* is identical to the one in figure 13 in diploid number, but pair 1 is fixed for a presumed unequal pericentric inversion (Cole, 1971b), so that this pair is now strongly subacrocentric. The karyotype formula for *S. pyrocephalus* would therefore be: 2n = 34 (8MM,2SMM,2SAM,20m,XX♀/XY♂), with the 2SAM term accounting for the new morphology of pair 1. As a second example, *S. merriami* has a karyotype characterized by fixation of presumed centric fissions for all six macroautosomal pairs, which has increased the total number of this part of the karyotype from 12 to 24 elements, and converted the morphology from all biarmed to all acrocentric macrochromosomes (Cole, 1971b). The microautosomal and sex chromosome systems of *S. merriami* are identical to the hypothetical ancestral karyotype, so its karyotype is written: 2n = 46 (24AM,20m, XX♀/XY♂). Photographs of the ancestral karyotype and various derived ones are presented in figures 14–17.

Figure 18 depicts several different sex chromosome heteromorphisms reported within *Sceloporus*. If the 2n = 34 (10MM, 2SMM,20m,XX♀/XY♂) karyotype (fig. 16A) is taken as the ancestral condition, which Hall concluded on the basis of the presence of the minute Y chromosome (fig. 18A, easily the smallest chromosome in the entire genome) in several species of *Uta* and *Sceloporus* (Pennock et al., 1969; Cole, 1971a, 1971b), then all others depicted are presumably derived at some level within *Sceloporus*. The heteromorphism illustrated in figure 18B is hypothesized to characterize *S. clarki* (2n = 40; 2MM,2SMM,16AM,18m,XX♀/XY♂; Hall, 1973: 89–92, figs. 9C and 10; Hall also interpreted some of the material reported by Cole, 1970, as evidence for this heteromorphism), in which the *S. clarki* X chromosome may be homologous to the X of the ancestral XY system. However, it is unclear how the relatively large acrocentric *S. clarki* Y chromosome and 18 microautosomes may have been derived from the minute Y and 20 microautosomes of the ancestral 2n = 34 karyotype, particularly if their X chromosomes are homologous.

Figure 18C depicts the conspicuous pair 7 XY heteromorphism reported for *S. lundelli* by Cole (1970; fig. 6), a species characterized by a 2n = 22 (10MM,2SMM,8m,XX♀/XY♂) karyotype. Figure 18D shows the $X_1X_1X_2X_2$♀/X_1X_2Y♂ system originally described by Cole et al. (1967) for *S. jarrovi* and *S. poinsetti*, and by Axtell and Axtell (1971) for another population of *S. jarrovi*. This type of system has since been reported in many other *Sceloporus* (fig. 17), including all grouped together by Hall (1973) into the large radiation of crevice-users (see below). Cole et al. (1967) originally hypothesized that this system likely evolved from an ancestral condition similar to that of female *S. jarrovi* and *S. poinsetti*. In other words, it was derived from a system with no, or perhaps only a slightly distinct, sex chromosome heteromorphism among the microchromosomes, presumably by a centric fusion between the nondifferentiated ancestral Y chromosome and an acrocentric microautosome (symbolized A_m in fig. 18D). This type of rearrangement would link a pair of autosomes to the sex chromo-


A
Y
B
Y
C
D
Y

some system, produce an unpaired biarmed large microchromosome in males, and reduce the male 2n count by one chromosome. The original ancestral X chromosome is now designated the X_1, the unfused microautosome becomes the X_2, and the fusion product bearing the original Y chromosome retains the designation of Y (fig. 18D). The evidence for homology presented by Cole et al. (1967) was the diakinetic pairing behavior of the X_1X_2Y chromosomes in meiosis in males; these three elements formed a trivalent in which the two X chromosomes were paired at opposite ends of the Y in an end-to-end arrangement. Cole et al. also showed that males segregated two types of spermatocytes, X_1X_2 and Y carrying gametes, in statistically equal numbers (50: 50).

Cole (1970) suggested possible homology between the large Y chromosome of the XY system of *S. lundelli* (fig. 18C) and the X_1X_2Y system of the crevice-users, on the basis of approximately equal sizes and similar morphologies. He also argued that this was likely because the Y chromosomes in both systems probably evolved in part by means of microchromosomal fusions. Hall (1973) carried this interpretation one step further by postulating that the original X chromosome in the ancestral XY system was one of the larger of the pair 8 microchromosomes in the 2n = 34 karyotype, and that one member of microchromosome pair 7 was the autosomal element involved in the Y chromosome-microautosome fusion that derived the submetacentric Y of the crevice-user X_1X_2Y system. Hall also postulated homology between the long arm of the crevice-user biarmed Y and the smaller acrocentric Y of *S. clarki* (fig. 18B, D).

Figure 18E illustrates a second X_1X_2Y heteromorphism reported for *S. melanorhinus*, a species characterized by a 2n = 40♀/39♂ (2 MM,2SMM,14AM,18m,$X_1X_1X_AX_A$♀/X_1X_AY♂) karyotype (Hall, 1973: 89–92). In this system, the short arm of the *S. melanorhinus* Y is postulated to be homologous to both the long arm of the submetacentric crevice-user Y (fig. 18D) and the acrocentric *S. clarki* Y chromosome, and was presumably derived via fusion of the ancestral *clarki*-like Y to an acrocentric fission product of macrochromosome pair 5 (symbolized A_5 in fig. 18E). This event thus linked a different autosomal pair to the sex chromosome system in such a way that the ancestral X is now X_1, the derived Y element is the ancestral Y fused to one of the acrocentric pair 5 chromosomes, and the homologous unpaired acrocentric 5 becomes X_2. These interpretations suggest the origin of a minimum of five different sex chromosome heteromorphisms within *Sceloporus*. One or two of these (*S. clarki* and/or *S. melanorhinus*; fig. 18B, E) need confirmation. In addition, there are sexually dimorphic karyotypes in *S. rufidorsum* that are hard to explain (discussed below; see fig. 14), and there are probably other sex chromosome systems as yet unrecognized, as microchromosomes are difficult to study and some differences in centromere position are quite subtle (discussed below; Reed et al., 1990).

CHROMOSOMAL DATA BASE

In the 1977 unpublished manuscript (formally declared to be in the public domain by

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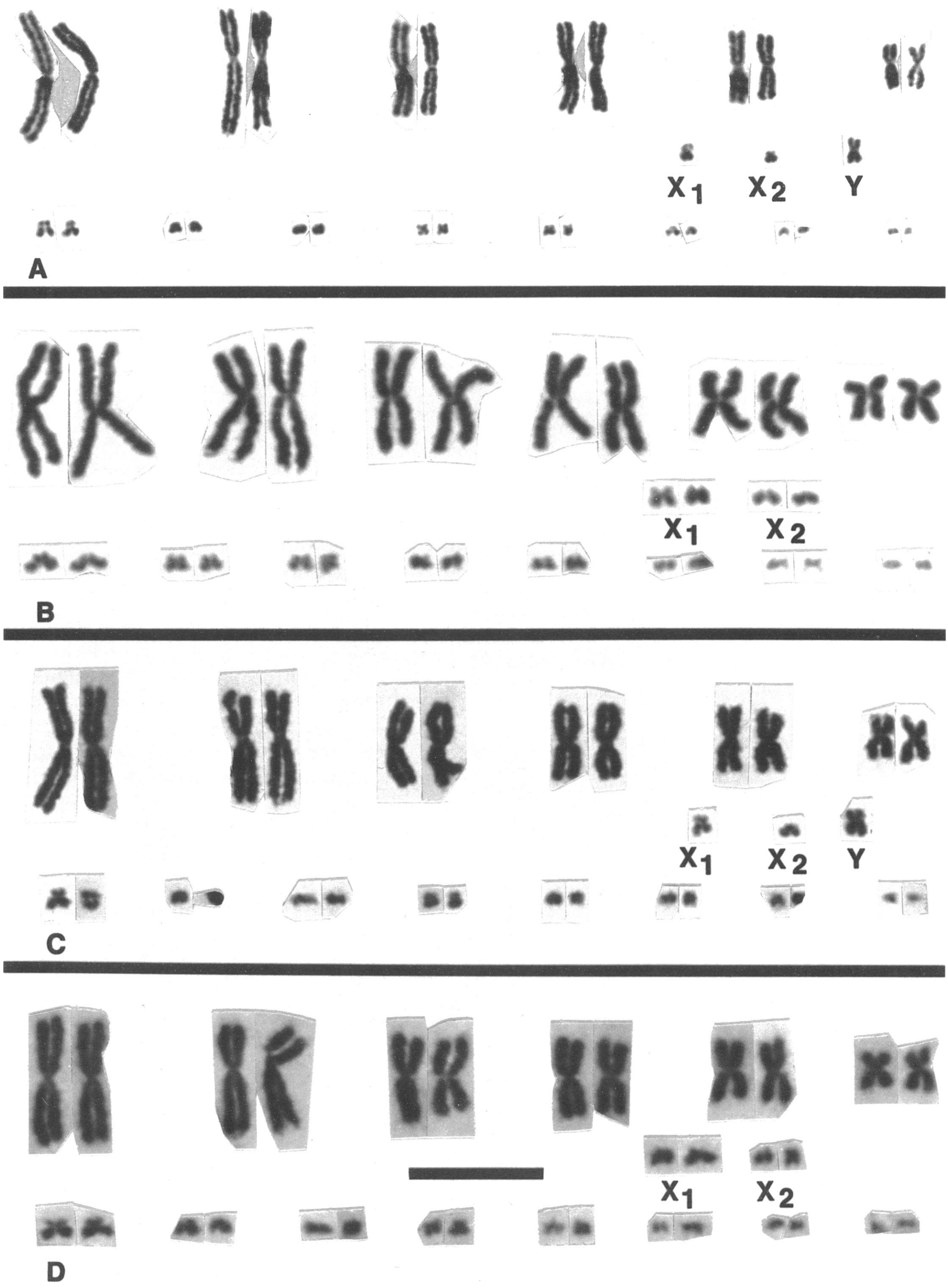
Fig. 16. Karyotypes of four species of *Sceloporus*. **A.** *S. orcutti*, male (2n = 34), AMNH 136776; note the minute Y, paired with the second smallest microchromosome for illustrative purposes, as in B and D, as the X chromosome is not individually recognizable in a conventionally stained mitotic karyotype. **B.** *S. chrysostictus*, male (2n = 34), UAZ 19077; note minute Y, and note secondary constrictions (arrow) near centromere on largest pair of microchromosomes, a feature unique (for *Sceloporus*) to this species and those in the *variabilis* species group; line represents 10 μm; same cell illustrated by Cole (1971b: 2). **C.** *S. scalaris*, male (2n = 24), UAZ 19826; note macrochromosome pair 1 is clearly submetacentric; same cell as illustrated by Cole (1978: 11). **D.** *S. merriami*, male (2n = 46), UAZ 24191; note the minute Y and secondary constrictions (arrow) on macrochromosome pair 1, which may be homologous to the long arm of macrochromosome pair 2 in the ancestral karyotype (panel A of this fig.); line represents 10 μm; same cell illustrated by Cole (1971b: 10).


X_1
X_2
Y
A
X_1
X_2
B
X_1
X_2
Y
C
X_1
X_2
D

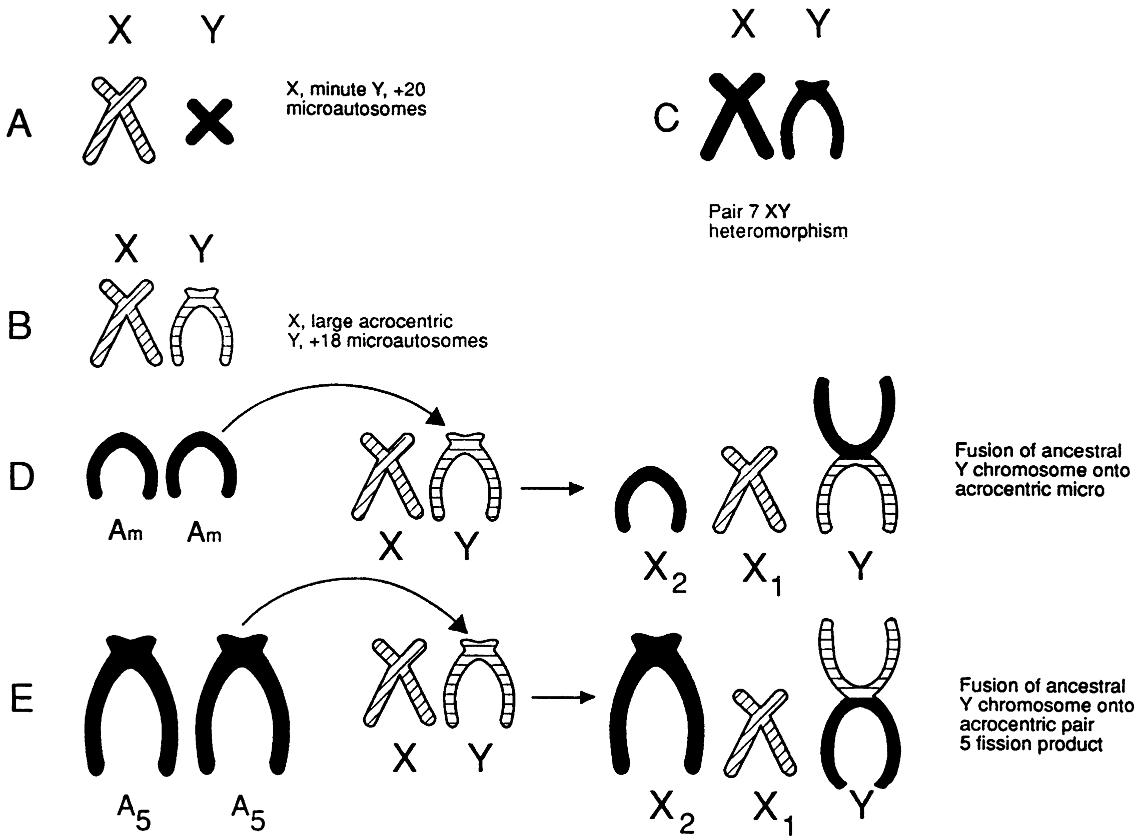


Fig. 18. Interpretations of five distinct sex chromosome heteromorphisms described within *Sceloporus*. Diagonal hatching indicates presumed homology between X element of the XY systems in A and B, and the X_1 element in both of the X_1X_2Y systems (D and E). Horizontal hatching indicates presumed homology between Y chromosome of the XY system in B, and the Y-autosomal fusion product of both of the X_1X_2Y systems (D and E). In C, the sex chromosomes are the largest microchromosomes; in A and B they are smaller.

Hall, 1983: 645), Hall updated a portion of his Ph.D. thesis, and presented a detailed hypothesis for a sequence of chromosomally mediated speciation events and phylogenetic relationships for all species groups of *Sceloporus*. Hall's hypothesis frequently involved rearrangements in the composition of some of the groups previously recognized by Smith, Larsen and Tanner, and Cole. In the 1977 paper, Hall summarized all available cytogenetic information for the genus in a large appendix (table 1 in the 1977 MS.), and de-

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Fig. 17. Karyotypes of two species of *Sceloporus* having the $X_1X_1X_2X_2$ (female):X_1X_2Y (male) sex chromosome system. **A.** *S. torquatus*, male (2n = 31), AMNH 106542. **B.** *S. torquatus*, female (2n = 32), AMNH 106541. **C.** *S. pictus*, male (2n = 31), AMNH 106469. **D.** *S. pictus*, female (2n = 32), AMNH 104458; line represents 10 μm. In both species, the Y is clearly recognized as a small metacentric or submetacentric chromosome in males. The X chromosomes, however, are not individually distinguishable among the microchromosomes in conventionally stained mitotic karyotypes; they are labeled only for illustrative purposes.

veloped his hypotheses for speciation mechanisms and patterns on the basis of this data set. In that table, Hall listed all species by diploid number and karyotype formula, as defined above, but maintained the original species groups of Smith (1939) and Smith and Taylor (1950), albeit with taxonomic emendations reflecting additions/deletions of species. We present an updated summary of this data base in table 4, but with three modifications. First, the species groups are arranged to conform to Hall's (1973, 1977, 1980) views of relationships, so far as these can be determined. Second, we have tried to extract from Hall's material the total number of localities sampled, and the total number of specimens karyotyped for each species. Third, we have incorporated C. J. Cole's unpublished data for species not previously reported (see also figs. 14–17). The information on sample sizes is readily available from published data sets, but the *Specimens Examined* section of Hall's dissertation is incomplete, so these numbers are only approximate for some species. In all cases, however, such summaries reflect conservative estimates of the total number of individuals karyotyped for each species. We have also provided the geographic distributions of all species groups as interpreted by Hall, to the extent that these are known.

SMALL-BODIED, SMALL-SCALED RADIATION

The first section of table 4 and figure 19 summarize Hall's views of species group compositions and relationships for the small-bodied, small-scaled radiation of *Sceloporus.* There are morphological features that presumably define this radiation as a monophyletic unit, although this remains to be demonstrated by an explicit cladistic analysis. Similarly, the morphological characters used by Hall to recognize particular species groups were poorly characterized in his papers. For now we simply present his phylogenetic hypothesis as an alternative to the others, and discuss subsequent modifications to his arrangement. As discussed by Paull et al. (1976), the consideration of any phrynosomatid genus as an outgroup to *Sceloporus—Callisaurus, Cophosaurus, Holbrookia, Petrosaurus, Phrynosoma, Sator* (the position of this genus in relation to *Sceloporus* is uncertain, so it is not listed as an outgroup in fig. 19; see below), *Uma, Urosaurus,* or *Uta*—will give the same conclusion of the symplesiomorphic karyotype within *Sceloporus,* although with less confidence in the presence of the subtle sex chromosome heteromorphism than in other karyotypic details. All of the outgroup genera are monotypic for the 2n = 34 (10MM, 2SMM,22m) karyotype, and at least five species of *Uta* are also characterized by the X/minute-Y sex chromosome heteromorphism (Pennock et al., 1969). This same karyotype has been documented in several groups of *Sceloporus* within the small-bodied radiation by Cole (1971a, 1971b; 1978) and Hall (1973), and Hall argued specifically that the 2n = 34 (10MM,2SMM,20m,XX♀/XY♂) karyotype was ancestral for the genus. However, if *Uta* is considered the second outgroup of *Sceloporus* and *Urosaurus* is the first outgroup (a proposition reasonably well supported in cladistic studies of osteological/morphological data sets; Etheridge, 1964; Presch, 1969; Etheridge and de Queiroz, 1988; see alternatives in Frost and Etheridge, 1989; and Wiens, 1993), and the minute Y heteromorphism is absent in *Urosaurus,* then this polarity is ambiguous. This type of karyotype was described and illustrated by Cole within *Sceloporus* (e.g., 1971a, 1971b), but with less detail on the microchromosomes, and he did not consider it ancestral for the genus at that time. The Y chromosome morphology remains poorly documented in *Urosaurus* (Paull et al., 1976), and the diminution of the Y occurs so frequently in evolution (Bull, 1983) that its independent derivation in several radiations sharing a common ancestral karyotype without such heteromorphism would not be surprising.

Hall's views of species group composition support those of Smith and Taylor (1950) with respect to the *chrysostictus, maculosus, merriami,* and *utiformis* groups. The first three of these groups are monotypic and distributed over small geographic areas; *S. chrysostictus* is confined to the Yucatan Peninsula, ranging through the Mexican states of Campeche, Yucatan, and Quintana Roo, and the Peten region of Guatemala and northern Be-

TABLE 4

Species of *Sceloporus* and a Summary of Chromosomal Data Updated from Hall (1973, 1977) and Including Unpublished Data of CJC

A question mark (?) denotes a taxon of uncertain status (see text), an asterisk (*) denotes species reallocated from a Smith (1939) species group to the present group by Hall or a new species group recognized by Hall, on the basis of karyotype; and two asterisks (**) identify the chromosomally extremely polytypic "species" *S. grammicus,* which may contain several genetically independent units yet to be described as species. Under Sources, specimens karyotyped by CJC but not previously reported are reported as follows: AMNH, American Museum of Natural History; LACM, Museum of Natural History of Los Angeles County; UAZ, University of Arizona.

Species groups of Hall	2n	Karyotype formula	No. examined	No. localities	Sources
SMALL-SIZED, SMALL-SCALED SPECIES:					
VARIABILIS					
couchii	34	(10MM,2SMM,20m,XX♀/XY♂)	4	3	Cole (1978); Hall (1973)
cozumelae	34	(10MM,2SMM,20m,XX♀/XY♂)	5	3	Cole (1978)
teapensis (?)	34	(10MM,2SMM,20m,XX♀/XY♂)	20	10	Cole (1978); Hall (1973)
variabilis	34	(10MM,2SMM,20m,XX♀/XY♂)			
CHRYSOSTICTUS					
chrysostictus	34	(10MM,2SMM,20m,XX♀/XY♂)	5	4	Cole (1971a, 1978); fig. 16B
UTIFORMIS					
utiformis	34	(10MM,2SMM,20m,XX♀/XY♂)	2	2	Cole (1971a); Hall (1973)
SINIFERUS					
carinatus	?	—	—	—	
siniferus	34	(10MM,2SMM,20m,XX♀/XY♂)	7	3	Cole (1978); Hall (1973)
squamosus	?	—	—	—	
JALAPAE*					
gadoviae	34	(10MM,2SMM,20m,XX♀/XY♂)	3	1	Cole (1971b); Hall (1973)
jalapae	34	(10MM,2SMM,20m,XX♀/XY♂)	6	4	Cole (1971b); Hall (1973)
ochoterenae	34	(10MM,2SMM,20m,XX♀/XY♂)	3	1	Cole (1978)
parvus	34	(10MM,2SMM,20m,XX♀/XY♂)	4	1	Hall (1973); Cole (1978)
MACULOSUS					
maculosus	34	(10MM,2SMM,18m,$X_1X_1X_2X_2$♀)	3	1	Cole (1971a)
	33	(10MM,2SMM,18m,X_1X_2Y♂)			
maculosus	~40	?	1	1	C. Axtell (pers. comm. to Hall [1973])
MERRIAMI					
merriami	46	(24AM,20m,XX♀/XY♂)	5	4	Cole (1971a); Hall (1973); Guillette & Smith (1985); fig. 16D
SCALARIS					
aeneus	24	(10MM,2SMM,10m,XX♀/XY♂)	9	2	Cole (1978); Hall (1973)

TABLE 4—(*Continued*)

Species groups of Hall	2n	Karyotype formula	No. examined	No. localities	Sources
bicanthalis (?)	24	(10MM,2SMM,12m) (XY not described)	5	1	Guillette & Smith (1985)
goldmani	24	(10MM,2SMM,12m) (XY indistinct)	6	2	Cole (1978)
scalaris	24	(10MM,2SMM,12m) (XY indistinct)	11	6	Cole (1978); Hall (1973); fig. 16C
subniger (?)	?	—	—	—	
LARGE-SIZED, LARGE-SCALED SPECIES:					
ORCUTTI*					
hunsakeri	34	(10MM,2SMM,20m,XX♀/XY♂)	1	1	Hall & Smith (1979)
licki	34	(10MM,2SMM,20m,XX♀/XY♂)	2	2	Cole (1970); Hall & Smith (1979)
nelsoni	34	(10MM,2SMM,20m,XX♀/XY♂)	6	4	Cole (1971b); Hall (1973)
orcutti	34	(10MM,2SMM,20m,XX♀/XY♂)	9	5	Cole (1970); Hall (1973); AMNH 136776; fig. 16A
pyrocephalus	34	(8MM,2SMM,2SAM,20m,XX♀/XY♂)	3	2	Cole (1971b); Hall (1973)
CLARKI*					
clarki	40	(2MM,2SMM,16AM,18m,XX♀/XY♂) (polymorphic for Em9)	94	26	Lowe et al. (1967); Cole (1970); Hall (1973)
melanorhinus	40	(2MM,2SMM,14AM,18m,$X_1X_1X_AX_A$♀)	13	7	Cole (1970); Hall (1973)
	39	(2MM,2SMM,14AM,18m,X_1X_AY♂) (polymorphic for Em9)			
ASPER*					
asper	32	(10MM,2SMM,16m,$X_1X_1X_2X_2$♀)	6	3	Hall (1973)
	31	(10MM,2SMM,16m,X_1X_2Y♂) (fixed for Em9)			
MEGALEPIDURUS					
megalepidurus	32	(10MM,2SMM,16m,$X_1X_1X_2X_2$♀)	6	1	Hall (1973); AMNH 106487–106489, 106491–106493
	31	(10MM,2SMM,16m,X_1X_2Y♂) (fixed for EM9 mutation)			
pictus (?)	32	(10MM,2SMM,16m,$X_1X_1X_2X_2$♀)	4	2	AMNH 104458, 106469, 106471–106472; fig. 17C, D
	31	(10MM,2SMM,16m,X_1X_2Y♂)			
megalepidurus × *pictus*	32	(10MM,2SMM,16m,$X_1X_1X_2X_2$♀)	3	1	AMNH 106483–106485
	31	(10MM,2SMM,16m,X_1X_2Y♂)			
GRAMMICUS					
heterolepis	32	(10MM,2SMM,16m,$X_1X_1X_2X_2$♀)	10	2	Hall (1973); Arevalo & Sites (in prep.)
	31	(10MM,2SMM,16m,X_1X_2Y♂)			
shannonorum (?)	32	(10MM,2SMM,16m,$X_1X_1X_2X_2$♀)	5	1	Hall (1973)
	31	(10MM,2SMM,16m,X_1X_2Y♂)			

TABLE 4—(*Continued*)

Species groups of Hall	2n	Karyotype formula	No. examined	No. localities	Sources
anahuacus (?)	32	(10MM,2SMM,16m,$X_1X_1X_2X_2$♀)	244+	7+	Hall & Selander (1973); Porter & Sites (1986); Arevalo et al. (1991); Sites et al. (1988); Gadsden et al. (1989)
	31	(10MM,2SMM,16m,X_1X_2Y♂) (some populations polymorphic for pair 1 fission)			
palaciosi	34	(8MM,2SMM,4AM,16m,$X_1X_1X_2X_2$♀)	270+	13+	Hall & Selander (1973); Hall (1973); Porter & Sites (1986); Arevalo et al. (1991); Sites et al. (1988); Gadsden et al. (1989)
	33	(8MM,2SMM,4AM,16m,X_1X_2Y♂) (fixed for pair 6 fission)			
*grammicus***	32	(10MM,2SMM,16m,$X_1X_1X_2X_2$♀)	507+	46+	Hall (1973); Sites (1983); Arevalo et al. (1991)
	31	(10MM,2SMM,16m,X_1X_2Y♂)			
	34	(8MM,2SMM,4AM,16m,$X_1X_1X_2X_2$♀)	62+	17	Hall (1973); Sites (1983)
	33	(8MM,2SMM,4AM,16m,X_1X_2Y♂) (fixed for pair 6 fission)			
	34	(8MM,2SMM,4AM,16m,$X_1X_1X_2X_2$♀)	90+	7+	Hall (1973); Arevalo et al. (1991)
	33	(8MM,2SMM,4AM,16m,X_1X_2Y♂) (fixed for pair 5 fission)			
	36	(6MM,2SMM,8AM,16m,$X_1X_1X_2X_2$♀)	230+	37	Hall (1973); Sites (1983); Arevalo et al. (1991)
	35	(6MM,2SMM,8AM,16m,X_1X_2Y♂) (fixed for pairs 5 & 6 fissions)			
	38	(6MM,12AM,16m,$X_1X_1X_2X_2$♀)	92+	6	Porter & Sites (1986); Arevalo et al. (1991)
	37	(6MM,12AM,16m,X_1X_2Y♂) (fixed for pairs 2, 5, 6 fissions)			
	40–44	(0–4MM,16–24AM,16m,$X_1X_1X_2X_2$♀)	66+	5	Hall (1973); Porter & Sites (1986); Arevalo et al. (1991)
	39–43	(0–4MM,16–24AM,16m,X_1X_2Y♂) (fixed for pairs 2, 3, 5, 6 fissions; segregate fission polymorphisms at pairs 1 & 4)			
	44–46	(0–2MM,20–24AM,18m,$X_1X_1X_2X_2$♀)	329+	23+	Hall (1973); Porter & Sites (1986); Arevalo et al. (1991)
	43–45	(0–2MM,20–24AM,18m,X_1X_2Y♂) (fixed for pairs 1, 2, 3, 5, 6, 14 fissions; segregate fission polymorphisms at pair 4)			
TORQUATUS					
bulleri	32	(10MM,2SMM,16m,$X_1X_1X_2X_2$♀)	2	2	Hall (1973); AMNH 106383–84
	31	(10MM,2SMM,16m,X_1X_2Y♂)			
cyanogenys (?)	32	(10MM,2SMM,16m,$X_1X_1X_2X_2$♀)	8	3	Hall (1973); UAZ 24181, 21676–21677, 24208
	31	(10MM,2SMM,16m,X_1X_2Y♂)			
dugesii	32	(10MM,2SMM,16m,$X_1X_1X_2X_2$♀)	8	4	Hall (1973); AMNH 106402, 106413, 136770; UAZ 29950
	31	(10MM,2SMM,16m,X_1X_2Y♂)			
insignis	?	—	—	—	

TABLE 4—(*Continued*)

Species groups of Hall	2n	Karyotype formula	No. examined	No. localities	Sources
jarrovi	32	(10MM,2SMM,16m,$X_1X_1X_2X_2$♀)	55	19	Axtell & Axtell (1971); Cole et al. (1967); Hall (1973)
	31	(10MM,2SMM,16m,X_1X_2Y♂)			
lineolateralis (?)	?	—	—	—	
macdougalli	?	—	—	—	
mucronatus	32	(10MM,2SMM,16m,$X_1X_1X_2X_2$♀)	28	15	Hall (1973); UAZ 29477, 29946, 29929
	31	(10MM,2SMM,16m,X_1X_2Y♂)			
ornatus	32	(10MM,2SMM,16m,$X_1X_1X_2X_2$♀)	8	4	Hall (1973); UAZ 24203
	31	(10MM,2SMM,16m,X_1X_2Y♂)			
poinsetti	32	(10MM,2SMM,16m,$X_1X_1X_2X_2$♀)	21	13	Cole et al. (1967); Hall (1973)
	31	(10MM,2SMM,16m,X_1X_2Y♂)			
prezygus (?)	?	—	—	—	
serrifer	32	(10MM,2SMM,16m,$X_1X_1X_2X_2$♀)	1	1	UAZ 28336 (female only)
torquatus	32	(10MM,2SMM,16m,$X_1X_1X_2X_2$♀)	49	24	Hall (1973); AMNH 106541, 129221, 106542, 109052, 129220; UAZ 29475–29476; fig. 17A, B
	31	(10MM,2SMM,16m,X_1X_2Y♂)			
GRACIOSUS					
graciosus	30	(10MM,2SMM,18m) (XY indistinct)	96	19	Cole (1971b, 1975); Thompson & Sites (1986a)
MAGISTER*					
magister	26	(8MM,4SMM,14m) (fixed for pair 1 pericentric inversion)	16	11	Lowe et al. (1967); Cole (1970); Hall (1973); fig. 14C
zosteromus (?)	30	(10MM,2SMM,18m) (XY indistinct)	?	?	Hall (1973)
lineatulus (?)	?	—	—	—	
monserratensis (?)	?	—	—	—	
rufidorsum (?)	30	(10MM,2SMM,18m♀)	5	3	AMNH 107491–107493, 136772–73; fig. 14A, B
	29	(10MM,2SMM,17m,X_1X_2Y♂?)			
HORRIDUS*					
cautus	22	(10MM,2SMM,10m) (XY indistinct)	4	2	Cole (1972); Hall (1973)
edwardtaylori	22	(10MM,2SMM,10m) (XY indistinct)	9	2	Cole (1970); Hall (1973)
exsul	22	(10MM,2SMM,10m) (XY indistinct)	1	1	Sites & Haiduk (1979)
horridus (?)	22	(10MM,2SMM,10m) (XY indistinct; geographic variation in pair 7 morphology)	8	7	Cole (1970); Hall (1973)
lundelli	22	(10MM,2SMM,8m,XY♂) (pair 7 = heteromorphic sex chromosomes)	13	2	Cole (1970)

TABLE 4—(*Continued*)

Species groups of Hall	2n	Karyotype formula	No. examined	No. localities	Sources
olivaceus	22	(10MM,2SMM,10m) (XY indistinct; heteromorphisms in pair 7)	12	4	Cole (1970); Hall (1973)
occidentalis	22	(10MM,2SMM,10m) (heteromorphisms in pairs 1 and 7)	103	21	Cole et al. (1967); Cole (1972, 1983); Jackson & Hunsaker (1970); Hall (1973)
spinosus	22	(10MM,2SMM,10m) (geographic variation in pair 7 morphology)	5	3	Cole (1970); Hall (1973)
undulatus	22	(10MM,2SMM,8m,XY♂) (geographic variation in pair 7 morphology; polymorphic for pair 3 aberration at one locality)	150	23	Cole (1972, 1975, 1977, 1983); Hall (1973); Reed et al. (1990)
virgatus	22	(10MM,2SMM,10m) (polymorphic for pair 1 aberration)	26	1	Cole & Lowe (1968); Cole (1972); Hall (1973)
woodi	22	(10MM,2SMM,10m)	7	1	Cole (1972); Hall (1973)
FORMOSUS					
acanthinus	?	—	—	—	
adleri	22	(10MM,2SMM,10m)	2	1	Hall (1973); AMNH 136766–67 (females only); fig. 15B
*cryptus**	22	(10MM,2SMM,10m) (XY indistinct)	?	?	Hall (1973)
formosus	22	(10MM,2SMM,10m) (XY indistinct; variation in pair 7 morphology)	9	5	Hall (1973); AMNH 104522, 104525, 106414, 106822–23, 106825; UAZ 29927, 29952, 29955; fig. 15A
internasalis (?)	?	—	—	—	
lunaei	?	—	—	—	
malachiticus	22	(10MM,2SMM,10m) (XY indistinct)	8	1	Hall (1973); UAZ 29928, 29930–31, 29937, 29943–44, 29958–59
salvini (?)	?	—	—	—	
smaragdinus	?	—	—	—	
stejnegeri	22	(10MM,2SMM,10m) (XY indistinct)	1	1	LACM 58080
*subpictus**	22	(10MM,2SMM,10m) (XY indistinct)	9	2	AMNH 106532–106537, 106539, 106890–106891; fig. 15C
taeniocnemis	22	(10MM,2SMM,10m) (XY indistinct)	3	1	UAZ 21615, 21862, 21864
tanneri	?	—	—	—	

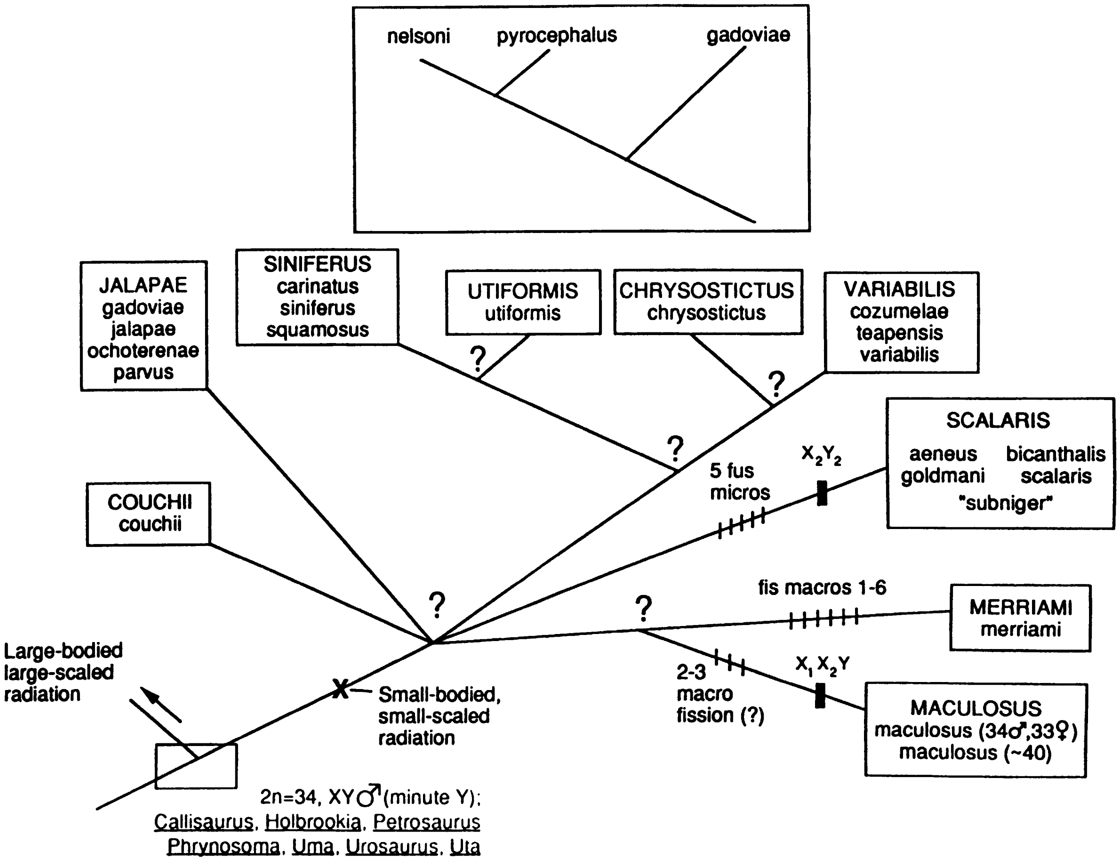


Fig. 19. Species groups (enclosed in squares) and phylogenetic relationships for the small-bodied, small-scaled radiation of *Sceloporus*, as presented by Hall (1977). Question marks indicate nodes represented without specific supporting evidence; vertical lines represent either chromosomal fission (fis) or fusion (fus) events; heavy vertical bars represent derivation of presumed novel sex chromosome heteromorphisms; and a heavy "X" represents hypothesized morphological similarities defining major clades. The three-species phylogeny inset at the top of the figure represents the relationships proposed for the *pyrocephalus* group by Cole (1971b).

lize (fig. 20). The total range of *S. maculosus* is a small xeric region in the north-central part of the Mexican Plateau, extending in a northeast-to-southwest arc in the states of Coahuila and Durango and with a peripheral isolate in northwestern Zacatecas (Baker et al., 1981; fig. 20). *Sceloporus merriami* is confined to the small north-central section of the Mexican Plateau, and ranges from the Big Bend area of Texas south through eastern Chihuahua and western Coahuila (fig. 21). The *utiformis* group (fig. 24) includes only *S. utiformis*, which ranges along the west coast of Mexico at low to moderate elevations, from southern Sinaloa south through northern Guerrero.

Although Hall (1977) provided no evidence for the relationship of *S. chrysostictus* to other species, Cole (1978) assigned this species to the *variabilis* group, based on a chromosomal synapomorphy (secondary constriction on the largest pair of microchromosomes; fig. 16B), and characters of external morphology.

The two species of *Sator*, a genus endemic to islands in the Sea of Cortez, have been considered the sister group of *Sceloporus utiformis* (Wyles and Gorman, 1978; Murphy,

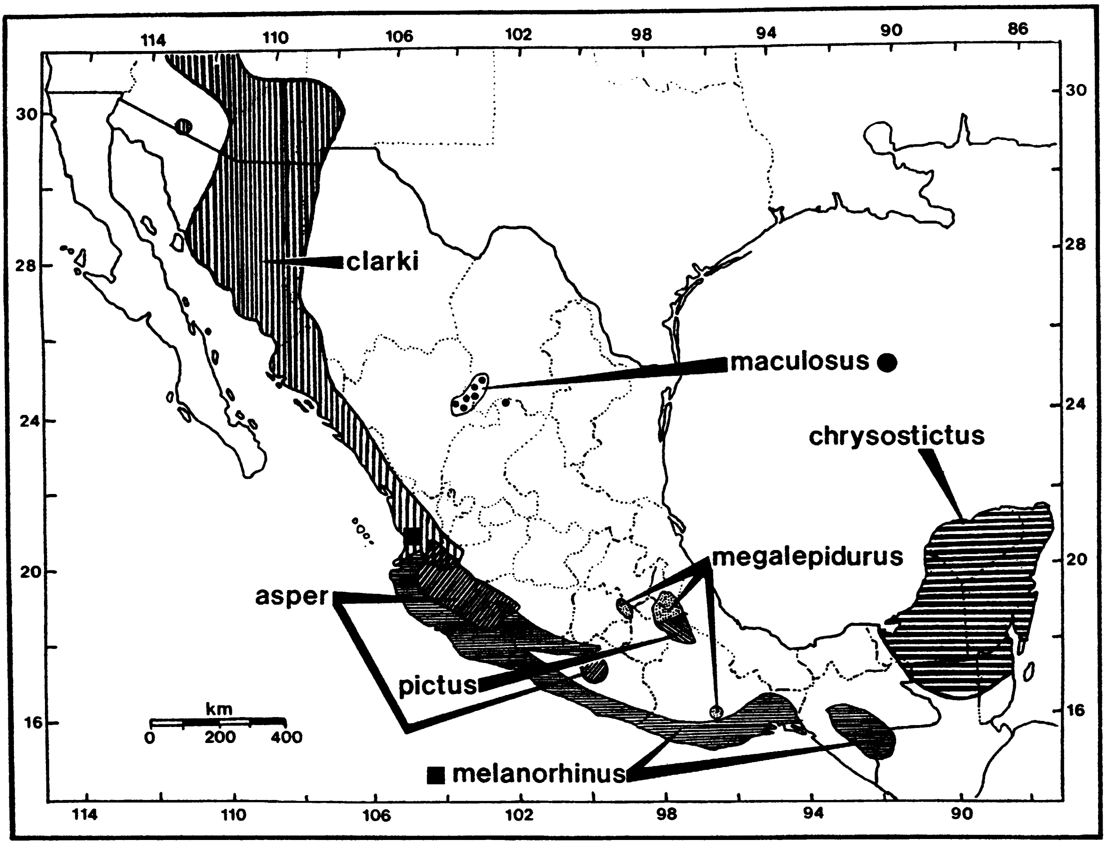


Fig. 20. Geographic distributions of the monotypic *chrysostictus* and *maculosus* groups of the small-bodied radiation (fig. 19), the monotypic *asper* group, and the *clarki* and *megalepidurus* groups of the large-bodied radiation (fig. 26).

1983a). *Sator angustus* is confined to the Gulf islands of San Diego and Santa Cruz, while *Sator grandaevus* occurs only on the island of Cerralvo (Murphy and Ottley, 1984). *Sator grandaevus* apparently has the same karyotype (Lowe and Robinson, 1971) as the hypothesized ancestral configuration (2n = 34) discussed above, which presents an interesting biogeographic problem (see below).

Hall (1973, 1977) modified other Smith and Taylor (1950) small-bodied groups by removing *S. gadoviae, S. jalapae, S. ochoterenae,* and *S. parvus* from the *pyrocephalus, scalaris, siniferus,* and *variabilis* groups, respectively, to form a distinct *jalapae* group (fig. 19). All of these but *S. jalapae* have karyotypes identical to those of their former (Smith and Taylor, 1950) groups (table 4), and Hall presumably used morphological and/or biogeographic criteria to support these changes, but these were never clearly discussed. The removal of *S. jalapae* from the *scalaris* group can be justified on the basis of chromosomal data (compare karyotypes for the *jalapae* and *scalaris* groups in table 4), and had previously been suggested on the basis of morphological distinctness (Thomas and Dixon, 1976). Hall (1977) also removed *S. couchii* from the *variabilis* group, and considered it basal to the entire small-bodied radiation.

These changes leave a *variabilis* group comprising two or three species (depending upon the validity of *S. teapensis*) with an extensive, linear north-to-south distribution (figs. 22, 23). Specifically, *S. variabilis* and

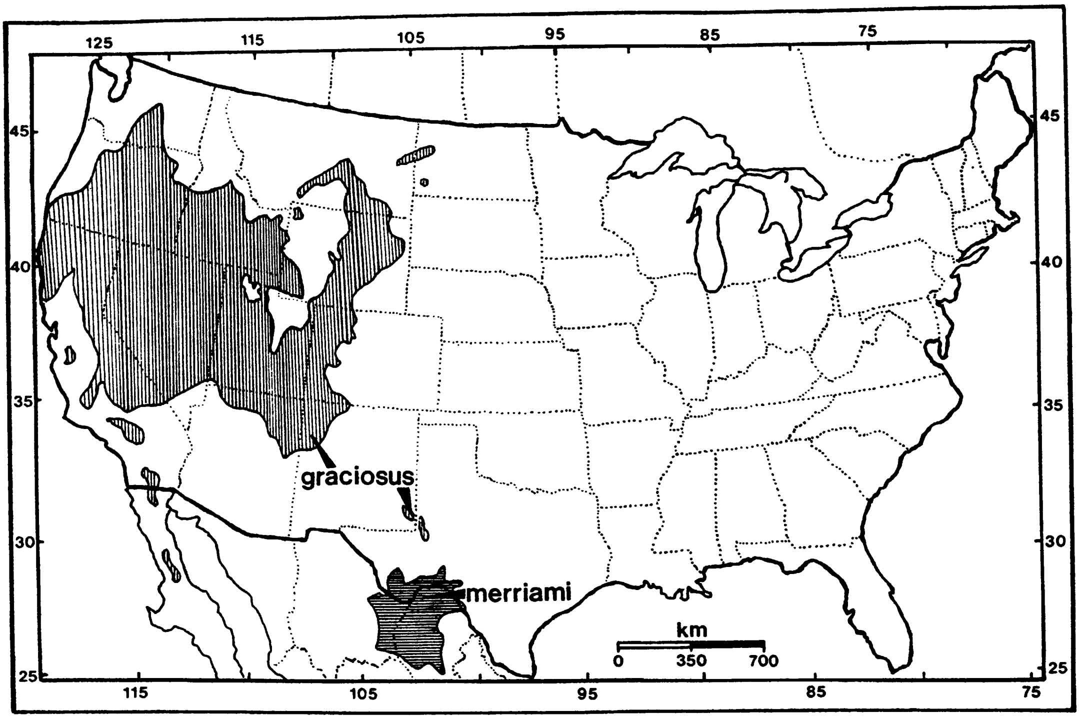


Fig. 21. Distributions of the monotypic *graciosus* and *merriami* groups of the large-bodied and small-bodied radiations, respectively.

teapensis range from the vicinity of San Antonio, Texas south along the entire east coast of Mexico, across the Isthmus of Tehuantepec to the Pacific Coast, and continuing south-southeast along both versants through much of Nuclear Central America. The southernmost distribution of *S. variabilis* on the eastern side of Central America terminates in northern Nicaragua, but it continues further south on the Pacific versant to the Guanacaste Province of Costa Rica (fig. 23). *Sceloporus cozumelae* is restricted to two isolated coastal sections of the Yucatan Peninsula. *Sceloporus couchii* is confined to a xeric montane/grassland area of the northeastern rim of the Mexican Plateau, along the Coahuila-Nuevo Leon border (fig. 22). The *siniferus* group is also left with three species, with *S. carinatus* being confined to uplifted areas of central Chiapas and western Guatemala, *S. siniferus* ranging along coastal regions from western Guerrero east through Oaxaca, Chiapas, and just into the southwestern corner of Guatemala (both illustrated in fig. 24), and *S. squamosus* extending along the Pacific versant of Nuclear Central America from southeastern Chiapas to northwestern Costa Rica (figs. 24, 31).

Hall's recognition of the *jalapae* group leaves the following hypothesized monophyletic units. The *scalaris* group, which may contain up to five species (fig. 19), is characterized by the highly derived 2n = 24 (10MM,2SMM,10m,XX♀/XY♂) karyotype (table 4; fig. 16C), and is distributionally centered mostly at high elevations at the southern end of the Mexican Plateau and in the transverse volcanic belt (fig. 25). Two exceptions include *S. goldmani,* restricted to isolated grassland habitats in southern Coahuila and northern San Luis Potosi (squares in fig. 25), and *S. scalaris,* which ranges across most of the high elevation areas of the Mexican Plateau, and extends northwest along the Sierra Madre Occidental just into Arizona and New Mexico (fig. 25). *Sceloporus aeneus* has

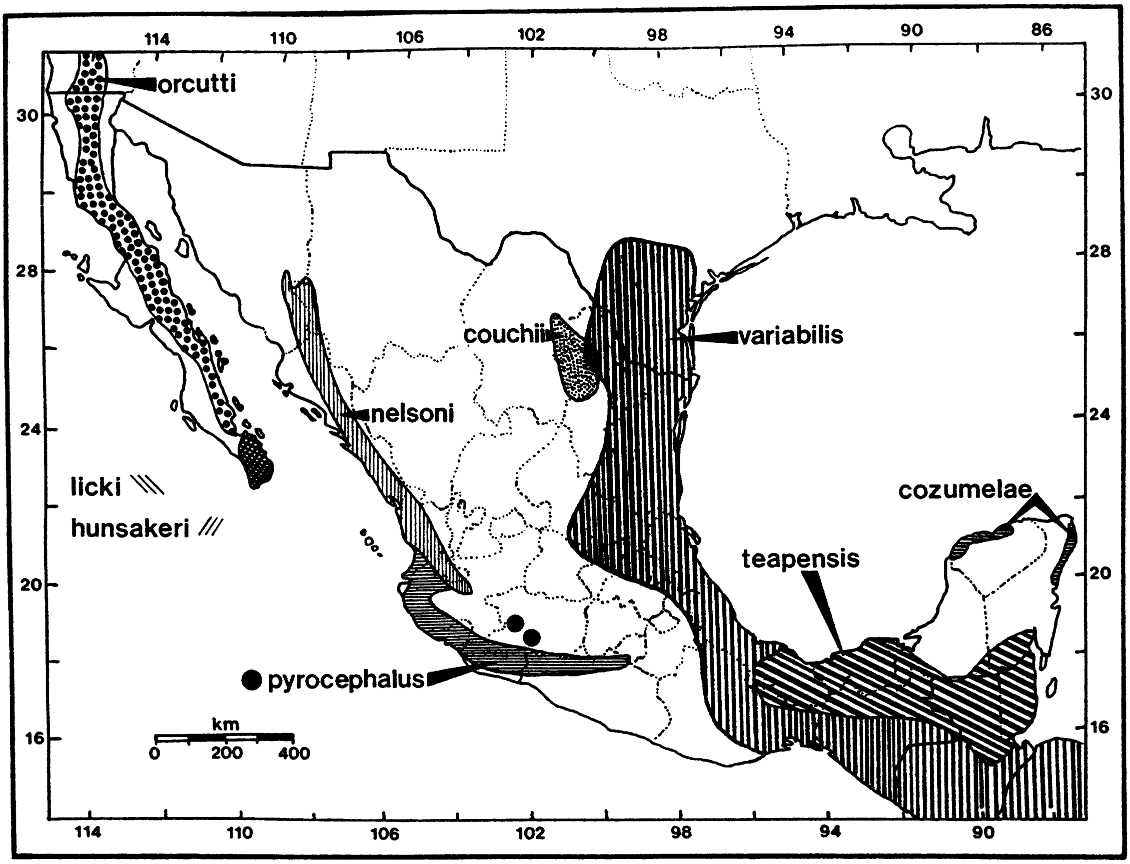


Fig. 22. Distributions of the *variabilis* and monotypic *couchii* groups of the small-bodied radiation, and the large-bodied *orcutti–nelsoni–pyrocephalus* group.

a disjunct distribution in the states of Mexico, Michoacan, and the Distrito Federal west of the Valley of Mexico; *S. bicanthalis* is confined to high elevations in the states of Hidalgo, Mexico, Puebla, and Tlaxcala east of the Valley of Mexico; and *S. subniger* is known only from the slopes of Nevado de Toluca in the state of Mexico (fig. 25). Both Hall (1973) and Cole (1978) found the same karyotype to characterize the *scalaris* group, but Cole considered the sex chromosomes to be undifferentiated. The *jalapae* group consists of the northern *S. parvus,* distributed linearly from north-to-south across the eastern section of the Mexican Plateau, and three southern species: *Sceloporus gadoviae* occupies an oval-shaped area centered in the states of Guerrero, Michoacan, Morelos, Puebla, and northwestern Oaxaca; *S. jalapae* is known from the highlands of north-central Oaxaca, Puebla, Tlaxcala, and the extreme western edge of central Veracruz; and *S. ochoterenae* is confined to southern Mexico (state), Morelos, and central Guerrero (fig. 25).

One other discrepancy between Hall's hypothesis and all others is the absence of a distinct *pyrocephalus* group. He removed *S. nelsoni* and *S. pyrocephalus* to a basal position in the large-bodied, large-scaled radiation, and allied both to the *orcutti* group for biogeographic and morphological reasons (figs. 22, 26). Cole (1971b) recognized the *pyrocephalus* group as a distinct unit, and proposed a sequence of speciation events in which *S. nelsoni* and *S. pyrocephalus* were derived relative to *S. gadoviae* (inset in fig.

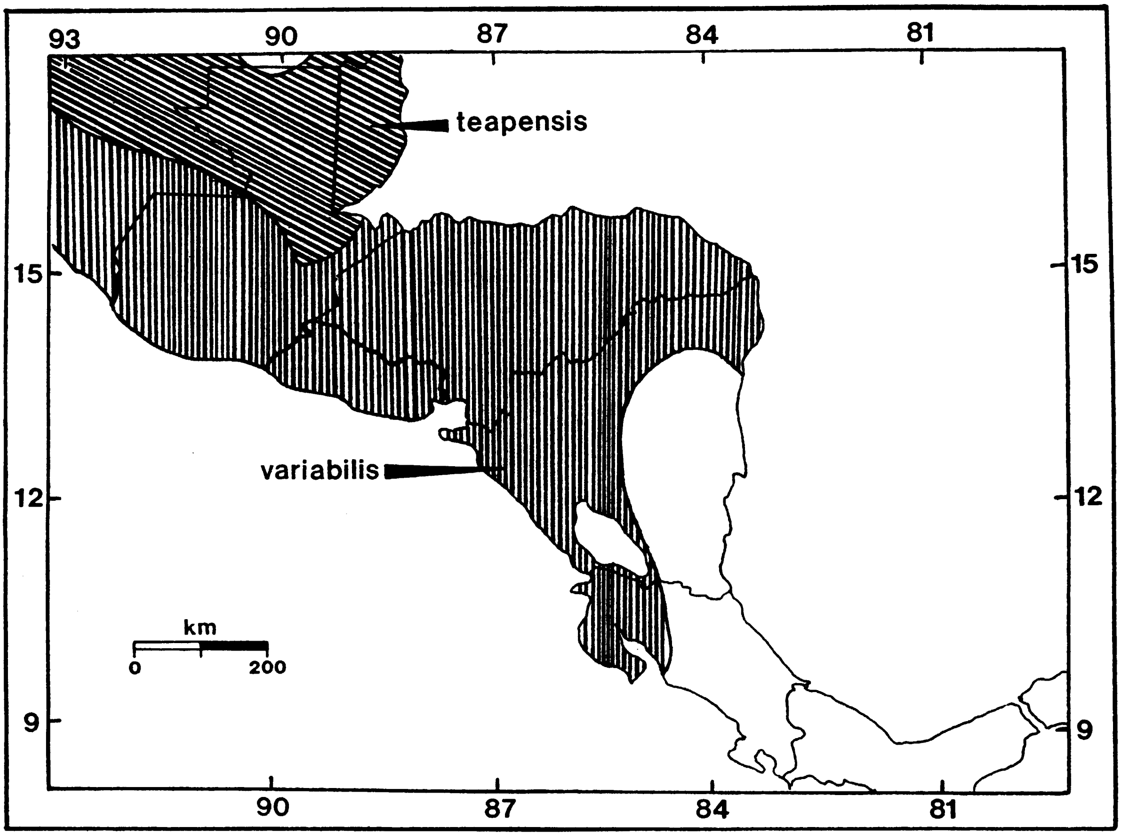


Fig. 23. Distribution of *S. variabilis* and *S. teapensis* in southern Mexico and Central America.

19). Hall's proposal contradicts a presumably derived morphological feature—the laterally compressed tail—that has been interpreted by others to diagnose the *pyrocephalus* group. Note that either arrangement is biogeographically plausible; *S. gadoviae* could either comprise the southernmost member of a three-species *pyrocephalus* group, or of the four-species *jalapae* group (compare figs. 22 and 25).

Since most of the species in this radiation retain the symplesiomorphic karyotype, chromosomal data are of only limited use for phylogenetic inference at the species-group level, and this is reflected in the pentatomy in figure 19. Hall did specify a phylogenetic arrangement in which sister-group status was recognized for the *siniferus* and *utiformis* groups as well as the *chrysostictus* and *variabilis* groups, and then suggested that all of these shared a common ancestor more recently with each other than with any other group of *Sceloporus*. This view is specified by the topology of figure 19, but the "?" indicates the tentative nature of the arrangement, and the absence of explicit synapomorphies defining these clades in Hall's proposal.

Chromosomal data can be used to define only three clades within the small-bodied radiation, the *maculosus, merriami,* and *scalaris* groups that deviate from the ancestral diploid number. A fourth group, not evident in table 4, is the abovementioned *variabilis* group, defined by the unusual location of a secondary constriction on a microchromosome pair (Cole, 1978; fig. 16B). These represent at least two independent sequences of karyotypic derivation away from the ancestral karyotype, but the chromosomal data do

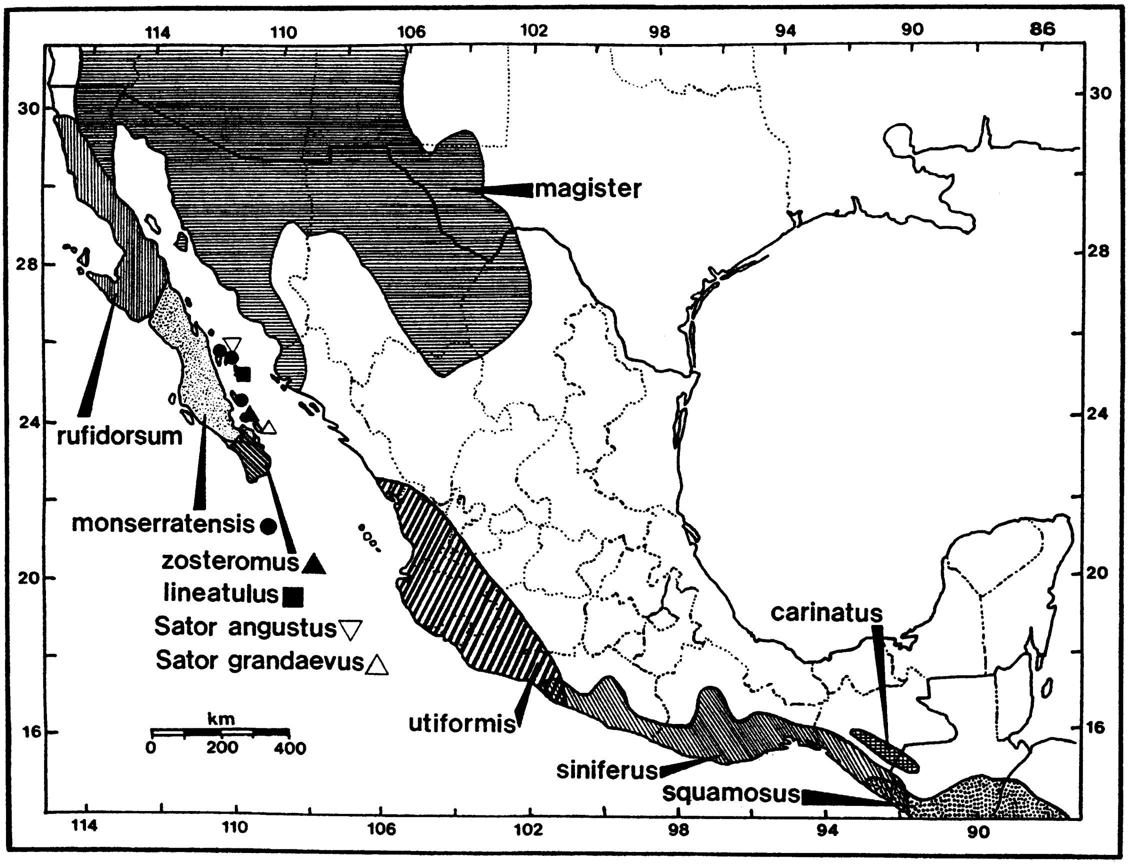


Fig. 24. Distributions of the *siniferus* and *utiformis* groups of the small-bodied radiation, and the *magister* complex of the large-bodied radiation. Within the latter, *S. lineatulus* is endemic to Santa Catalina island (■), *S. monserratensis* to Carmen, Coronados, Monserrate, and San Jose, as well as the main Baja Peninsula (●), and *S. zosteromus* to the Cape region of the Peninsula and to Espiritu Santo-Partida Sur (▲). The two species of *Sator* are denoted as *angustus* (▽) on San Diego and Santa Cruz, and *grandaevus* (△) on Cerralvo (distributions taken from Murphy and Ottley, 1984).

not permit inferences to be made about how these groups might relate to each other (but see comments below for the *maculosus* and *merriami* groups), or to the other groups in this radiation. Hall (1977: 9) argued that *S. merriami* probably represents the oldest sequence of chromosomal derivation in the genus, and postulated that its 2n = 46 (24AM,20m,XX♀/XY♂) karyotype was derived from the ancestral type by fissions of all six pairs of macroautosomes (table 4). This hypothesized early, independent derivation of *S. merriami* would imply that it should be one of the most distinctive members of the genus, a view supported by behavioral and morphological studies suggesting a phylogenetically early derivation (Purdue and Carpenter, 1972a, 1972b; Larsen and Tanner, 1974, 1975; see also Wiens, 1993).

Some populations of *S. maculosus* may show an intermediate stage in the sequence of macroautosomal fissioning from which the *S. merriami* karyotype was derived. Cole (1971a) reported a 2n = 34♀/33♂ (10MM,2SMM,18m,$X_1X_1X_2X_2$♀/X_1X_2Y♂) system in *S. maculosus* (based on 3 individuals sampled from a single locality, table 4), which gives it a sex-chromosome heteromorphism unique to this radiation. Hall (1977: 8) discussed a single specimen of *S.*

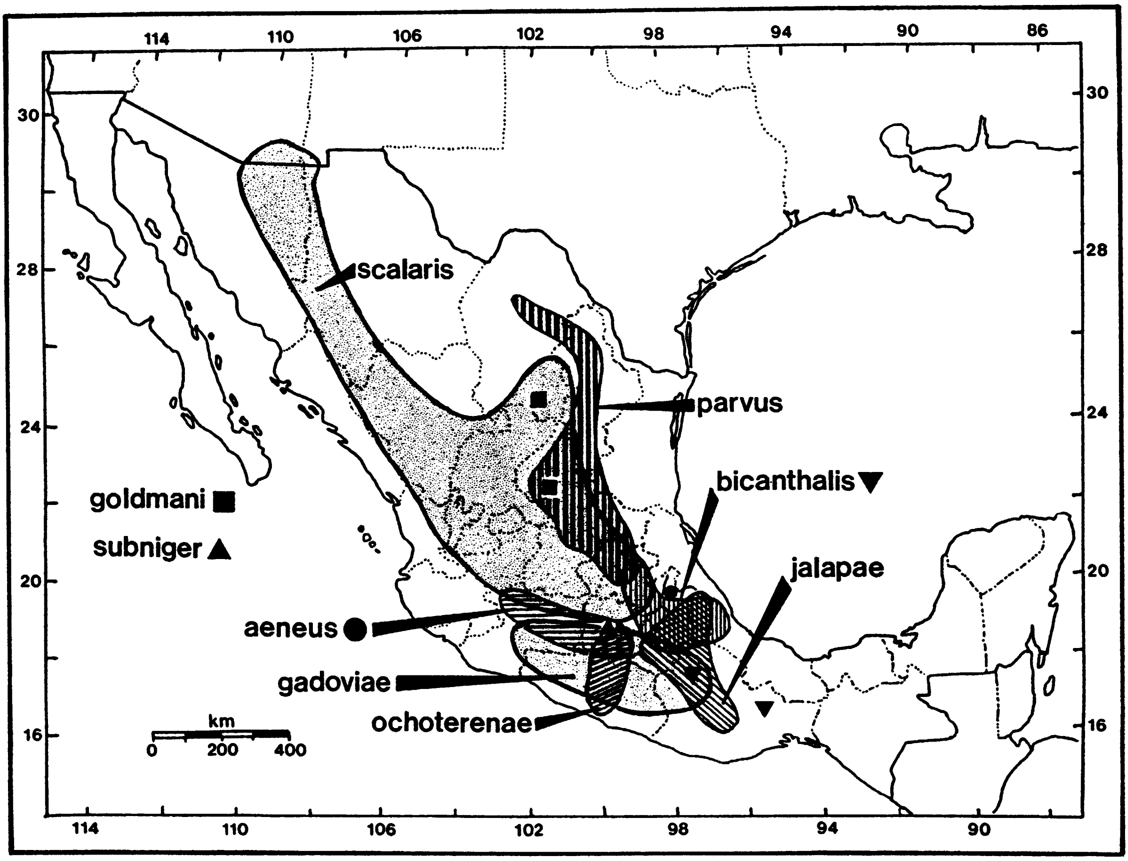


Fig. 25. Distributions of the *jalapae* and *scalaris* groups of the small-bodied radiation of *Sceloporus*.

maculosus reported by Carol Axtell from near the type locality, and which possessed a 2n ≈ 40 karyotype. Hall examined Axtell's slides and confirmed the high diploid count, although he could not specify which macroautosomes had been fissioned, nor comment on the presence/absence of an X_1X_2Y heteromorphism. Nevertheless, it is possible that a cryptic species resides in *S. maculosus*, and that the 2n = 40(?) *S. maculosus* could represent a sister group of *S. merriami*. Given the paucity of data points available thus far, coupled with strong evidence for intraspecific chromosomal polytypy and a unique sex chromosome system, the *S. maculosus* problem merits further study.

The other unequivocal sequence of chromosomal derivation from the ancestral karyotype within this group is the derivation of the *scalaris* group. In contrast to Hall's (1973, 1977) earlier reports, all recognized species have now been karyotyped (Cole, 1978), and all possess a 2n = 24 (10MM,2SMM,10m,XX♀/XY♂) karyotype (table 4). This karyotype was presumably derived by fixation of five fusions among the original 10 microautosomal pairs, and appears to corroborate a distinct clade (after removal of *S. jalapae*). Geographically, these species range from the mountains of southern Arizona and New Mexico to the southern slopes of the Eje Volcanica Transversal (fig. 25), where they are largely restricted to mesic grassland or grassland-forest habitats.

LARGE-BODIED, LARGE-SCALED RADIATION

By far the majority of Hall's unpublished work deals with his interpretations of the large-bodied, large-scaled radiation. He proposed several new groupings on the basis of

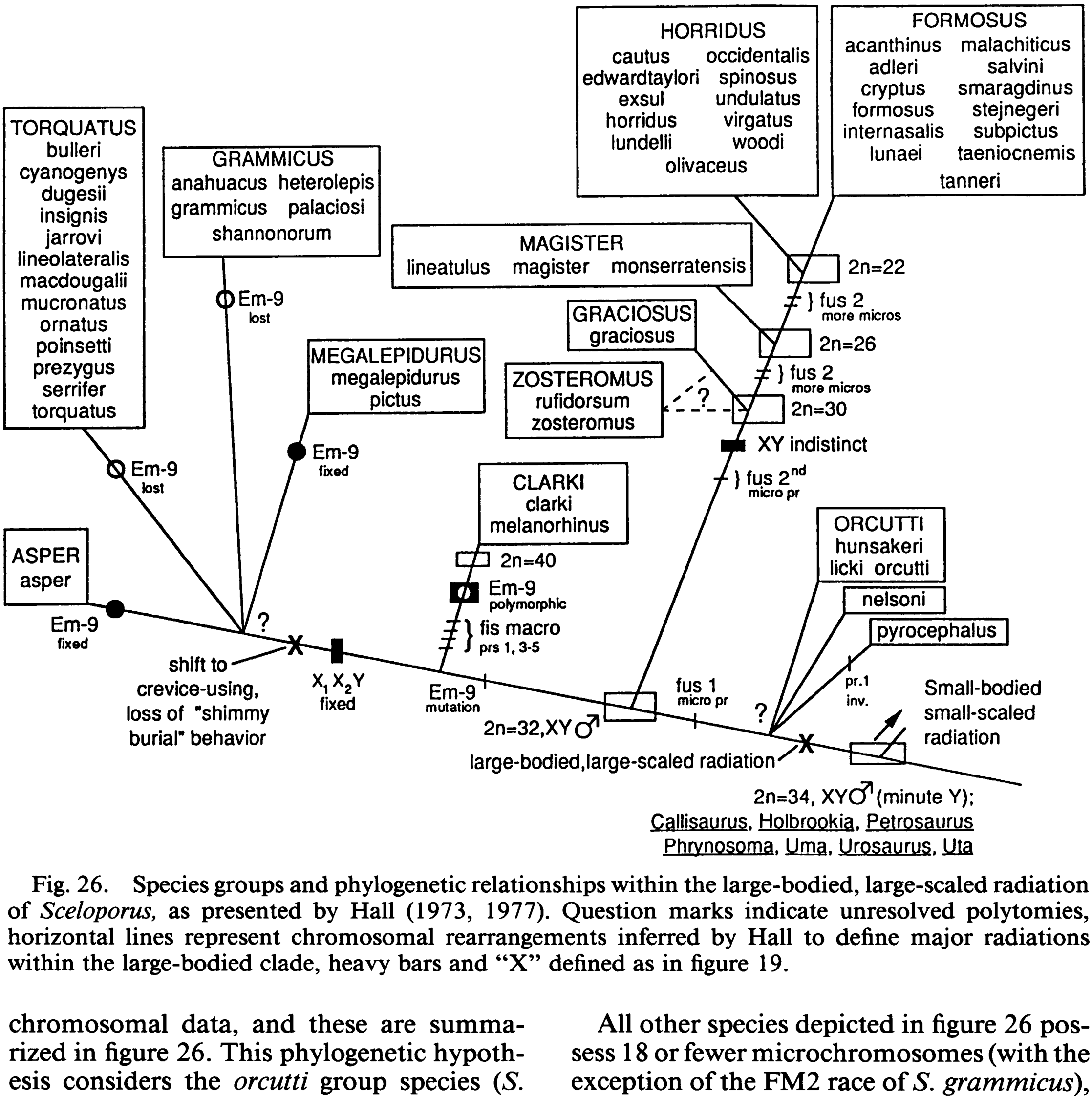


Fig. 26. Species groups and phylogenetic relationships within the large-bodied, large-scaled radiation of *Sceloporus,* as presented by Hall (1973, 1977). Question marks indicate unresolved polytomies, horizontal lines represent chromosomal rearrangements inferred by Hall to define major radiations within the large-bodied clade, heavy bars and "X" defined as in figure 19.

chromosomal data, and these are summarized in figure 26. This phylogenetic hypothesis considers the *orcutti* group species (*S. hunsakeri, S. licki,* and *S. orcutti*), along with *S. nelsoni* and *S. pyrocephalus,* as basal to the entire radiation. All of these possess the 2n = 34 (10MM,2SMM,20m,XX♀/XY♂) karyotype (with the exception of the fixed pair 1 pericentric inversion in *S. pyrocephalus*), and are restricted either to the Baja California peninsula (the *orcutti* group proper, figs. 22 and 27) or the west coast of mainland Mexico (fig. 22). The ranges of *S. nelsoni* and *S. pyrocephalus* appear to be separated by the lower reaches of the Rio Grande de Santiago, which also serves as a barrier between several other presumably closely related species of *Sceloporus* (see below).

All other species depicted in figure 26 possess 18 or fewer microchromosomes (with the exception of the FM2 race of *S. grammicus*), so the next hypothesized step in the evolutionary derivation of the large-scaled radiation was the loss of an unspecified microchromosome pair by a presumed translocation event. This would have generated a 2n = 32 (10MM,2SMM,18m,XX♀/XY♂) karyotype in an extinct ancestor, which then gave rise to two different lineages of further chromosomal divergence. A second microchromosomal fusion event generated the 2n = 30 (10MM,2SMM,18m,XY indistinct) karyotype presumably similar to those found today in *S. graciosus* and possibly *S. zosteromus.* Since this derived karyotype is only the first stage in a presumed transformation se-

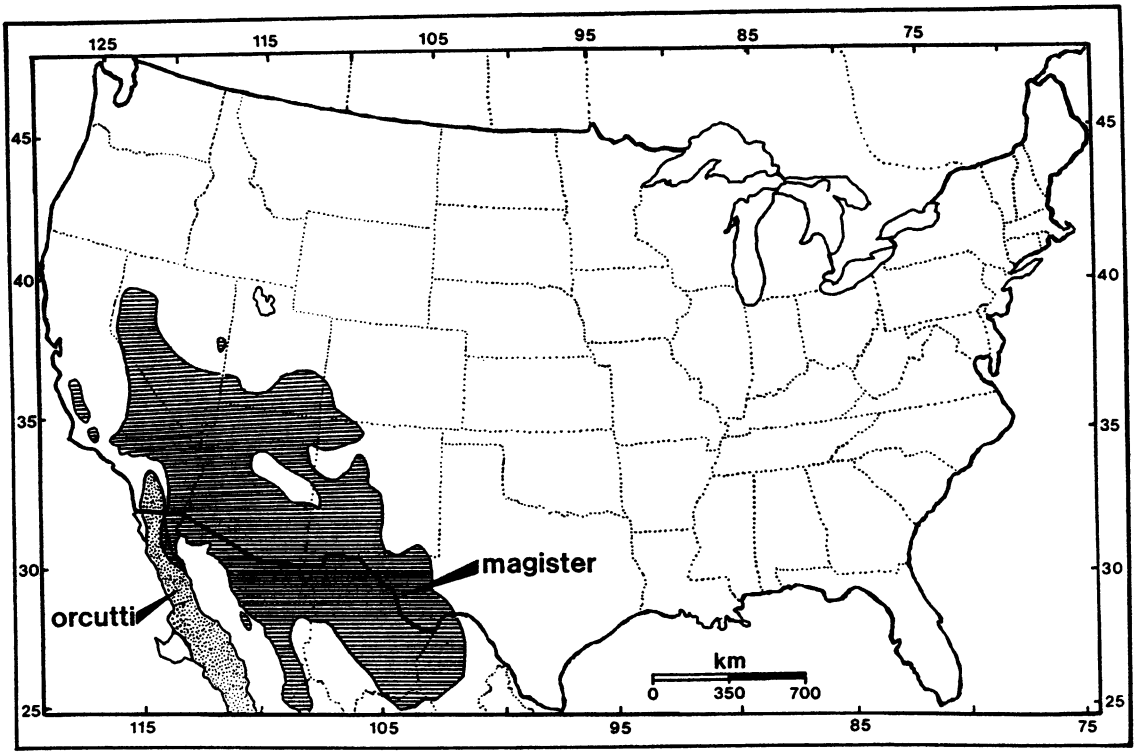


Fig. 27. Distributions of *S. magister* and *S. orcutti* in northern parts of their ranges; both are part of the large-bodied radiation.

ries, these two (and possibly a third, *S. rufidorsum*) species are not necessarily sister taxa, although such a relationship is not incompatible with the postulated derivation of the karyotypes. Two additional microchromosomal fusions are postulated to derive the 2n = 26 (8MM,2SMM,2SAM,14m, XY indistinct) karyotype of the *magister* group. An important point here is that the Baja endemics *S. lineatulus, S. monserratensis,* and *S. rufidorsum* are unknown karyotypically from Hall's data (1973, 1977, 1980; but see Murphy, 1983a and our fig. 14), and their specific status needs further confirmation. Fixation of two additional microchromosome fusions is then postulated to derive a large, diverse radiation of 2n = 22 (10MM,2SMM,10m, XY indistinct) *Sceloporus,* which itself diverged into two clades, one maintaining the ancestral reproductive mode of oviparity (the *horridus* group), while the second evolved viviparity (the *formosus* group). Note that this arrangement does not specify any apomorphies for the oviparous group.

The distributions of both the *magister* and *orcutti* complexes have been previously described, and are illustrated in figures 22 and 24. *Sceloporus graciosus* is widely distributed across elevated regions within and adjacent to the Colorado Plateau, Great Basin Desert, and associated mountain ranges and grasslands of the western United States. Disjunct populations are known from the northern Great Plains of Montana and North Dakota, the Yellowstone region of Wyoming, a series of sand dunes in New Mexico and Texas, and several isolated mountain ranges in California and the northern Baja Peninsula (fig. 21).

The oviparous *Sceloporus,* having a karyotype of 2n = 22 (10MM,2SMM,10m, XY indistinct; fig. 15), includes 11 species (the *horridus* group) distributed widely across most of North America north of the Isthmus of Tehuantepec (figs. 28, 29). *Sceloporus woodi* has a relictual distribution in Florida (fig. 28), *S. exsul* is known only from a few specimens from the type locality in Queretaro, and *S. cautus* and *S. edwardtaylori* are confined to

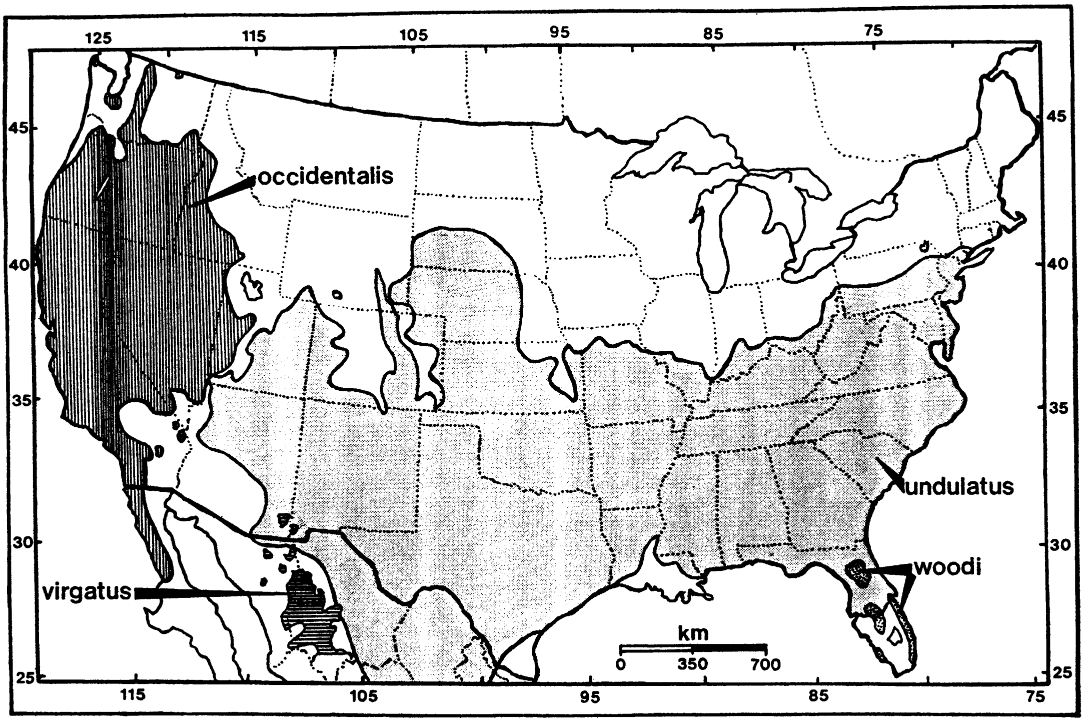


Fig. 28. Distributions of several northern species of Hall's (1973, 1977) *horridus* group; all are components of the large-bodied *Sceloporus* radiation.

relatively small geographic regions (fig. 29), but for the most part species of the *horridus* group are widespread and common. The southern limits of the distributions of *S. undulatus* and *S. virgatus* are unknown (fig. 29).

Hall (1973, 1977) defined the *formosus* radiation of 2n = 22 (10MM,2SMM,10m, XY♂ indistinct) *Sceloporus* groups on the basis of their independently derived, synapomorphic, viviparous reproductive mode. He did not try to define species limits within this group, and it remains by far the most poorly known of all species groups within the genus. The group has a relatively small total geographic range, and several species are known either only from their type localities (*S. subpictus, S. tanneri*), or from very restricted ranges (*S. adleri, S. cryptus, S. lunaei, S. salvini, S. stejnegeri*; figs. 30 and 31). *Sceloporus formosus* is relatively well known from higher elevations in Guerrero, Oaxaca, and Puebla (fig. 30), but distributional limits and species boundaries are extremely poorly defined for the *malachiticus* complex (fig. 31). This group includes at least four species (*S. internasalis, S. malachiticus, S. smaragdinus,* and *S. taeniocnemis*), and the distributions of these frequently overlap with each other or with those of other species (*S. acanthinus*), or are zoned altitudinally on several volcanic peaks in Chiapas and Guatemala, or overlap or are parapatric with populations not yet assigned to one of the known species (Stuart, 1971). The northern isolate in the San Andres Tuxtlas region of Veracruz appears to be assignable to *S. internasalis* (fig. 30), and the southern high-elevation populations in Costa Rica and Panama appear to be *S. malachiticus* (fig. 31), but the entire complex is in need of extensive study.

The second major radiation within the large-bodied group presumably begins with the origin of the "enlarged-micro" or Em mutation for microautosome pair 9. Hall (1973: 86–88) argued that microchromosomal similarities between the *clarki* group (including *S. clarki* and *S. melanorhinus*) and the "crevice users" (see below) were sufficient to hypothesize that all of these may have shared a common ancestry within the large-scaled

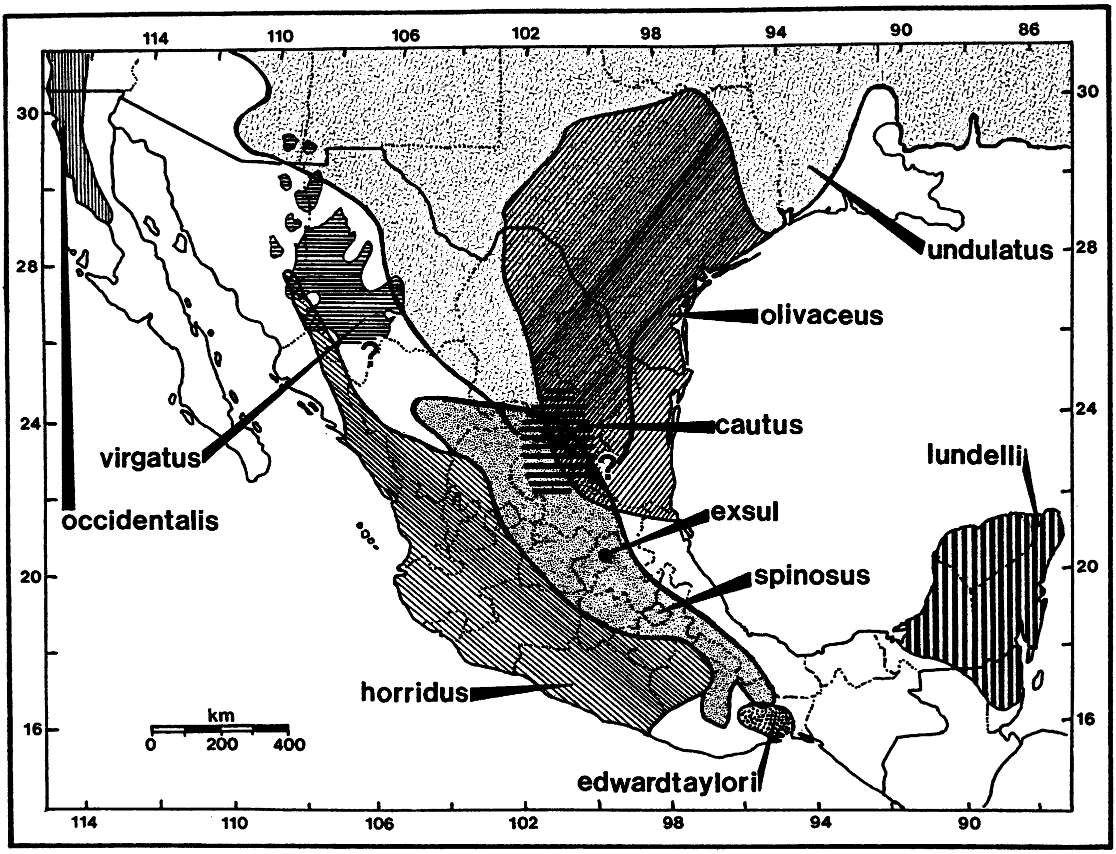


Fig. 29. Distributions of the majority of species in the *horridus* group; question marks denote uncertainties regarding the southern distributional limits of *S. undulatus* and *S. virgatus*.

Sceloporus division. Both species of the *clarki* group have female karyotypes with 20 microchromosomes (table 4), and this arrangement is indistinguishable from that of the "standard" karyotype of female crevice users, although male microchromosomal patterns in the *clarki* group species differ considerably from each other and the crevice users. Also, both *clarki* group species are polymorphic for the Em-9 mutation, which is fixed in some of the crevice users. This polymorphism was originally reported by Cole (1970) as an enlarged microchromosome and designated as the KB pattern, but was interpreted by Hall (1973: 87) as indistinguishable from the fixed Em mutation in *S. asper* and the *megalepidurus* group. Hall interpreted the Em mutation as an enlargement of microchromosome pair 9, on the basis of its size and morphology. The Em chromosomes are intermediate in size between the Y and macrochromosome pair 6, and distinctly submetacentric (see figs. 4E, F, 9E, and 10H in Hall, 1973). Thus, figure 26 presents the Em-9 mutation as a synapomorphic change that, as a *polymorphism,* diagnoses the radiation of crevice users, with the *clarki* group as the sister group of the crevice-user radiation. Both of the *clarki* group species retain the Em-9 polymorphism, but this group is defined by fixation of fissions for macrochromosome pairs 1, 3, 4 and 5. *Sceloporus clarki* itself is further derived by possessing an enlarged Y chromosome and a presumably autapomorphic XY heteromorphic system (fig. 18B). *Sceloporus melanorhinus* is then further derived via the aforementioned Y–pair 5 fusion to fix an autapomorphic X_1X_2Y system (fig. 18E). In our opinion, however, homology of the Em-9 microchromosome of *S. clarki* and the largest microchromosomes of the *megalepidurus* group has yet to be demonstrated (see below).

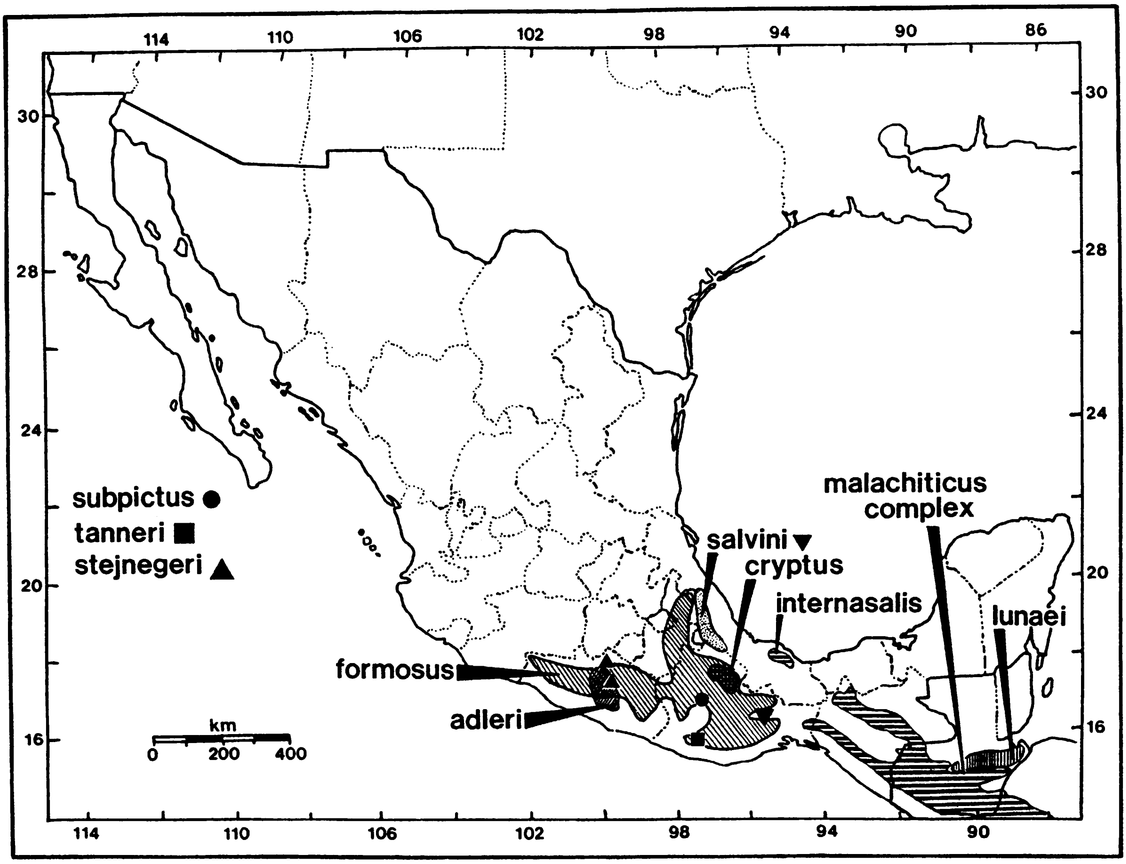


Fig. 30. Distributions of the viviparous *formosus* group of large-bodied *Sceloporus* as defined by Hall (1973, 1977); the *malachiticus* complex includes *S. internasalis, S. malachiticus, S. smaragdinus,* and *S. taeniocnemis.* See text for details.

The next hypothesized step in the sequence was the derivation of the $X_1X_1X_2X_2$♀/X_1X_2Y♂ sex-chromosome system originally described by Cole et al. (1967; see also figs. 17 and 18D), which in Hall's view is the synapomorphic chromosomal character uniting the four groups of crevice-using *Sceloporus* (*asper, grammicus, megalepidurus,* and *torquatus* groups; fig. 26). This heteromorphism is hypothesized to be derived from a *clarki*-like XY system (Hall, 1973: 95). The Em-9 polymorphism is hypothesized to have carried through this speciation event (the one giving rise to the *clarki* and crevice-user groups) as a polymorphism (Hall, 1973: 88), to have been fixed and independently in the *asper* and *megalepidurus* groups, and to have been lost in the *grammicus* and *torquatus* groups.

This crevice-user radiation shows rather pronounced morphological diversity despite the similarity of karyotypes. Members of the diverse *torquatus* group are generally specialized for the use of rock crevices, while the *grammicus* group (identical in composition to the Smith and Taylor update depicted in fig. 3), and the *megalepidurus* group (consisting only of *S. megalepidurus* and *S. pictus* of the Smith-Taylor group), all use some form of plant crevices. Hall (1973: 96) transferred *S. cryptus* from the *megalepidurus* to the *formosus* group on the basis of its 2n = 22 (10MM,2SMM,10m, XY indistinct) karyotype (table 4, fig. 15), and removed *S. asper* from the *formosus* group and allied it with the crevice users on the basis of its 2n = 32♀/31♂ (10MM,2SMM,16m,$X_1X_1X_2X_2$♀/X_1X_2Y♂) karyotype. Hall considered *S. asper* sufficiently distinct to treat it as a monotypic group, even though it shares the fixed Em-9 mutation with both *megalepidurus* group

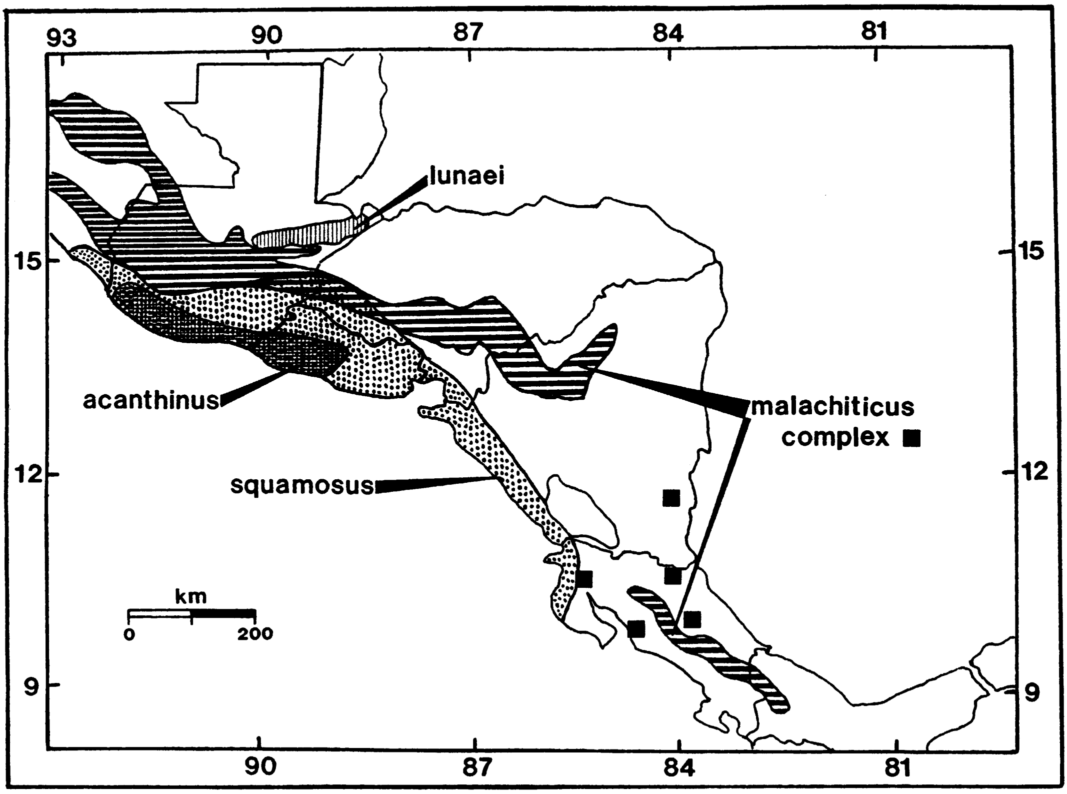


Fig. 31. Distributions of extreme southern elements of the *formosus* group, as defined in fig. 26, and *S. squamosus,* a member of the small-bodied *siniferus* group (see fig. 19). The *malachiticus* complex defines the same four species as those mentioned in figure 30.

species, and therefore could be the sister group of the *megalepidurus* group. *Sceloporus subpictus* (table 4, fig. 15) is karyotypically similar to the species in the *formosus* group, which is consistent with Hall's (1973) transfer of *S. subpictus* to that group (from the *megalepidurus* group), based on external morphology. Note that, with the exception of fixation versus loss of the Em-9 mutation, chromosomal data provide no resolution of phylogenetic relationships among the four crevice-user species groups recognized by Hall (fig. 26).

All four of these groups are restricted to mainland Mexico. *Sceloporus asper* is restricted to disjunct upland regions at the western edge of the transverse volcanic range, in Jalisco and Michoacan, while the two-species *megalepidurus* group occupies disjunct highlands in mountain ranges east and south of the Valley of Mexico (fig. 20). The *grammicus* group consists of several high-elevation species confined largely to the Mexican Plateau and associated mountain ranges. Both *S. anahuacus* and *S. palaciosi* are confined to a few volcanic peaks near the Valley of Mexico, while *S. heterolepis* and *S. shannonorum* are restricted to mountain ranges at the western margin of the transverse volcanic range and the Mexican Plateau, respectively (fig. 32). *Sceloporus grammicus* ranges across all but the hottest sections of the Mexican Plateau, and extends north into the lower Rio Grande valley of Texas. This "species" includes a number of chromosomally distinct populations that may in some instances represent additional, as yet unrecognized, cryptic species. These are currently under study by JWS and G. Lara-Gongora. The *torquatus* group contains about 13 species distributed across most mid- to high-elevation environments of Mexico north of the Isthmus of Tehuantepec (fig. 33). The only exceptions are *S. cyanogenys, S. serrifer,* and *S. prezygus,* which inhabit lowland areas on the Gulf side of Mexico from southern Texas south across the Isthmus of Tehuantepec to the Yucatan

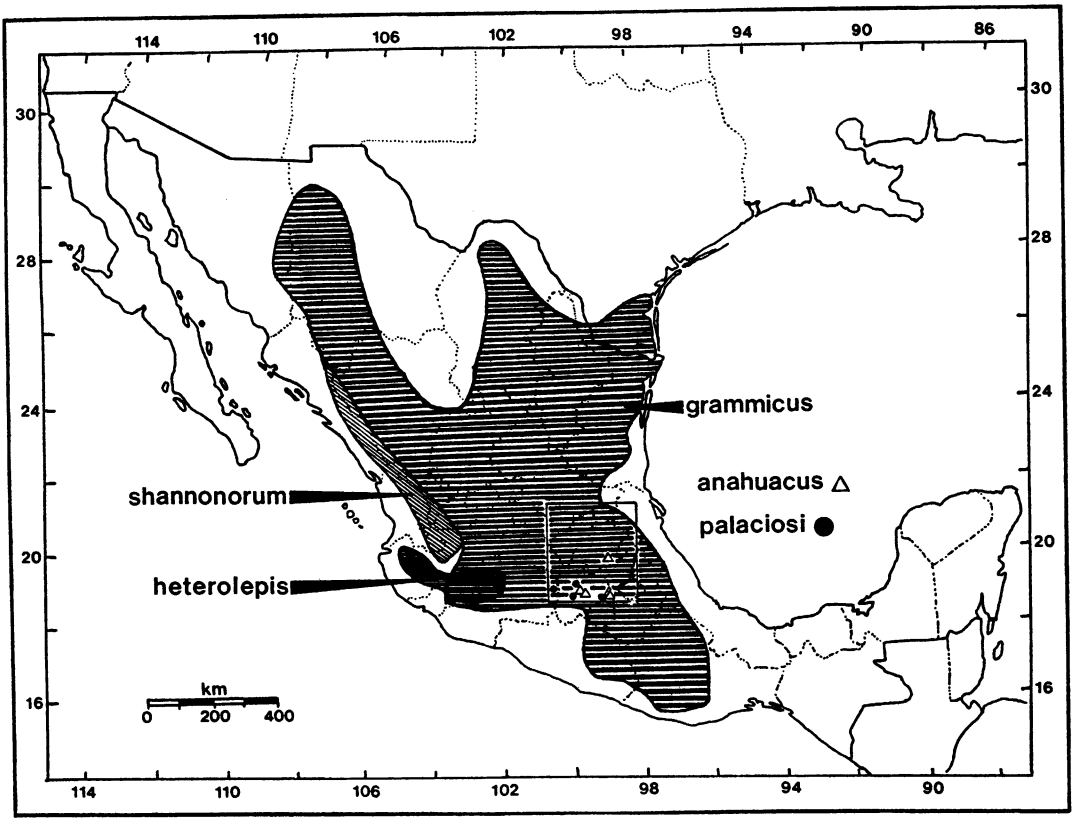


Fig. 32. Distributions of the *grammicus* group species within the large-bodied radiation of *Sceloporus*; the rectangle defines the area mapped in detail by Arevalo et al. (1991), in which the distributions of several chromosome races within *S. grammicus* are known from large sample sizes.

Peninsula, and extending just into northwestern Guatemala (*S. cyanogenys* is considered a subspecies of *S. serrifer* by Olson, 1987). Of the remaining species, *S. bulleri, S. dugesii, S. insignis,* and *S. macdougalli* have restricted ranges in southern or western Mexico, while *S. lineolateralis* and *S. ornatus* have restricted ranges on the north-central part of the Mexican Plateau. *Sceloporus mucronatus* has a moderate range south of the Mexican Plateau, while *S. jarrovi, S. poinsetti,* and *S. torquatus* are widely distributed across large sections of the central Mexican Plateau (fig. 33).

ADDITIONAL CHROMOSOMAL DATA AND COMMENTS ON TAXONOMIC PROBLEMS

In general, CJC published on karyotypes of *Sceloporus* as he accumulated complete representation of the species composing the species groups recognized by Smith (1939). Consequently, a considerable amount of his material was unpublished also, and nearly all of this (excepting new data on variation in *S. undulatus*) is included here (table 4; figs. 14–17). These data agree extremely well with Hall's unpublished data (table 4) and have vouchers in the form of individual specimens as well as sheets recording observations for the cells examined, on file at the American Museum of Natural History. In the course of pursuing these studies, CJC uncovered several problems warranting further research. These are mentioned here in the order in which pertinent species are listed in table 4. Reference is made to some published material also, in the context of Hall's data discussed above.

All of the species in the *variabilis* species group including *S. couchii,* and only one other species in the genus, *S. chrysostictus,* share the apparent karyotypic synapomorphy of a

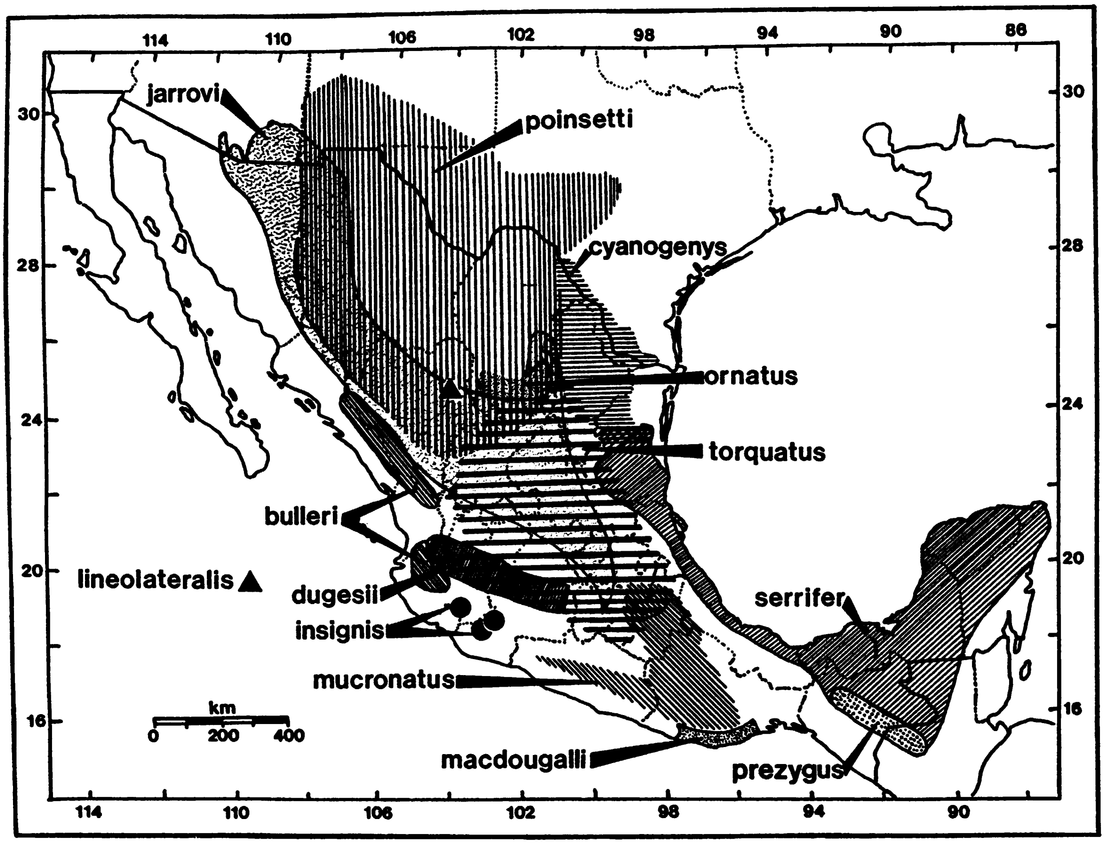


Fig. 33. Distributions of 13 species constituting the *torquatus* group of large-bodied *Sceloporus* recognized by Hall (1973, 1977).

secondary constriction near the centromere on one of the largest pairs of microchromosomes (subtelocentric) and absence of the constriction on the second largest pair of macrochromosomes (Cole, 1971b, 1978; fig. 16), perhaps reflecting a translocation of ribosomal DNA. This could be reflected in the cladogram (fig. 19) by reassociating *S. couchii* with or near the *variabilis* group (Cole, 1978).

We agree with Hall's assignment of *S. cryptus* and *S. subpictus* to the *formosus* group (from the *megalepidurus* group) based on their shared possession of a highly derived karyotype (2n = 22) and similarities in external morphology (table 4; fig. 15). The two remaining species in the *megalepidurus* group, *S. megalepidurus* and *S. pictus,* are morphologically similar, are known to interbreed, and therefore might form a single species. The intermediates listed in table 4 were collected on 21 July 1970 at the following locality: Mexico, Puebla; 10 km (by MX Hwy 150D toll road) W Esperanza.

Although we agree with Hall's reassignment of specimens referred to as *S. cryptus* and *S. subpictus* to his *formosus* group, we question whether these two and *S. adleri* actually represent three species distinct from each other and from *S. formosus.* However, OFV has collected both *S. adleri* and *S. formosus* at Omiltemi, Guerrero, and finds these to be easily and consistently distinguishable on the basis of morphological characters.

Eight of the nine specimens of *S. formosus* from four localities examined by CJC were karyotypically similar to each other in all details (table 4). The exception was the only male collected at the following locality: Mexico: Oaxaca; 2.3 mi [by Oaxaca Hwy 125] NE San Andres Chicahuaxtla [locality = 22 mi by rd SW Tlaxiaco]). This male was heteromorphic for the seventh largest pair of chromosomes (one submetacentric; one subtelocentric; fig. 15A), whereas all other *S. formosus* examined by CJC, including four males from two other localities, were homomorphic (submetacentric) for chromosome pair 7.

The karyotype of *S. rufidorsum* apparently is similar to that of *S. zosteromus* (table 4; fig. 14), consistent with their distribution on the Baja California Peninsula, and similar external morphology. Their karyotypic differences from *S. magister* suggest that neither is conspecific with that species. In addition, it is possible that *S. rufidorsum, S. zosteromus,* and other populations in the Baja region previously referred to *S. magister* actually constitute only a single species rather than several.

CJC's unpublished karyotypic data for *S. undulatus* (not included in table 4) now include hundreds of individuals, with a large series from an intergrade zone in Arizona where *S. u. elongatus* and *S. u. tristichus* freely interbreed. The data suggest that it would be premature to elevate subspecies of *S. undulatus* to the status of full species (sensu Frost and Hillis, 1990).

Hall noted (tables 4, 5) that *S. orcutti* is one of the species with a minute Y chromosome. This had not been noted by Cole (1970), so we recently examined another male (table 4) and confirm that the minute Y is present in this species (fig. 16A).

We discussed above Hall's suggestion that an enlarged microchromosome (Em-9) was a synapomorphy for the following species groups: *asper, clarki, grammicus, megalepidurus,* and *torquatus* (fig. 26). However, we think that the homology of "Em-9" has yet to be demonstrated among these groups, for two reasons. Firstly, the enlarged microchromosome described by Cole (1970) in the KB karyotype of *S. clarki* (also found in *S. melanorhinus*) appears to be a larger chromosome than that which Hall referred to as the Em-9 in *S. megalepidurus.* Secondly, in figure 17 we do not recognize what would represent "Em-9 fixed" for *S. pictus* versus "Em-9 lost" for *S. torquatus* (fig. 26). Perhaps Hall did not sufficiently consider individual variation in the appearance of microchromosomes from cell to cell in his report on Em-9. If the Em-9 character proves to be unreliable, external morphology of these lizards may reveal alternative placements for *S. clarki* and *S. melanorhinus.*

In an early report on karyotype evolution in *Sceloporus,* Cole (1970) accepted the view then prevailing among cytogeneticists, that karyotypic evolution proceeded via centric fusion, and proposed that the ancestral karyotype of Smith's (1939) *spinosus* group was represented by the karyotypes of *S. clarki* and *S. melanorhinus* (2n = 40). We all agree now, however, that sufficiently detailed comparative investigations (e.g., Paull et al., 1976) of a relevant variety of lizard species indicate that the 2n = 34 karyotype (figs. 13, 16A) represents the ancestral condition for *Sceloporus* and for the Phrynosomatidae. In fact, studies on the *S. grammicus* complex (Hall, 1980; Arevalo et al., 1991), in the context of karyotypic evolution in the Phrynosomatidae, provide some of the best evidence in lizards that karyotypic evolution sometimes occurs by means of centric fission (see also Webster et al., 1972). This pattern has also been documented in other tetrapod groups (Cole, 1974, for example). Most major patterns of karyotypic evolution, including inversions, and centric fusions and fissions, are apparent and available for additional investigation in *Sceloporus* (figs. 14–17, 19, 26).

PHYLOGENETIC SUMMARY

We have now summarized three different "phylogenetic" hypotheses for the genus *Sceloporus*: Smith's (1939) treatment (including the Smith and Taylor 1950 revisions); the multivariate/phenetic work of Larsen (1973) and Larsen and Tanner (1974, 1975); and the chromosomally based hypotheses of Hall (1973, 1977, 1980). Some common patterns are reflected in all of these schemes, but each also suggests different derivations for some species.

The differences are most pronounced between the hypotheses of Smith (1939) and Hall (1973, 1977, 1980). The phylogeny of Larsen and Tanner (1974, 1975) is very much intermediate between these two and contains similarities to both. Both Hall and Larsen and Tanner extensively rearranged the relationships of Smith's small-scaled radiation. For the most part, Hall was unable to resolve the relationships between the groups within this radiation (fig. 19). In fact, the resolutions he proposed for the *siniferus, utiformis,* and the *chrysostictus–couchii–variabilis* clade (itself supported by data from Cole, 1978) were not supported by substantive data. In contrast, Larsen and Tanner (1975) proposed that four of Hall's groups, whose intergroup relationships were unresolved (*jalapae, couchii, merriami,* and *maculosus*), formed a monophyletic group (their Group I) and were sufficiently distinct to merit generic status, *Lysoptychus.*

Larsen and Tanner's Group II contains four species groups: (1) the remaining species in Hall's small-scaled radiation; (2) the species of Smith's small-scaled radiation that Hall removed to the large-scaled radiation (*S. nelsoni* and *S. pyrocephalus*); (3) the species of the *grammicus* and *megalepidurus* groups that (a) Smith (1939) considered to occupy phylogenetically intermediate positions in the large-scaled radiation, and (b) Hall (1977, 1980) united in the crevice-dwelling complex of the large-scaled radiation including the *torquatus* group species; and (4) *S. asper* (2n = 32), which Smith placed in the *formosus* group, the latter having a very derived karyotype (2n = 22). Hall also placed this species in the crevice-dwelling complex.

In part, a major rearrangement of the small-scaled radiation seems warranted on the basis of the present understanding of the higher-level systematics of the Phrynosomatidae. The aforementioned studies which place *Urosaurus* and *Uta* as first and second outgroups to *Sceloporus* (Etheridge, 1964; Presch, 1969; Etheridge and de Queiroz, 1988; Frost and Etheridge, 1989), as opposed to originating within *Sceloporus,* minimally require Smith's (1939) phylogeny to be rerooted. However, the composition of Larsen and Tanner's Group II is distinctly different from both Smith's and Hall's phylogenies, regardless of how that early hypothesis would be rooted. As mentioned previously, both Smith (1939) and Larsen and Tanner (1975) placed the *pyrocephalus* group in the small-scaled radiation while, in contrast, Hall (1977, 1980) placed the two species he considered to be members of that group at the base of the large-scaled radiation. Several of the hypotheses of relationships among groups of small-scaled, small-bodied *Sceloporus* provide interesting zoogeographic scenarios appropriate for further testing. For example, the *pyrocephalus* group contains two species distributed along the west coast of Mexico while its sister group (in the Larsen-Tanner hypothesis), the *scalaris* group, is distributed east of the Sierra Madre Occidental on the central Mexican Plateau. Similarly, species of the Larsen-Tanner *variabilis* group are distributed on the east coast from Texas to Yucatan and then through much of northern Central America (figs. 20, 22, 23), while its sister group, the *utiformis* group, occurs along the west coast of Mexico and the Sierra Madre Occidental south into Central America, but primarily along the Pacific half of the area (fig. 24).

Within the large-scaled radiation all three hypotheses show substantial differences in the relationships among the major species groups, in the relationships of species within groups, and, to a lesser extent, in the membership of species in groups. The Smith and Larsen-Tanner hypotheses are surprisingly consistent in the membership and relationships of the *formosus, spinosus, undulatus,* and *graciosus* groups. As mentioned previously, Smith's *formosus* group is paraphyletic with the *spinosus* and *grammicus/megalepidurus* groups being derived from it (fig. 5), and in particular from subspecies of *S. formosus.* Larsen and Tanner hypothesized a monophyletic *formosus* group with the *spinosus* group being its sister group (fig. 11). They placed *S. lundelli* in the *formosus* group while Smith placed it as a member and sister group of the remainder of the *spinosus* group. Within the *formosus* group there is substantial agreement in the arrangement of species between the Smith and Larsen-Tanner hypotheses. However, in the *spinosus* group the hypothesized relationships differ substantially and provide an interesting area for investigation both phylogenetically and zoogeographically. For example, *S. edwardtaylori*, which has a geographic range restricted to southern Oaxaca, is placed in the Larsen-Tanner hypothesis as the sister group of *S. horridus* and *S. spinosus* (fig. 11). These two species have ranges extending from northern Oaxaca to north-central Mexico (fig. 29). In contrast, Smith (fig. 6) placed *S. edwardtaylori* as the sister species of a clade including *S. melanorhinus, S. clarki*, and the *orcutti* complex. The *orcutti* complex and *S. clarki* are distributed in Baja California and the northwest coastal region of Mexico while the distribution of *S. melanorhinus* extends from northern Michoacan through all of southern Oaxaca (fig. 20). Zoogeographic scenarios are plausible for either of these distributions and sets of relationships, but would imply distinctly different speciation scenarios. Karyotypically, and morphologically, *S. clarki* and *S. melanorhinus* are distinct (2n = 40) while *S. edwardtaylori* resembles the *spinosus* group (2n = 22), supporting the Larsen-Tanner hypothesis. Although this would seem conclusive evidence, the highly derived nature of the *clarki* and *melanorhinus* karyotype is clearly autapomorphic and the question of the relationship of this clade to the other species in the large-scaled radiation remains problematical.

On the basis of derived karyotypes, Hall united not only the *spinosus* and *formosus* groups (exclusive of the *orcutti, nelsoni*, and *clarki* groups), but the *undulatus* and *graciosus* groups as well (fig. 26). The uniting of the *undulatus* group with the *spinosus* group is a distinct conflict with the relationships proposed by both Smith (fig. 3) and Larsen and Tanner (fig. 11). The Smith and Larsen-Tanner hypotheses agree completely on the relationships proposed for these species groups except in the placement of *S. cautus*—placed in the *undulatus* group by Smith and the *spinosus* group by Larsen and Tanner. Either of these latter two placements makes sense zoogeographically (fig. 29).

Hall's proposed crevice-using radiation (fig. 26) conflicts substantively with both Smith's hypothesis (fig. 3) and that of Larsen and Tanner (fig. 7). Hall as well as Larsen and Tanner removed *S. asper* from the *formosus* group, where it was placed by Smith, and associated it with the *grammicus, heterolepis, megalepidurus* groups. However, while Hall's hypothesis united these with the *torquatus* group into a single crevice-user group, the Larsen-Tanner hypothesis placed these three species in their Group II radiation of small-scaled species. Both of these hypotheses are in distinct conflict with Smith's placement of the groups.

Since all of the *torquatus* group species are identical karyotypically, Hall could not form an hypothesis of relationships among them. In contrast, both Smith and Larsen and Tanner provided detailed hypotheses, and although they agree in the species membership of the two groups, they conflict in entirety regarding the relationships within the groups. Within the *jarrovi* group, the primary split of the Larsen-Tanner hypothesis is a north-south division between *S. dugesii* and the other more northern species. In contrast, Smith's hypothesis implies successive speciation of peripheral isolates from the extensively distributed *S. jarrovi*. Within the large-scaled *torquatus–poinsetti* group, the Larsen-Tanner hypothesis has a major north-south split between *S. poinsetti* and the other species. The species with more southern distributions are then split into a group with species having small, relatively peripheral distributions (*S. macdougalli, S. bulleri, S. insignis*, and *S. cyanogenys*) and ones with relatively large and/or central distributions (*S. torquatus, S. serrifer*, and *S. mucronatus*). In contrast, Smith's hypothesis has a primary split between two species with northern distributions (*S. poinsetti* and *S. cyanogenys*) plus *S. mucronatus* (a species with an extremely southern distribution) and a large group with primarily central distributions (except *S. macdougalli*). The only other resolved hypothesis separates a Central Mexican Plateau species (*S. torquatus*) from Sierra Madre Occidental species (*S. bulleri* and *S. insignis*).

Obviously, independent lines of evidence will be needed to resolve the conflicts raised by these three competing hypotheses and to date only limited data sets are available (e.g., Mindell et al., 1989; see below). We emphasize at this point that we are acutely aware that since the Smith and Larsen-Tanner studies are based on nonphylogenetic assumptions while Hall's approach was basically phylogenetic, we are in an epistemological sense comparing apples and oranges. Nevertheless, the intent of all authors was to recover the phylogeny of *Sceloporus,* and here we simply draw attention to similarities and differences in conclusions. Hall (1973), however, developed additional arguments which seemed to support his chromosomal hypothesis for phylogenetic relationships among some groups within the large-bodied, large-scaled radiation. These arguments are principally behavioral and ecological in nature, in that they are based on the general biology of crevice using, but they reflect the synthetic nature of his overall hypothesis.

We have briefly alluded to the propensity of the *grammicus, megalepidurus,* and *torquatus* group species to use different classes of crevices for sleeping and escape. Hall interpreted this aspect of their biology as phylogenetically significant, and argued that it was indicative of both a common ancestry (i.e., a synapomorphic behavior for all species with the $2n = 32♀/31♂$ $X_1X_1X_2X_2♀/X_1X_2Y♂$ karyotype in fig. 26), and sufficient to explain the morphological differences between radiations using rock versus plant crevices (Hall, 1973: 106–113).

Hall's arguments are based on the premise that most species of *Sceloporus* will "shimmy bury" (Axtell, 1956) into loose soil or sand to sleep, or to escape in the absence of trees or burrows. This is true even for the tropical cloud-forest *S. formosus* that never encounters loose sand in its habitat (Hall, 1973: 107; Etheridge and de Queiroz [1988] considered this behavior ancestral for *Sceloporus,* and Frost and Etheridge [1989] also noted it as plesiomorphic within the Phrynosomatidae). The only *Sceloporus* species which Hall observed *never* to display this behavior were the crevice users, although he only tested four species under controlled conditions (*S. grammicus* from Oaxaca, *S. mucronatus, S. pictus,* and *S. torquatus*). These and all other crevice users, however, are always found closely associated with some kind of crevice into which they quickly retreat at the slightest disturbance. Almost all species in the *torquatus* group, for example, are restricted to rock-crevice type habitats (primarily rock outcrops and stone fences), where they take cover in crevices and cracks formed along bedding and fracture planes. Two apparent exceptions appear to be *S. serrifer,* reputed to be semiarboreal (Smith, 1936), and *S. cyanogenys,* occasionally found on *Yucca* plants. Rarely, individuals of most other species may be found on other substrates (fallen logs or hollow trees) that provide alternative crevice cover, but Hall notes that in many thousands of observations of these species in the wild, he never saw *torquatus* group species use burrows in the ground for cover, nor found them far from crevices (1973: 108).

The plant-crevice-users exploit a variety of crevicelike spaces in plants, such as the hollowed interiors of *Opuntia* pads, spaces under or between the swordlike leaves of *Agave* and *Yucca* plants, cracks in split logs and trees, and under loose bark on *Yucca, Opuntia,* dead standing trees, fallen logs, and stumps. The *grammicus* group species inhabit most of these crevice types within their respective ranges, as do most of the chromosome races of *S. grammicus,* but the latter also readily take to stone walls, houses, archaeological ruins, and rock faces along road cuts in human-modified habitats. In contrast, *S. megalepidurus* and *S. pictus* seem to be much more restricted to *Agave* and *Yucca,* and spend more time on the ground at the base of these plants than does *S. grammicus.*

The conclusions Hall draws from these observations are that: (1) crevice using is a derived character; and (2) the loss of "shimmy burial" behavior also appears to be derived in the same groups. This latter inference is especially relevant in view of the fact that many crevice users live in habitats where loose sand or soil is closely juxtaposed to their crevice cover, implying to Hall that the crevice users had made a major ecological shift in their use of the environment. Many other species of *Sceloporus* use trees, logs, and other plants for preferred cover, but are not restricted to them. For example, *S. formosus, S. melanorhinus, S. olivaceus* (all tree users), and *S. spinosus* (a rock-tree-*Yucca* user) will all shimmy bury in sand almost as readily as will *S. magister* collected from sand dunes (Hall, 1973). In addition, two of the species of the *S. orcutti* complex (*S. orcutti* and *S. hunsakeri*) are petricolous and use rock crevices while the other species of the complex (*S. licki*) is arboreal (Hall and Smith, 1979), but also uses rock crevices (Alvarez et al., 1988). The available evidence suggested to Hall that the shift to crevice using and the concomitant loss of the shimmy burial behavior had evolved only once in *Sceloporus,* and these traits diagnosed the clade of crevice users depicted in figure 26.

Within the framework of his crevice-user radiation hypothesis, Hall then proposed an early split into the rock- versus plant-crevice-using radiations to explain the pronounced morphological differences between these groups. *Sceloporus megalepidurus* and *S. pictus* utilize the complex crevice systems between the leaves of *Agave* and *Yucca* plants. They exhibit mainly behavioral adaptations to these microhabitats, and generally escape by moving away from a potential predator through the complex system of spaces. Their scales are intermediate in size between those of the *grammicus* and *torquatus* groups, and are comparatively smooth for a large-scaled *Sceloporus.* Smooth scales presumably facilitate passage through the crevice matrix, and *megalepidurus* group species are usually cryptically striped in dorsal color. However, keels and other aspects of scale structure improve locomotion in tight places and defend against extraction by predators (Cole and Van Devender, 1976), especially after the body is inflated (see below).

Species of the *grammicus* group often will wedge themselves into a rock or wood crevice when being pursued, and their generally smaller, almost granular scales allow them to work their way out of a crevice when a threat has passed. Most *grammicus* group species have dorsal patterns of undulating bars, which are cryptic against bark.

Species of the *torquatus* group use rough-textured rock crevices that are completely rigid to their natural predators. Typical escape behavior involves a lizard wedging itself into a crevice head-first, facing away from a predator, and then arching its back and inflating its body to set the stiff spines of the larger scales against the rock surface. When the threat passes, the lizard deflates and easily extricates itself. Most species of this group are often large-bodied, and possess large keeled scales, and most live in open habitats where they can see potential predators approaching in time to reach a nearby crevice for cover.

As a final note, Hall (1973) pointed out that virtually nothing is known of the behavioral ecology of *S. asper* except that all specimens seem to have been taken on live trees. On the basis of subjective comparisons, Hall suggested that this species might be morphologically intermediate between the *megalepidurus–grammicus-torquatus* crevice users, and the other large-bodied, large-scaled *Sceloporus.* Phenetically, *S. asper* appeared closest to *S. heterolepis* among the crevice users examined by Larsen (1973) and Tanner and Larsen (1974, 1975), and possibly represents a comparatively ecologically unspecialized, early derivative of the ancestor from which the more specialized crevice users (the *grammicus, megalepidurus,* and *torquatus* groups) later evolved.

Hall's proposals are of great heuristic value, but require two additional qualifications. Firstly, he based some of his hypotheses on *microchromosome* morphologies, which are difficult to study at the level of resolution afforded by conventional light microscopy. Electron microscopic scanning of surface-spread synaptonemal complexes offers additional resolution (Reed et al., 1990), but even at this level, arm homologies within and between species can only be tentatively assigned. Secondly, Hall's suggestion that the Em-9 mutation (assuming that the above-discussed homology problems can be resolved), as a *polymorphism,* diagnoses the entire crevice-user radiation, contradicts a philosophical position adopted by some cladists: character state *transformations* only (the complete substitution of one state for another) contain a phylogenetic signal distinct from polymorphisms of only tokogenetic utility (Nixon and Wheeler, 1990). We do not argue that polymorphic characters lack phylogenetic information (see Swofford and Berlocher, 1987), but point out that a number of unresolved questions have recently been raised with regard to how much phylogenetic information is present in such characters, and what sampling protocol(s) is (are) necessary to recover it (Crother, 1990).

Other studies. One early molecular study of a small part of *Sceloporus* was carried out by Wyles and Gorman (1978) and is discussed in detail below. The unpublished Ph.D. dissertation of Wyles (1980) also includes immunological and allozyme comparisons of selected species of *Sceloporus,* chosen to represent many of the species groups recognized by Smith (1939), relative to all of the sceloporine (= phrynosomatid) genera. Wyles' comparisons were based on distance estimates, and he suggested that some species groups of *Sceloporus* were more closely related to some sceloporine genera than they were to other species groups of *Sceloporus.* He viewed *Sceloporus* as part of an "evolutionary grade" that he did not clearly define, but suggested a possible polyphyletic origin for the genus. He recommended including *Sceloporus* and all of the "close in" (as measured by allozyme and immunological distances) sceloporine genera (*Petrosaurus, Sator, Streptosaurus, Urosaurus,* and *Uta*) together in a single genus, and then defining monophyletic subgenera after additional study.

A third phylogenetically oriented molecular study is available from the work of Mindell et al. (1989). These workers resolved enzyme products from 23 variable protein loci for 19 species of *Sceloporus,* and analyzed 69 phylogenetically informative allozyme characters by parsimony methods. Of the taxa surveyed, *S. merriami* was designated as the outgroup, to which all other species were rooted. Of the 18 ingroup taxa, four represented three groups within the small-bodied, small-scaled radiation, including: (1) *S. cozumelae* and *S. variabilis* of the *variabilis* group; (2) *S. chrysostictus*; and (3) *S. siniferus.* The remaining 14 ingroup species represented four species groups, including: (1) *S. clarki*; (2) *S. grammicus* (S race); (3) *S. occidentalis, S. olivaceus, S. spinosus, S. undulatus,* and *S. virgatus* (*horridus* group); and (4) *S. cyanogenys, S. dugesii, S. jarrovi, S. mucronatus, S. poinsetti, S. serrifer,* and *S. torquatus* (*torquatus* group). Numerical parsimony analysis with the PAUP program produced three equally parsimonious cladograms for these groups, but all had several features in common. First, all of the *torquatus* group species *except S. serrifer* consistently formed a well-supported clade (supported by from 4 to 6 character changes on the basal branch), with *S. grammicus* consistently forming the sister group of the *torquatus* clade. With the noted exception of *S. serrifer,* the crevice-user group identified by the allozyme matrix supported the expectations of Hall's hypothesis. *Sceloporus serrifer* consistently grouped with the five *horridus* group species, which was itself deeply divided into a strongly supported *occidentalis–undulatus–virgatus* clade (based on 10–12 state changes at the basal branch) and a weakly supported *olivaceus–serrifer–spinosus* group (3–4 state changes on the basal branch). The entire clade forms a sister group of the crevice users. Three of the four small-bodied, small-scaled species consistently form an extremely well-supported clade (*chrysostictus–cozumelae–variabilis*), while *S. siniferus* is the sister group of this trio, and *S. clarki* is the sister taxon of all of these. The position of *S. clarki* does not support Hall's proposal, that *S. clarki* should be the sister group of the crevice-user clade. Because of small sample sizes for both the species surveyed and the number of loci resolved, results from this analysis must be considered tentative, but the study does suggest that there is a great deal of potentially very informative biochemical/molecular information yet to be explored in this group.

One other study currently in press (Wiens, 1993) deserves comment because it represents a cladistic evaluation of the most extensive character set available for the eight phrynosomatid genera. Wiens defined unambiguous states for a total of 45 characters representing osteological, squamation, soft anatomy, coloration, chromosome 2n number, and behavioral data sets. A parsimony analysis of these data revealed support for a "*Sceloporus* group" with a topology of [*Uta* + [*Urosaurus* + [*Sator* + [*Sceloporus merriami* + all other *Sceloporus*]]]]. One synapomorphy supported monophyly for a *Sator* + *Sceloporus* clade (interruption or loss of the gular fold); a second supported monophyly of the *S. merriami* + all other *Sceloporus* clade (reduction from 6 to 4 postrostral scales); and a third supported monophyly for all remaining *Sceloporus* (dorsal scales pointed and overlapping). *Sceloporus utiformis* appears to be more closely related to the *siniferus* group than to the genus *Sator.* Note that this topology is in marked contrast to, and provides an explicit alternative to, all other hypotheses described above.

DISCUSSION

The above review outlines the basic phylogenetic hypotheses formulated for the genus *Sceloporus*. It summarizes the available morphological, chromosomal, and isozyme data, and highlights many of the major unresolved systematic issues. However, we wish to emphasize the value of this genus as a research resource for addressing many basic issues in ecology and evolutionary biology. Among the more obvious issues in need of serious investigation, we suggest that study of *Sceloporus* would be of value in at least the following areas: (1) historical biogeography; (2) the evolution of viviparity; (3) the evolution of heteromorphic sex chromosomes; (4) speciation/hybridization issues; (5) social behavioral and sexual selection; (6) ecology and the evolution of life history strategies; and (7) other issues. Because some of the issues of historical biogeography complement previously discussed phylogenetic hypotheses, these will be treated first, and the remaining topics reviewed in the order presented above.

I. HISTORICAL BIOGEOGRAPHY

The genus *Sceloporus* was hypothesized to constitute part of the Young Northern Element of the New World herpetofauna defined by Savage (1982), and if true, postdates many important tectonic events. Savage (1982: 522, fig. 22) did note the disjunct montane distribution of some elements of the *formosus* group, and suggested that this pattern may record vicariant events associated with recent orogenies, but in general the relatively recent origin inferred for most groups makes them less than optimal for retrieving "deep history" vicariant events that greatly influenced the evolutionary histories of many other groups. However, an alternative possibility was presented by Frost and Etheridge (1989) in which the phylogenetic arrangement [Crotaphytidae + [Phrynosomatidae + [Tropiduridae + [Opluridae]]]] (fig. 15, topology 1; p. 28 of that paper) gives an area cladogram of [North America + [North America + [South America + [Madagascar]]]]. If this is the real history, it suggests an origin in the Cretaceous, or possibly earlier, for the Phrynosomatidae. This alone does not reveal the age of the genus *Sceloporus*, but implies that it *could* have predated the origin inferred by Savage. Regardless, some species and groups are confined to small geographic areas and/or specific habitats, and do offer the potential for historical biogeographic analysis (Smith, 1941; Flores-Villela, 1992). Explicit biogeographic hypotheses have been advanced by Hall (1973: 114–127) and Murphy (1983a, 1983b), and are testable by phylogenetic methods. We discussed the Larsen and Tanner hypotheses above and do not treat them further here, but both the Hall and Murphy hypotheses are diagrammatically illustrated in figure 34, and since Hall's scenario is broader in taxonomic scope, it will be treated first.

With respect to Hall's phylogenetic interpretation of the large-sized, large-scaled radiation (fig. 26), those with the presumed symplesiomorphic 2n = 34 XY♂ karyotype include the three *orcutti* group species, and *S. nelsoni* and *S. pyrocephalus*. The *orcutti* group is essentially confined to the Baja California Peninsula (fig. 22), where *S. orcutti* and *S. hunsakeri* are rock dwellers in comparatively xeric habitats, while *S. licki* is a tree and rock dweller confined to the relictual oak-conifer woodland of the Cape Region. *Sceloporus nelsoni* and *S. pyrocephalus* were postulated by Hall (1973) to be the closest mainland relatives of the *orcutti* group, although the unresolved polytomy he presented (fig. 26) provides for alternative relationships (i.e., *S. nelsoni* and *S. pyrocephalus* are not depicted as the sister group of the *orcutti* group). Both of these species are largely rock or ground dwellers, with *S. nelsoni* confined to xeric thorn scrub habitats, and *S. pyrocephalus* inhabiting moderately open areas of the generally more mesic tropical deciduous forest. These two species are distributed in a narrow north-south belt in western Mexico, and appear to be separated by the lower reaches of the Rio Grande de Santiago, which drains the Lago Chapala–Rio Lerma system (fig. 22). Biogeographically, this interpretation places the chromosomally most primitive species (species of the *orcutti* group, *S.*

nelsoni, and *S. pyrocephalus* all retain the postulated plesiomorphic karyotype, with the exception of a pair 1 pericentric inversion in *S. pyrocephalus*) of the large-bodied, large-scaled radiation around the periphery of the hottest parts of the Colorado-Sonoran Desert, mostly north of the Rio Grande de Santiago (fig. 34).

Murphy (1983a) provided electrophoretic evidence in support of Hall's recognition of a monophyletic *orcutti* complex, and identified this group as part of a more inclusive Transpeninsular Xerophilic Species Track on the Baja Peninsula. Murphy further hypothesized that, on the basis of electrophoretic similarities, *S. hunsakeri* and *S. licki* were sister species relative to *S. orcutti,* and that the ancestor of this pair had diverged in isolation from *S. orcutti* south of the Isthmus of La Paz after the Cape Region had rafted to and joined with the Baja Peninsula (see biogeographic details in Murphy, 1983a: fig. 8; tectonic data in Larson et al., 1968; and Atwater, 1970). A cladistic analysis supporting these hypotheses is predicted to show that the *orcutti* group is monophyletic, with *S. hunsakeri* and *S. licki* being sister taxa, and that the *orcutti* group is the sister group of the *S. nelsoni–S. pyrocephalus* clade.

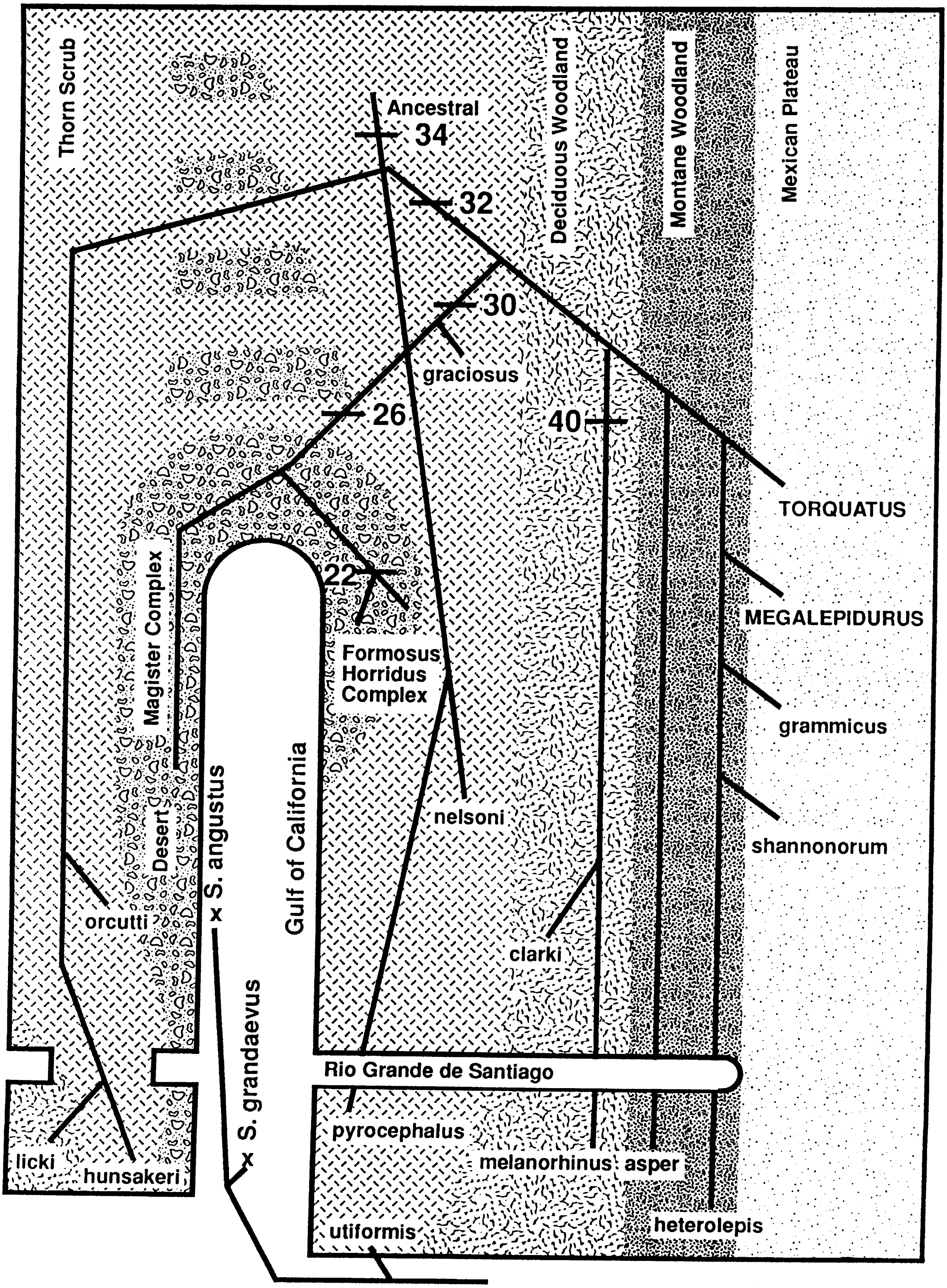
Note that the above relationships are not predicted from karyotypic data; these species form an unresolved polytomy on this basis (fig. 26). Chromosomal data, however, do suggest the next sequence of speciation events within this radiation, and these data in part form the basis of the biogeographic hypotheses of Hall. The "loss" of a single microchromosome pair is hypothesized to be a synapomorphic character transformation (the $2n = 32$, 10MM,2SMM,18m,XY♂ karyotype) corresponding with divergence of the remaining large-bodied, large-scaled radiation from a common ancestor with the *orcutti–nelsoni–pyrocephalus* polytomy. This was presumably followed by further reductions in the number of microchromosomes to derive *S. graciosus* ($2n = 30$), and additional microchromosomal reductions to derive the *magister* group ($2n = 26$) and the $2n = 22$ radiations (fig. 26). This chromosomal sequence was hypothesized by Hall (1973) to be biogeographically plausible on the basis of present ranges of *S. graciosus* and the *magister* group (figs. 21, 24, 27), and the $2n = 22$ radiations are hypothesized to have undergone extensive speciation either in the mountains of western Mexico and/or on the Mexican Plateau. The ancestral $2n = 22$ radiation is hypothesized to have diverged into one group retaining the ancestral oviparous reproductive mode (Hall's *horridus* group, with a generally more northern distribution), and a second supported by the independent origin of a viviparous reproductive mode (Hall's *formosus* group, with a generally southern distribution—note that Hall did not specify any derived characters diagnostic of this group). As previously discussed, neither the phylogenetic nor biogeographic details of these radiations are well understood, but if Hall's groups are shown to be monophyletic then, as we describe below, his biogeographic scenario makes refined predictions about phylogenetic relationships of the groups depicted in unresolved polytomies in figure 26.

Murphy (1983a) identified the *magister* complex as part of a Transpeninsular Mesophilic Track, and suggested that the proto-*magister* stock was one of several "waves" of desert forms that invaded the Baja Peninsula from the northeast. Specifically, dispersal was postulated from a Sonoran refugium via "turning the corner" around the head of the Sea of Cortez (1983a: 12, fig. 5E), and speciation then proceeding from north to south as this lineage colonized the peninsula. Murphy proposed a $2n = 30$ karyotype as derived, but in Hall's scheme this is ancestral to the $2n = 26$ and $2n = 22$ karyotypes (fig. 26). Murphy (1983a: 32) stated that the karyotypes of *S. monserratensis, S. rufidorsum,* and *S. zosteromus* are $2n = 30$, but we can only find evidence for this karyotype in *S. zosteromus* in Hall's thesis and manuscripts, and in *S. rufidorsum,* the karyotype of which is presented here (fig. 14; table 4). We have therefore listed *S. monserratensis* and *S. lineatulus* as unknowns in table 4. We note that Murphy's general interpretation is consistent with both Hall's overall placement of the *magister* group in the chromosomal phylogeny, and with his interpretation of the general sequence of speciation events in western Mexico (fig. 34). That is, the *magister* group is predicted to have a sister-group relationship to both of the $2n = 22$ species groups (i.e., the *formosus* and *horridus* groups, which are postulated to be sister groups of each other), and these three groups are then predicted to form a sister clade of *S. graciosus* (figs. 26, 34). Detailed karyotypic data are needed for all species in the *magister* group, because the sequence of speciation events, which is predicted to be from north to south on the basis of Murphy's (1983a, 1983b) biogeographic evidence, is incompatible with the limited chromosomal data base. Distributional data suggest that *S. zosteromus,* currently confined to the Cape Region of the Peninsula (fig. 24), is presumably the most recently derived species in the sequence (fig. 26), but it retains the 2n = 30 karyotype hypothesized to be ancestral to the 2n = 26 karyotype of *S. magister* (fig. 26).

The next sequence of events proposed for further derivations within the large-bodied, large-scaled radiation involved the origin of the Em-9 mutation, which is hypothesized to diagnose the *clarki* group plus the crevice-user radiation, and then fissioning of macrochromosome pairs 1 and 3–5 to derive the two *clarki* group species (fig. 26). Hall noted that the distributions of these two species are approximately parallel, but are more extensive than those of the *S. nelsoni–S. pyrocephalus* pair (compare ranges depicted in figs. 20 and 22). *Sceloporus clarki* occurs north of the Rio Grande de Santiago in generally xeric habitats, while the chromosomally more derived *S. melanorhinus,* possessing an autapomorphic X_1X_2Y sex chromosome heteromorphism (fig. 18E), is restricted to more mesic habitats south of this river (fig. 20).

Hall then hypothesized another synapomorphy—the origin of another unique X_1X_2Y sex chromosome system—to diagnose the crevice-user radiation (the *asper, grammicus, megalepidurus,* and *torquatus* groups; fig. 26). He postulated that the derivation of this radiation was associated with ecological shifts to plant and rock crevices and the colonization of woodland and Plateau habitats at higher elevations east of the presumed ancestral habitats (fig. 34). *Sceloporus asper,* previously suggested by Hall as possibly the earliest derivative of the crevice-user radiation, occurs at intermediate elevations (1000–2000 m) in the valley of the Rio Grande de Santiago and in the western sections of the transverse volcanic range (fig. 20). Hall hypothesized that the two *megalepidurus* group species were early derivatives of the radiation leading to the *grammicus* group, on the basis of unspecified morphological considerations (1973: 116–117). These species are found in xeric basins at the eastern end of the transverse volcanic range (fig. 20). *Sceloporus shannonorum* and *S. heterolepis* were considered to be well-differentiated species (contra Webb, 1969), but both more closely related to the "standard" (2n = 32♀/31♂) *S. grammicus* chromosome race than to either of the *megalepidurus* group species. The distributions of *S. shannonorum* and *S. heterolepis* parallel the *S. nelsoni–S. pyrocephalus* and the *S. clarki–S. melanorhinus* species pairs in apparently being separated by the Rio Grande de Santiago and/or its major tributaries, the Rios de Huaynamota and Bolaños (fig. 32). Hall further hypothesized that, as in the other two species pairs, the southernmost species *S. heterolepis,* was the more recently derived of the two. This species possesses very conspicuous rows of enlarged paravertebral scales, an extreme state of a feature unique to the *grammicus* group. South of the Rio Grande de Santiago and its tributaries, *S. heterolepis* appears to be found in pine or pine-oak forests above 2000 m, while north of this barrier *S. shannonorum* is restricted to intermediate elevations (1500–2000 m) in oak or pine-oak forests. The northern "standard" populations of *S. grammicus* are probably parapatric with *S. shannonorum* along the crest of the Sierra Madre Occidental (fig. 32), but *S. grammicus* generally occurs at higher elevations and usually on the east-facing slopes. Hall suggested a close relationship between *S. shannonorum* and the S chromosome race (northwestern populations) of *S. grammicus,* and that divergence between the two may have been precipitated by separation on either side of the Sierra Madre Occidental during the coldest Pleistocene periods.

Because species constituting the rock-crevice using *torquatus* group are so well-differentiated from other large-bodied, large-scaled *Sceloporus,* and all have apparently identical karyotypes (table 4), Hall could not infer which member of this group might be the earliest derivative within the group. He sug-


Thorn Scrub
Deciduous Woodland
Montane Woodland
Mexican Plateau
Ancestral
34
32
30
graciosus
26
40
22
TORQUATUS
MEGALEPIDURUS
grammicus
shannonorum
Magister Complex
Formosus Horridus Complex
nelsoni
Gulf of California
S. angustus
Desert
orcutti
clarki
Rio Grande de Santiago
S. grandaevus
pyrocephalus
melanorhinus
asper
heterolepis
utiformis
licki
hunsakeri

gested that *S. jarrovi,* mainly a species of the Mexican Plateau and its flanking mountain ranges (fig. 33), might fit this category, based primarily on its "comparatively primitive" (i.e., basal position in a branching tree) position in Larsen's (1973) numerical phenetic analysis. This hypothesis is in distinct contrast to that of Larsen and Tanner (1975), who proposed the origin of this group in the Gulf Coastal Plain, followed by a post-Pleistocene expansion. Largely for previously discussed ecological reasons, Hall suggested that the *torquatus* radiation diverged into a rock-crevice-using radiation separate from the plant-crevice-using *grammicus–megalepidurus* groups. Hall implied, however, that the common ancestor of all of these groups was a crevice dweller. If true, then the rock- and plant-crevice groups might not be separate, but one radiation within the other, an hypothesis contradicted by Hall's interpretation of the Em-9 character. In contrast to the unresolved chromosomal polytomy for the four crevice-user groups depicted in figure 26, the ecological/biogeographic hypothesis together with the Em-9 character predict a cladistic hypothesis in which the *grammicus* and *megalepidurus* groups are sister groups composing a plant crevice-users clade, which is the sister group to the rock-crevice user *torquatus* group, and these radiations collectively have a sister-group relationship with *S. asper* (fig. 34).

In figure 34, we have tried to summarize all of Hall's biogeographic interpretations, as described above, in light of the chromosomally based hypotheses for the large-bodied, large-scaled radiation depicted in figure 26. Hall's synthesis is based on the predominantly linear ranges along the west coast of Mexico and/or the Baja Peninsula, of most of the groups considered above. These generally follow five major vegetation zones as these are determined by elevation, temperature, soil, and humidity, including: (1) hot desert, generally with a sand/bare rock substrate, no trees, and scattered thorn bushes; (2) thorn scrub, with an adobe/rocky soil substrate, scattered thorn bushes, succulent xerophytes, and trees along drainages; (3) xeric woodland, with generally deeper and more friable soil, ranging from oak woodland with juniper and *Agave* in the north to thorn forest and tropical deciduous forest in the south; (4) cool montane forest, with oak and mixed conifer; and (5) xeric plateau, with few or no trees, scattered bushes and grass, much exposed rock, less equable and cooler climates. On the basis of the chromosomal phylogenetic hypothesis and present distributions, Hall proposed that early divergences in the large-bodied, large-scaled radiation were restricted to the western coastal slopes of mainland Mexico north of the present Rio Grande de Santiago, and involved ecological shifts outward from the thorn scrub community. As depicted in figure 34, many of the earliest speciation events likely involved ecological shifts from ground/rock-dwelling to thorn scrub to woodland/arboreal habitat use. Some of these speciation events were associated with, or in Hall's views (1973, 1977, 1980, 1983) causally related to, chromosomal rearrangements that diagnosed subsequent lines of descent.

As speciation events and concomitant ecological shifts promoted movement of incipient lineages to higher elevations, ancestral

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Fig. 34. Diagrammatic representation of southwestern North America, emphasizing western mainland Mexico, the Gulf of California (Sea of Cortez), and the Baja Peninsula. Exaggerated constriction near the southern end of the Peninsula represents the Isthmus of La Paz, which separates the Cape Region from the main Peninsula. Generalized distributions of vegetation zones from the west coast of mainland Mexico eastward to the Mexican Plateau are based on elevation, temperature, moisture, and soils. The extensive cladogram superimposed over most of the figure represents Hall's (1973, 1977) interpretations of the sequence of speciation events defining major clades within the large-bodied, large-scaled *Sceloporus.* Events defined by presumed chromosomal synapomorphies are shown with horizontal bars with diploid chromosome numbers, simplified from figure 26, while other sequences are defined by morphological, behavioral, ecological, and/or distributional evidence (see text). The *Sator angustus–S. grandaevus–utiformis* clade represents the phylogenetic hypothesis for this group based on the trans-gulfian vicariance model described by Murphy (1983a).

crevice users presumably adjusted to these vegetation zones, and in so doing became susceptible to geographic isolation and additional speciation on or between different mountain ranges (i.e., those divided by the Rio Grande de Santiago). Subsequent secondary contact and sympatry during climatic optima could have led to size and/or ecological displacement within the broad range of crevice-using niches. Further, breaching the crest of the Sierra Madre Occidental from the western slopes would have opened the Mexican Plateau and its associated highlands to subsequent speciation within the crevice-using and 2n = 22 radiations.

Hall's phylogenetic and biogeographic reconstructions are not the only histories that could account for the present-day geographic relationships of the various chromosomal lineages in the radiations depicted in figure 34, but his interpretations require fewer longitudinal shifts and/or long-distance dispersal events than do distributions based on the phylogenetic hypotheses of Smith (1939) or Larsen (1973). Further, a modification of Murphy's (1983a) hypothesis for relationships within the *magister* group can be accommodated within Hall's proposals.

We note that Hall's scenario provides a basis for developing and testing rigorous biogeographic hypotheses (e.g., Platnick and Nelson, 1978). One approach (Rosen, 1978; Nelson and Platnick, 1981) requires the construction of independent taxon cladograms for three or more taxa, the conversion of these to area cladograms, and a search for congruence among the latter. The western slopes of the Sierra Madre Occidental and the adjoining Pacific lowlands constitute one of three areas of Mexico in which reptilian endemism is high, and the endemic component is well represented by phrynosomatid lizards (Flores-Villela, 1992). Hall's proposal can be used to independently formulate three-taxon statements and three-area cladograms for the Baja endemic *S. orcutti* and the west coast endemics *S. nelsoni* and *S. pyrocephalus*, and Baja endemics in the *S. magister* complex relative to the west coast *S. clarki* and *S. melanorhinus* pair. These groups were not proposed independently of the historical biogeographic hypothesis under consideration, but by incorporating other groups of organisms, the hypothesis becomes amenable to some form of quantitative biogeographic parsimony analysis (Brooks, 1985; Wiley, 1987, 1988; Kluge, 1988; Mayden, 1988; Page, 1988; see also Cracraft and Prum, 1988; Brooks, 1990). This approach is not without limitations (see discussions by Cracraft, 1988; Kluge, 1988; Noonan, 1988), but it has proven useful for many groups.

Another explicit biogeographic hypothesis depicted in figure 34 was clearly elaborated by Murphy (1983a, 1983b) with regard to the *Sceloporus utiformis–Sator* group within the small-bodied, small-scaled radiation. This is the Transgulfian Vicariance hypothesis (see also Murphy, 1975; Seib, 1980) advanced to explain the island distributions of both species of *Sator,* and their previously proposed close morphological relationship to *S. utiformis.* Specifically, the islands occupied by the two species of *Sator* (refer to fig. 34) are old islands that, on the basis of independent geological evidence (reviewed by Murphy, 1983a, 1983b), appear to be derived from part of the Mexican mainland, and they harbor other taxa (one species of *Leptotyphlops,* Murphy, 1975) whose closest relatives appear to be restricted to the lowlands of western Mexico. Thus, the two species of *Sator* are predicted to be sister species in a cladistic analysis, and the *Sator* clade should then be the sister taxon of *Sceloporus utiformis.*

In figure 35 we present an alternative hypothesis for the phylogeny and biogeography of the genus *Sceloporus,* modified from figure 34. This hypothesis is consistent with the chromosomal data for the genus and the biogeography of western North America, and assumes that the ancestor of *Sceloporus* originated in western Mexico before the geological drift of Baja California and the Cape Region toward the northwest, as proposed by Robinson (1973) for certain lizards of the teiid *Cnemidophorus deppei* group. Indeed, this geological drift could have been a major vicariant event for the divergence of the *graciosus, formosus–horridus, magister, orcutti,* and *zosteromus* groups in isolation from other ancestral groups of *Sceloporus* on the mainland of western Mexico (fig. 35). This is also consistent with the observed reduction in diploid chromosome number from south to north on the Baja California Peninsula, hypothesized to represent the ancestral to derived states, respectively.

Other vicariant hypotheses are possible but have not been explicitly developed. For example, several species representing a number of different species groups have relatively small distributions in the southwestern U.S. and/or arid parts of the northern part of the Mexican Plateau, suggesting that these species may be relicts of a more widespread lizard fauna that contracted and differentiated in response to increasing aridity. These species include *S. cautus* and *S. virgatus* (*horridus* group), *S. lineolateralis, S. ornatus,* and *S. cyanogenys* (*torquatus* group), and *S. couchii, S. maculosus,* and *S. merriami.* Species restricted to higher elevations along the transverse volcanic belt and/or the Sierra Madre del Sur in central and southern Mexico, including some members of the *formosus, grammicus, jalapae, megalepidurus,* and *scalaris* groups, may have speciated in association with recent orogenic activities and/or Pleistocene climatic events (Flores-Villela, 1992). These and additional historical biogeographic hypotheses may become apparent once strongly supported cladograms are available for all monophyletic groups.

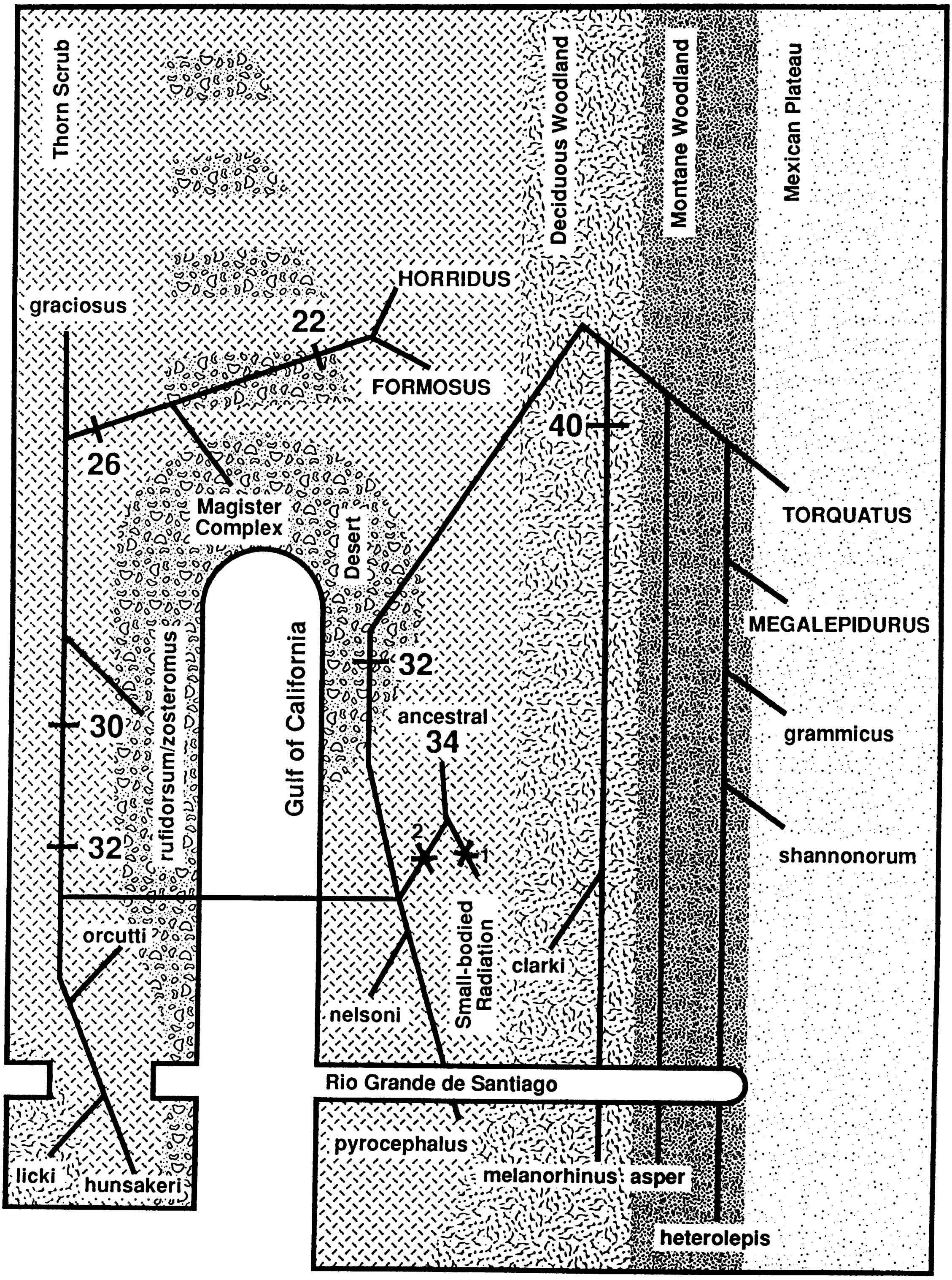
II. EVOLUTION OF VIVIPARITY

A number of recent reviews of viviparity in reptiles suggest that, based on the number of independent origins of this mode in squamates, it may be relatively "easy" in an evolutionary context to become viviparous (Blackburn, 1982; Shine, 1983a, 1983b, 1985; Shine and Bull, 1979). However, these authors emphasize that analysis of the process(es) and/or mechanism(s) for the evolution of viviparity in squamate reptiles is difficult, and like most studies of evolutionary mechanisms, relies on inferences made from indirect studies of assumptions of various models based on groups with well-corroborated phylogenies (Shine, 1983a). Shine (1985) reviewed several hypotheses advanced to explain the origin of viviparity, and suggested that its derivation from oviparity was almost certainly gradual. That is, intermediate or transitional stages are likely required based on the known anatomical/physiological differences between closely related oviparous and viviparous species, which in turn requires advantages for the transitional states so that natural selection can drive the process (Shine, 1985: 615–616, 624).

Shine (1985) conducted a phylogenetic survey of the distribution of viviparity in squamate reptiles, and concluded that it probably evolved independently between four and six times within the genus *Sceloporus.* These conclusions were derived by overlaying the distribution of viviparity on the phylogenies advanced by Smith (1939) and Smith and Taylor (1950). The upper number of Shine's estimate, six independent origins for viviparity in *Sceloporus,* was obtained by suggesting that this mode may have independently evolved two or three times in the *scalaris* group alone (once in *S. goldmani,* and perhaps twice in *S. aeneus*).

Shine's (1985) analysis extended an earlier study by Guillette et al. (1980) that provided a detailed investigation of *Sceloporus* alone. Guillette et al. (1980) noted that at least 28 of the 68+ species are viviparous, and statistically evaluated the environmental, geographic, phylogenetic, and life-history correlates of viviparity and oviparity. Smith's (1939) phylogenetic hypothesis was chosen to correlate parity types primarily because he did not use parity mode as a phylogenetic character. This study showed significant environmental correlates with viviparity (i.e., a greater number of montane than lowland species were viviparous), and that viviparity is completely correlated (i.e., fixed) in all species groups of *Sceloporus* where it occurs (the *asper, formosus, grammicus,* and *torquatus* groups) excepting the *scalaris* group. Guillette et al. concluded (1980: 211) that "phylogenetic relationships do not fully account for significant environmental correlations with mode of reproduction." A limitation to this conclusion is that, for all abovementioned species groups with fixed viviparity, the individual species do not represent independent sampling units in any statistical analysis (Felsenstein, 1985).

The alternative phylogenetic hypotheses discussed in this review differ significantly from the original Smith (1939) proposal, but regardless of which is closer to the real history of the genus, the conclusion is inescapable that viviparity has had multiple origins with-


Thorn Scrub
Deciduous Woodland
Montane Woodland
Mexican Plateau
graciosus
HORRIDUS
22
FORMOSUS
26
40
Magister Complex
Desert
TORQUATUS
MEGALEPIDURUS
32
Gulf of California
rufidorsum/zosteromus
30
ancestral
34
grammicus
2
1
32
shannonorum
Small-bodied Radiation
clarki
orcutti
nelsoni
Rio Grande de Santiago
pyrocephalus
melanorhinus
asper
licki
hunsakeri
heterolepis

in *Sceloporus*. In this context, both the large-bodied and small-bodied radiations (if both are monophyletic groups) pose some interesting problems regarding the evolution of viviparity. For example, if we accept Hall's scenario for the large-bodied, large-scaled radiation, as depicted in figure 26, we would conclude that the viviparous mode evolved once in the tropical montane 2n = 22 *formosus* group, and independently in the crevice-user radiation after its divergence from a common ancestor with the *clarki* group. The distribution of reproductive parity types within the crevice users is as follows: all species in the *asper, grammicus,* and *torquatus* groups are viviparous, while *S. megalepidurus* is *oviparous* (table 1, Guillette et al., 1980). On the basis of chromosomal characters, the four groups constitute an unresolved polytomy in figure 26 (provided that the Em-9 loss/fixation is ignored) and little independent evidence has been presented upon which to assess their relationships. If the *megalepidurus* group is basal to the other three, then viviparity would be parsimoniously interpreted as a synapomorphic trait uniting the *asper, grammicus,* and *torquatus* groups. However, any other arrangement, such as the biogeographic hypothesis just discussed above, would place the *megalepidurus* group internal to this node, and allow for the possibility that *S. megalepidurus* (the reproductive mode of *S. pictus* is unknown) had reverted back to oviparity. It is also possible, of course, that even if *S. megalepidurus* was internally placed in a monophyletic crevice-user group, it might still retain the plesiomorphic parity mode, while viviparity could have evolved independently in the other groups. However, given earlier assertions that viviparity is irreversible once it has evolved (Packard et al., 1977; Tinkle and Gibbons, 1977), the possibility of a reversal in *S. megalepidurus* would be an extremely interesting result.

A second fruitful line of inquiry is offered by the small-bodied, small-scaled radiation with respect to the phylogenetic position of, and relationships within, the *scalaris* group (fig. 4B). This is the one group for which both parity modes are well documented (Guillette et al., 1980), and if it can be confirmed as monophyletic, meets a major requirement necessary (alternative parity types existing in closely related species) for evaluating selective forces actually driving the transition from oviparous to viviparous modes (Shine, 1985: 672). The *S. aeneus–bicanthalis* complex has been especially well studied by Guillette (1981, 1982; see also Guillette and Lara, 1986), and offers great potential because the system either represents a single species polymorphic for both parity modes (Thomas and Dixon, 1976), or perhaps two distinct species that are extremely closely related (Davis and Smith, 1953; Guillette and Smith, 1985). Guillette (1981) showed that *S. a. aeneus* was oviparous but displayed prolonged egg retention; most females held eggs in the oviducts until embryos were developed to stages 28–30, and after deposition, embryos develop through stages 30–35, and normally hatch at stage 36. Populations of *S. a. bicanthalis* collected from different mountains, but at similar elevations (3200–3600 m) were similar in body weight, snout-vent length, and clutch size, but were viviparous. Embryos were retained in the body through stage 35, and born at stage 36. These results confirmed the suggestion advanced by Packard et al. (1977) that if egg retention is an intermediate step to viviparity, both modes should occur in geographic proximity. Though collected from separate volcanic peaks, both populations sampled by Guillette (1981) were adjacent to the Valley of Mexico and in close proximity

←

Fig. 35. Our preferred phylogenetic and biogeographic scenario, alternative to that presented in figure 34. Modifications are as follows: (1) X_1, hypothesized synapomorphies for major small-scaled, small-bodied clade of *Sceloporus*, X_2, same for large-scaled, large-bodied clade; (2) consistent with morphology, *S. nelsoni* and *S. pyrocephalus* share a lineage separate from that of *S. orcutti,* instead of a trichotomy; (3) the lineage of *S. orcutti* had a transgulfian vicariant origin; (4) consistent with biogeography, the apparent loss of one pair of microchromosomes occurred independently in the *asper-clarki* lineage and the *formosus-zosteromus* lineage; and (5) *S. rudiforsum* is associated with *S. zosteromus* rather than with *S. magister,* based on new chromosome data (table 4).

to each other. In a followup study, Guillette (1982) showed that the longer egg retention in *S. a. aeneus* was accompanied by increased vascularity of the oviduct and embryonic membranes, which is expected if this is a transitional stage in the evolution of viviparity because longer egg retention may pose gas exchange problems. The detailed documentation of the reproductive cycles in these two populations (Guillette, 1981, 1982) has contributed to the development of more refined models of the endocrinological and physiological shifts predicted to accompany the evolution of viviparity in high-elevation squamates (Guillette, 1985). A recent model by Shine and Guillette (1988), for example, combines both proximate (physiological) and ultimate (evolutionary) processes and suggests that: (1) the duration of egg retention is controlled by circulating levels of progesterone; and (2) progesterone is secreted by adrenals in response to environmental cues, with increased stress inducing greater progesterone secretion, which in turn prolongs egg retention. If this is a realistic mechanism, it could constitute a large phenotypic component of variance in egg retention in a natural population, which would in turn accelerate the rate of change in egg retention inducible by selection. One prediction of this model is that endocrinological comparisons of phylogenetically closely related oviparous and viviparous species should reveal differences in rates or durations of progesterone secretion by corpora lutea and/or adrenals, or the extent of oviductal contractions induced by progesterone. Other predictions, both ecological and physiological, are provided by Shine and Guillette (1988: 48–49), and make a compelling case for a thorough phylogenetic study of the entire *scalaris* group, including all isolated populations scattered across the transverse volcanic range in central Mexico.

III. EVOLUTION OF HETEROMORPHIC SEX CHROMOSOMES

Most of the different sex chromosome systems within *Sceloporus* have been discussed above. Since some of these systems have been interpreted as synapomorphic states diagnostic of monophyletic groups, there is some circularity in discussing possible multiple origins of these systems in the absence of strong independent phylogenetic support. This is also a conservative interpretation, however, in that it minimizes the apparent amount of evolution of sex chromosomes, and unless the true phylogeny of *Sceloporus* is very different from any of the proposed hypotheses, multiple origins for sex chromosomes within the genus is an inescapable conclusion. We therefore point out some of the more interesting and unresolved questions regarding the evolution of sex chromosome heteromorphisms, and why these would repay further study in *Sceloporus.*

The term sex chromosome implies that the sex-determining locus (or loci) is (are) inherited within a larger chromosome segment that has a low incidence of crossing-over in the heterogametic sex. Thus, the sexes differ at expanded groups of loci linked to the sex factor(s). Bull (1983) devoted three chapters to a review of sex chromosome evolution, and emphasized two major themes. First, the majority of observations of sex chromosome evolution in animals appears to fall into a single evolutionary process. Second, this process appears to consist of two major stages: (1) the suppression of crossing-over between the X and Y; and (2) the subsequent degeneration of the Y chromosome in the heterogametic sex (Muller, 1914). The initial mechanism for crossover suppression may involve either chromosomal rearrangements that shift the location(s) of crossing-over to regions other than that containing the sex factor(s) or locus, or the origination of satellite DNA on the Y element (Ohno, 1967; Singh et al., 1976, 1980). The Y chromosome presumably degenerates either due to the operation of "Muller's ratchet" (the accumulation of sex-linked recessive lethals in the nonrecombining portion of the Y; Felsenstein, 1974), and/or "genetic hitchhiking" (the fixation of deleterious mutations linked to other beneficial loci; Maynard-Smith and Haigh, 1974; Rice, 1987). Many of these suggestions are based on theoretical considerations, and as pointed out by Bull (1983), the big gap between cytological and genetic studies of sex chromosomes makes it difficult to provide a comprehensive theory of sex chromosome evolution. Nevertheless, the process of sex chromosome evolution is viewed as proceeding from an initial state of identity toward extreme heteromorphism.

Theoretical limitations notwithstanding, the X and Y chromosomes are commonly observed to differ from each other in size and/or shape, gene content, and chromatin or DNA content (Bull, 1983). They also frequently differ from the autosomes in size or shape, although the X is frequently typical of some of the autosomes. It is primarily the Y that is depauperate of typical genes, reduced in size relative to the X, and partially or entirely heterochromatic. There is no general consensus on the process(es) of heterochromatization, although Jones (1984) proposed a mechanism whereby the sex-determining locus "hijacks" a locus controlling chromosomal condensation during the cell cycle (via a rearrangement that forms a tight linkage group between the two). Such a mechanism would cause an entire sex chromosome to condense and decondense in response to the functional state of the sex determiner. Since mitotically condensed chromosomes are genetically inert, such "hijacking" would insure that all loci on this element could be subsequently expressed at a time and place appropriate to sex determination. Jones (1984) developed this hypothesis from a consideration of sex chromosome systems of mammals (XY systems) and snakes (ZZ/ZW systems, female being heterogametic), both of which are much more conservative than many monophyletic groups of lizards. The hypothesis is, however, testable in a number of groups with modern cytogenetic techniques.

The XY systems considered above are the "simple" sex chromosome heteromorphisms which often serve as a substrate for the further derivation of multiple sex-chromosome systems (White, 1973: ch. 17). Multiple sex-chromosome heteromorphisms appear to evolve from XY systems via translocation of an autosome onto either the original X or Y. Additional theoretical considerations have been devoted to these systems (White, 1957; Lucchesi, 1978; Charlesworth and Charlesworth, 1980; Charlesworth, 1991), but substantial progress is not likely until appropriate comparative data can be collected from groups with well-understood phylogenies (Charlesworth et al., 1987).

Sceloporus represents an ideal system for such studies in many respects. All species are dioecious; no parthenogenesis is known, nor is sex suspected of being determined by temperature in any species, even though this is common in many other reptilian groups, including some lizards (Bull, 1983; Bull et al., 1988). These observations suggest the operation of phylogenetic constraints that permit only *genetic* sex determination in *Sceloporus,* which eliminates some potentially complicating factors. Perhaps more importantly, not all species have morphologically recognizable sex chromosomes (although this may be an observational bias, since morphologically similar XY chromosomes in early stages of differentiation would be hard to detect), but in those that do, males are always the heterogametic sex (as opposed to groups such as geckos, Bull, 1980). Male heterogamety facilitates detailed meiotic studies (Hedin et al., 1990), and in *Sceloporus,* both simple and multiple sex-chromosome systems are well documented (summarized in table 5).

As previously discussed, Hall (1973, 1977) considered the XY system with a minute Y chromosome to be the ancestral state for *Sceloporus.* His premise was that *Uta* was the first outgroup of *Sceloporus,* although he did not use that term, and this type of heteromorphism is well documented in *Uta* (Pennock et al., 1969). The Y chromosome is by far the smallest element in the *Uta* genome, and although C-banding has not been conducted to confirm its presumed heterochromatic nature, its size and limited meiotic crossing-over with the larger X accords well with conventional wisdom of sex chromosome evolution. Table 5 and figures 19 and 26 show that many species inferred to be basal in both the small-bodied and large-bodied radiations retain this same system. Within these species, the minute Y is well documented from conventional Giemsa-stained karyotypes (i.e., no C bands) in the *chrysostictus, merriami, utiformis,* and *variabilis* groups (table 5). The morphology of the Y chromosome is uncertain in the *jalapae* and *siniferus* groups, and at least part of the *scalaris* group. Within the *scalaris* group, however, Hall (1973) reported, but did not illustrate, large XY elements in *S. aeneus* (not seen by Cole, 1978). If verified with more

TABLE 5

Summary of Sex Chromosome Data for *Sceloporus*, Condensed from table 4, but with Expanded Comments on Y-chromosome Heteromorphisms

(An asterisk (*) denotes the presence of a multiple sex-chromosome system)

Species groups of Hall	2n	Sex chromosome heteromorphism	Sources
SMALL-SIZED, SMALL-SCALED SPECIES:			
VARIABILIS	34	XX♀/XY♂ (minute Y)	Cole (1978); Hall (1973)
CHRYSOSTICTUS	34	XX♀/XY♂ (minute Y)	Cole (1971a); fig. 16B
UTIFORMIS	34	XX♀/XY♂ (minute Y)	Cole (1971a)
SINIFERUS	34	XX♀/XY♂ (uncertain Y morphology)	Cole (1978)
JALAPAE	34	XX♀/XY♂ (uncertain Y morphology)	Cole (1971b, 1978); Hall (1973)
MACULOSUS*	34/33 ~(?)	$X_1X_1X_2X_2$♀/X_1X_2Y♂ (Y-autosomal fusion)	Cole (1971a); table 4
MERRIAMI	46	XX♀/XY♂ (minute Y)	Cole (1971a); fig. 16D
SCALARIS	24	XX♀/XY♂ (large XY micros in *S. aeneus*)	Hall (1973)
LARGE-SIZED, LARGE-SCALED SPECIES:			
ORCUTTI	34	XX♀/XY♂ (minute Y of uncertain morphology)	Hall (1973); Hall & Smith (1979); fig. 16A;
CLARKI*	40 or 40/39	XX♀/XY♂ (minute Y) $X_1X_1X_2X_2$♀/X_1X_2Y♂ (Y-autosomal fusion)	Hall (1973)
ASPER*	32/31	$X_1X_1X_2X_2$♀/X_1X_2Y♂ (Y-autosomal fusion)	Hall (1973)
GRAMMICUS*	32/31–46/45	$X_1X_1X_2X_2$♀/X_1X_2Y♂ (Y-autosomal fusion)	Summarized in Arevalo et al. (1991)
MEGALEPIDURUS*	32/31	$X_1X_1X_2X_2$♀/X_1X_2Y♂ (Y-autosomal fusion)	Hall (1973); fig. 17C, D
TORQUATUS*	32/31	$X_1X_1X_2X_2$♀/X_1X_2Y♂ (Y-autosomal fusion)	Axtell & Axtell (1971); Cole et al. (1967); Hall (1973); fig. 17A, B
GRACIOSUS	30	XY indistinct	Cole (1971, 1975); Thompson & Sites (1986a)
MAGISTER	26–30	XY indistinct but see *S. rufidorsum* (fig. 14)	Cole (1970); Hall (1973)
HORRIDUS	22	XY indistinct except for enlarged pr. 7 XY♂ in *S. lundelli*; but see Reed et al. (1990)	Cole (1970, 1972, 1975, 1977, 1983); Cole & Lowe (1968); Hall (1973)
FORMOSUS	22	XY indistinct	Hall (1973); fig. 15

sophisticated mitotic and meiotic techniques, this may represent the enlargement of the Y from an ancestral minute element. The only multiple-sex chromosome system known from the small-bodied radiation is the 2n = 34♀/33♂ ($X_1X_1X_2X_2$♀/X_1X_2Y♂) heteromorphism described in the *maculosus* group (Cole, 1971a: table 5). This system presumably evolved by some sort of microautosome–minute Y translocation such as that depicted in figure 18D, but this will require independent cytogenetic confirmation. If *S. maculosus* is found to be a member of a monophyletic small-bodied, small-scaled radiation that does not contain *S. melanorhinus* or the crevice users, as illustrated in figure 19, then it would represent an independent derivation of this type of multiple sex chromosome system.

The large-bodied, large-scaled radiation appears to contain several different independently evolved multiple sex chromosome systems (fig. 26). *Sceloporus clarki* is hypothesized to possess a uniquely derived enlarged Y chromosome (fig. 18B), which then provided a substrate for the derivation of the $X_1X_1X_2X_2$♀/X_1X_2Y♂ heteromorphism characteristic of *S. melanorhinus* (fig. 18E). This system is almost certainly independent of all other multiple sex chromosome heteromorphisms in the genus because the autosomes involved in the autosome–Y translocation appear to be one of the pairs of acrocentric products resulting from the fixed pair 5 fission that, along with three other fissions, defines the *clarki* group (fig. 26). The entire crevice-user radiation (the *asper, grammicus, megalepidurus,* and *torquatus* groups) is postulated to be diagnosed by a third independently derived $X_1X_1X_2X_2$♀/X_1X_2Y♂ system homoplasious to that previously described for *S. maculosus.* The microautosomes involved in the Y chromosome translocation may represent different pairs, or independent translocations of the same pairs in the crevice-using and *maculosus* groups.

Elsewhere within the large-bodied radiation, Hall postulated the derivation of the "XY indistinct" system in which the direction of change is presumably from an extremely heteromorphic XY system characterized by the minute Y, toward a system of XY homomorphism (fig. 26). Conventional wisdom holds that, because the X chromosome appears to retain most of its original functions while the Y loses most functions, accumulates heterochromatin, and generally becomes reduced in size, such accumulated differences will *maintain* the heteromorphism. In other words, extreme sex chromosome heteromorphism is one of a small class of evolutionary phenomena postulated to be irreversible (Bull and Charnov, 1985). In view of the possibility of reversibility of sex chromosome heteromorphisms in the ancestor of the *formosus, graciosus, horridus,* and *magister* groups relative to the basal *orcutti–nelsoni–pyrocephalus* polytomy (fig. 26), the recent study by Reed et al. (1990) is especially interesting. These investigators showed that, on the basis of high-resolution synaptonemal complex (SC) analyses of meiotic pairing in *S. graciosus* and *S. undulatus,* both species possessed length heteromorphisms in microchromosomes that were undetectable at the level of resolution afforded by light microscopy. Furthermore, in both species, the heteromorphic microchromosomal pairs (pair 7 in *S. undulatus* and pair 8 in *S. graciosus*) showed unpaired "buckle" configurations in the SCs indicative of asynchronous synapsis, strongly suggesting that these pairs represent heteromorphic sex chromosomes. (Pair 7 is also interpreted to represent uniquely derived X and Y chromosomes in another species in the *horridus* group, *S. lundelli.*) The buckle configurations represent the differences in amount or degree of contraction of chromatin between the synapsed elements. Since the data presented by Reed et al. (1990) do not provide enough information to determine which element is the Y chromosome, the differences in chromatin content could be explained either by the addition or deletion of genetic material. The evolutionary implications, however, are that reversals of minute Y chromosome heteromorphisms may be possible. Again additional phylogenetic and cytogenetic corroboration is needed, but structurally at least, Y chromosome heteromorphism may be more evolutionarily labile than previously thought.

Finally, the sex chromosome heteromorphism in *S. rufidorsum* (tables 4, 5; fig. 14A, B) requires further documentation as it remains quite puzzling. In this species, females have a somatic diploid number of 30, and males 29. In all details resolved by light microscopy, the karyotypes of both sexes are identical except males have one microchromosome fewer than females. This might suggest an XX♀/XO♂ sex chromosome system; however, this is unknown for lizards and is inconsistent with the presumed mode of sex determination for all other *Sceloporus* (actively genetically determined males), which make this hypothesis untenable. It is possible that *S. rufidorsum* has a minute Y chromosome that CJC overlooked in the slide preparations, but CJC has recognized such minute chromosomes in other species. In addition, the presumed closest relative of *S. rufidorsum, S. zosteromus,* was not reported by Hall to have recognizable sex chromosomes (table 4). Consequently, we hypothesize that an ancestral minute Y translocated onto a much larger autosome, which is difficult to resolve, and this represents an independently evolved X_1X_2Y sex chromosome heteromorphism of a type unique in the genus. This hypothesis can be tested by meiotic analysis in males.

IV. SPECIATION AND HYBRIDIZATION ISSUES

Many topics previously discussed or to be discussed are not completely independent of this section, and in fact there is considerable overlap among some. For example, the biogeographic hypotheses presented above have major implications for patterns of speciation in major radiations within *Sceloporus,* and the evolution of sexual selection and/or mate choice differences between breeding groups is the presumed causal basis for divergence in many animal speciation models (reviewed by Lande, 1989). However, studies of speciation may focus on a number of interrelated questions at both infraspecific and supraspecific levels (Otte and Endler, 1989), and in this section we wish to emphasize several speciation-related issues at both levels for which various components of *Sceloporus* are particularly well suited for further study.

We note at the outset that an understanding of the concept of a "species" is crucial to these sorts of studies, and that the traditionally revered biological species concept (BSC) has come under increasing criticism (reviewed by Cracraft, 1987; Frost and Hillis, 1990, among others). The BSC and several non-historically oriented concepts (see Paterson, 1985; Templeton, 1989) do not provide for the unambiguous recovery of species in phylogenetic studies, and may consequently be misleading. We endorse the general view emphasized by Frost and Hillis (1990) that defining species in contexts relying on recovered phylogenetic history (reviewed in Nixon and Wheeler, 1990), which is not without inferential limits (see especially the important qualifications at lower hierarchical levels discussed by de Queiroz and Donoghue, 1988, 1990), offers the best epistemological basis for identifying independently evolving lineages. Thorough phylogenetic studies are a necessary step in investigating any of the above issues.

Comparative studies of speciation. There is renewed interest in the rigorous application of phylogenetic methods to Recent monophyletic groups in studies of macroevolutionary phenomena (Mayden, 1986; Gould et al., 1987; Jablonski, 1987; Slowinski, 1990; Slowinski and Guyer, 1989a, 1989b; Guyer and Slowinski, 1991), and in this regard *Sceloporus* offers an almost untapped resource. The recent papers by Slowinski and Guyer are especially intriguing in that they attempt to develop null models for patterns of speciation, as inferred from phylogenetic studies, against which to statistically test the relative frequencies of asymmetrical topologies of cladograms. The focal point of these papers aims to test whether species-diverse versus species-poor sister clades represent accelerated rates of speciation and/or reduced rates of extinction in the diverse clade relative to its depauperate sister clade, or whether such asymmetrical topologies cannot be distinguished from random processes. In view of the charge that adaptational explanations for the evolutionary success (i.e., high species diversity) of a particular clade are weak and speculative (Raikow, 1988), and the open question of the relationship (if any) between demonstrable natural selection and groups that appear to be radiating rapidly (Endler, 1986), the conceptual studies of Slowinski and Guyer represent an extremely important line of inquiry. Many of the macroevolutionary questions raised by these studies can be addressed either within *Sceloporus,* or between *Sceloporus* and its close relatives (see fig. 12 in Frost and Etheridge, 1989, for the alternative sister groups), *once well-corroborated cladograms are obtained.*

A second interesting idea concerns the role of punctuated equilibrium (Eldredge and Gould, 1972) in generating macroevolutionary patterns. This idea was originally advanced in discussions of morphological change in fossil groups (see also Gould and Eldredge, 1977; Stanley, 1979), but was extended to considerations of molecular (allozyme) divergence within Recent groups by Avise and Ayala (1975). Specifically, this model examined the consequences of punctuated equilibrium (also referred to as rectangular evolution in the Avise-Ayala papers) versus phyletic gradualism based on the distribution of genetic distances among living species in highly diverse versus species-poor groups of equal age. Both allozyme (Avise and Ayala, 1976; Avise, 1977) and morphological (Douglas and Avise, 1982) tests in fishes failed to support the rectangular model.

Mayden (1986) criticized this approach on the basis of difficulties in interpreting genetic distance data and failure to meet assumptions that comparisons are made between (1) monophyletic groups, (2) taxa of equal age, and (3) taxa experiencing similar degrees of extinction and homoplasy. Mayden (1986) argued that the species-rich (family Cyprinidae) and species-poor (Centrarchidae) fish radiations examined by Avise and Douglas (*Notropis* and *Lepomis*, respectively), were dubiously qualified on all of the above points.

Mindell et al. (1989) provided an alternative allozyme test with the genus *Sceloporus* in which the amounts of discrete character change relative to an outgroup were compared between sister species. This test required the assumption of similar extinction rates in the groups compared, but was conceptually more rigorous than earlier tests with respect to the issues of monophyly, equal age of taxa, and the distribution of homoplasious character states. Parsimony analysis of 68 informative allozyme characters among 19 species of *Sceloporus* (18 ingroup species rooted to *S. merriami*) revealed a pattern of allozyme change consistent with the rectangular hypothesis. This finding has stimulated some debate (Sanderson, 1990; Mindell et al., 1990b), and the results of this and related studies (Mindell et al., 1990a) must be regarded as tentative. In this case, however, punctuated change appears to be a viable explanation for the distribution of allozyme characters among species of *Sceloporus*.

Hybrid zone dynamics. The precise connection between the origin of zones of hybridization between genetically differentiated populations (as defined by Woodruff, 1973) and speciation processes is not clear. Natural hybrid zones do, however, offer experimental material for the quantification of some of the genetic differences in the genomes, morphologies, ecologies, and behaviors of hybridizing populations, and thereby they provide a "window" to some of the divergence causally related to or associated with speciation (sensu Mayr, 1963) (Barton and Hewitt, 1985, 1989; Hewitt, 1988, 1989; Harrison, 1991). The most informative studies are those based on comparative assessments of hybridization dynamics among several different zones of contact within the same species or species complex. These cases provide either replicates of contacts between the same pair of populations (or species) in different geographic settings, or in some cases, contacts between pairs of populations showing different levels of divergence (many examples reviewed in Barton and Hewitt, 1989; Hewitt, 1988, 1989; Harrison, 1991). The genus *Sceloporus* offers possibilities for in-depth studies relating to both of these criteria.

Two early studies described in some depth the dynamics of hybrid zones in two different species groups of *Sceloporus*. Jackson (1973a) reported the results of morphometric and ecological studies at three points of contact between *Sceloporus undulatus* and *S. woodi* in central Florida. In this case, a very narrow zone of hybridization was identified (by morphological markers) at each locality in an ecotone between very different plant associations; *S. woodi* was confined to sand-pine scrub associations, while *S. undulatus* inhabited longleaf-pine/turkey oak associations. Jackson (1973a) concluded that hybridization had probably occurred at these ecotones for the past 100,000 years, and that the hybrids were probably fertile.

In another study, Hall and Selander (1973) used unambiguous genetic markers, consisting of one fixed chromosomal and two fixed allozyme differences, to assess the dynamics of hybridizing chromosome races of the *S. grammicus* complex. These workers established a transect along an elevational gradient on the volcanoes forming the eastern divide of the Valley of Mexico, and showed that the point of contact centered on an ecotone between different vegetation types. At intermediate elevations (3000–3400 m), the F6 race (2n = 34, ♀/33♂ 8MM,2SMM,4AM, 16m,$X_1X_1X_2X_2$♀/X_1X_2Y♂; listed as *S. palaciosi* in table 4) inhabited relatively humid fir forests, while at higher elevations (~3400 m–tree line), the S race (2n = 32♀/31♂, 10MM, 2SMM,16m,$X_1X_1X_2X_2$♀/X_1X_2Y♂; listed as *S. anahuacus* [?] in table 4) was confined to drier open pine woodland. The screening of three unambiguous genetic markers allowed Hall and Selander (1973) to clearly distinguish between S × F6 F_1 hybrids (heterozygous at all three markers) versus various backcross combinations (heterozygous at one or two markers), and to document in detail the approximate width of this zone (400–500 m). They concluded that no apparent introgression occurred from S into F6, but that a low level of introgression occurred in the opposite direction. Hall and Selander argued that: (1) backcross individuals survived poorly; (2) those that survived to maturity did not reproduce; and (3) the contact between these populations was at least 7000 years old. Hall later (1980: 318) argued that F_1 individuals *and* the first generation of backcrosses were sufficiently fertile to allow significant introgression beyond the first generation of backcrossing. This contradicted conclusion no. 2 of the earlier paper, but the evidence unequivocally demonstrated random mating, hybrid fertility, and successful backcrossing within the zone, while the zone itself was functioning as a complete barrier to genetic introgression *in either direction over a distance of about 3 km.*

These studies were carried out prior to the development of both an extensive body of theoretical literature concerning the dynamics of hybrid zones (Asmussen et al., 1989; Barton and Hewitt, 1989; Harrison, 1991), and the deployment of more refined molecular techniques applicable to studies of population structure and gene flow (Hillis and Moritz, 1990). Both of the complexes just described provide additional research opportunities in light of these developments, especially with regard to questions related to the origin and evolutionary role of chromosomal rearrangements.

Chromosomal rearrangements have been implicated in both phyletic evolution (by adaptive divergence of genetic linkage groups) across broad taxonomic levels, and in speciation processes at the population level (reviewed by Baker et al., 1987; Sites and Moritz, 1987), yet with regard to the latter, the major predictions remain largely untested. Most hypotheses of chromosomal speciation predict that individuals heterozygous for one or more chromosomal rearrangements, formed as a consequence of random mating in a zone of hybridization between chromosomally differentiated populations, should display reduced fitness relative to chromosomal homozygotes (but see Imai et al., 1986; and Rowell, 1990; for alternatives). Reduced fitness may result from any number of genetic mechanisms (Sites and Moritz, 1987; Searle, 1988), and the meiotic mechanisms themselves may be confounded by factors other than structural chromosomal heterozygosity per se. For example, studies of lab lines of *Mus* have shown that meiotic pairing behavior and anaphase segregation patterns may be drastically different *for the same rearrangement* on different genetic backgrounds (de Boer, 1986). These and related findings indicate that studies of meiotic chromosome behavior in interspecific or interpopulation hybrids must be interpreted with caution if the genic effects are unknown (John, 1981, 1983; John et al., 1983), and that the latter should be evaluated where possible (for a well-documented example in the grasshopper complex *Caledia captiva,* see Coates and Shaw, 1985; Shaw and Coates, 1983, Shaw et al., 1986, 1990).

In a recent update of population-level chromosomal variation in the *S. grammicus* complex in central Mexico, Arevalo et al. (1991) mapped the location of seven different zones of parapatric hybridization. These included the three zones originally described by Hall (1973) and Hall and Selander (1973), and four new zones discovered by field sampling efforts by Sites and collaborators. These zones, plus an eighth identified by Sites and Davis (1989), involve six different combinations of chromosome races (see table 8 in Arevalo et al., 1991), with chromosomal divergence ranging from a single to as many as six rearrangements (S × F6 and S × FM2, respectively; see table 4 for details). Studies in progress will provide estimates of levels of nuclear and mitochondrial genomic divergence, as well as the phylogenetic relationships of all races involved in the contacts. When this information is available, it will then be possible to evaluate the meiotic and fitness consequences of chromosomal heterozygosity in the context of a known range of chromosomal and nuclear/mtDNA divergences. Interpretations of meiotic behavior in hybrid zones can now be extended beyond those traditionally derived from conventional light microscopy, by the application of high-resolution electron-microscopic scanning techniques (Hedin et al., 1990; Reed et al., 1990). Further, estimates of mis-segregation frequencies can be made with reference to meiotic data scored from chromosomal homozygotes and heterozygotes collected from polymorphic populations of nonhybrid origin (Porter and Sites, 1985, 1987), which provide internal controls for hybrid zone samples. Outside of the *S. grammicus* complex, the *S. undulatus* × *S. woodi* contacts in Florida offer additional experiments in which to evaluate the meiotic consequences of hybridization between species having structurally identical karyotypes (these are both 2n = 22 species, table 4; see Pounds and Jackson [1981] for additional data on differentiation in *S. undulatus*).

Mutational components of chromosomal polytypy. Occasional cytogenetic oddities have been reported within *Sceloporus,* such as the apparently spontaneous low-frequency production of arm breakage (in *S. virgatus,* Cole and Lowe, 1968), and rare triploid individuals (in *S. occidentalis,* by Cole, 1983; *S. graciosus,* by Thompson and Sites, 1986b; and in *S. grammicus,* by Porter, 1988). All of these likely represent nothing more than mutational aberrancies that would be expected on occasion in any large group for which adequate chromosomal surveys had been carried out. In several other cases, however, within-sample chromosomal polymorphisms are sufficiently common and unusual to warrant further investigation, because any evolutionary consequence of a given chromosomal rearrangement is a function of the frequency with which the rearrangement originates, as well as its subsequent fixation probability. The fixation probability is in turn a function of population structure and selection regimes, while the frequency of origination is likely a function of intrinsic mutation rate and the molecular architecture of the chromosome.

One of these cases involves a population of *S. undulatus cowlesi* from the White Sands area of New Mexico; Cole (1977) reported two separate collections of five animals each in which one individual was heterozygous for a macrochromosome pair 3 aberration. Specifically, one arm of this element was roughly twice as long as its normal homolog (see fig. 2 in Cole, 1977). In meiosis, diakinesis arrays for the heterozygous pair usually showed (18 of 21 bivalents) a ringlike configuration between the aberrant and normal-length sister chromatids (fig. 3 in Cole, 1977). Cole interpreted the extra length of the aberrant arm as a likely duplication or addition of heterochromatin, although he did not C-band the material. His meiotic studies of the single heterozygous male revealed the presence of crossover products at both prophase II and metaphase II, providing the first cytological demonstration of meiotic crossing-over in a reptilian system. The estimated 20 percent frequency of this aberration in this population makes it readily accessible to further study.

Cole (1970) also reported local polymorphisms in karyotypes for *S. clarki, S. melanorhinus,* and *S. olivaceus,* and later for *S. occidentalis* (Cole, 1983). The polymorphism in *S. clarki* is particularly attractive for additional study for the following reasons: (1) it involves several distinctive chromosomes (see fig. 1 in Cole, 1970); (2) several states occur in reasonably high frequencies; (3) the lizards are abundant, readily collected, and available in southern Arizona; and (4) according to Hall's interpretation, sex chromosomes may be involved.

Along the same line of inquiry, the most extensive meiotic study of the *S. grammicus* complex by Porter and Sites (1987) is interesting because it showed an appreciable frequency of spontaneous germ-line chromosomal rearrangements in several individuals. Five of 31 males examined, from five different localities, carried fission rearrangements in some of their metaphase II cells that were not present in mitotic karyotypes prepared from bone marrow, and these were interpreted as spontaneous germ-line mutations. All else being equal, high mutation rates for a particular class of rearrangement will provide for a higher frequency of fixation, and there is evidence from a variety of organisms that both natural and experimental hybridization will elevate chromosomal mutation rates (Peters, 1982; Shaw et al., 1983; Hagele, 1984; Naviera and Fontdevila, 1985; Adkins et al., 1991). There is strong suggestive circumstantial evidence for this in the *S. grammicus* complex independent of the meiotic data reported by Porter and Sites (1987). Arevalo et al. (1991) reported two extremely polymorphic samples of *S. grammicus* from two different localities in Central Mexico (see fig. 5 in Arevalo et al., 1991), and although transect samples were inadequate to document with certainty that both were hybrid-zone populations, both were located geographically between other races (FM1 × FM2, and FM2 × FM3), and were heterozygous for the appropriate chromosome markers. Of greater interest, however, was the fact that both populations were segregating for some rearrangements that had not been identified anywhere else in the range of this complex (see figs. 8 and 9 in Arevalo et al., 1991; also fig. 7 in Porter and Sites, 1986). These observations suggest that hybridization in this complex may result in dysgenic-type events that elevate background chromosomal mutation levels. Hybrid dysgenesis in the strict sense refers to the simultaneous occurrence of a number of associated genetic traits resulting from transposable element (TE) activity (reviewed by Kidwell, 1990), of which increased chromosomal aberrations are only one. Since the molecular basis for the mutational phenomena in *S. grammicus* is unknown, we refer to the dysgenic-type manifestation only in a general sense. Current technologies, however, make it possible to identify the base-pair composition of some TEs, and to localize them in the genome (see Ajioka and Eanes, 1989, for an example in *Drosophila*). Molecular cytogenetic studies of the populations of *S. grammicus* and *S. undulatus* just described, when coupled with high-resolution meiotic studies (Hedin et al., 1990; Reed et al., 1990), may yield data allowing inferences about chromosome architecture and the propensity for certain classes of rearrangements.

In a broader context, the molecular probes now being developed for a variety of repeated DNA sequences in vertebrates (Meyne et al., 1990), will permit detailed comparisons of the molecular structure of chromosomes between sister taxa of *Sceloporus* (Porter et al., 1991; for example). At low hierarchical levels, informative comparisons could be made between chromosomally highly polytypic populations of *S. grammicus* versus those that are largely monomorphic. At higher levels, one could compare chromosome structures between monophyletic groups of *Sceloporus* retaining the symplesiomorphic $2n = 34$ karyotype, versus those that have diverged from this arrangement by various means. Within the framework of well-corroborated phylogenies, the meiotic and molecular cytogenetic techniques provide a powerful combination of complimentary approaches to either understanding some aspects of chromosomal evolution or inferring phylogenetic relationships in *Sceloporus* at several hierarchical levels.

V. SOCIAL BEHAVIOR AND SEXUAL SELECTION

The overwhelming majority of species of *Sceloporus* show pronounced between-sex differences in behavior, coloration, and/or body size. An acceptable explanation for these differences rests on the theory of sexual selection (Arnold, 1983; Bradbury and Anderson, 1987; Lande and Arnold, 1985; O'Donald, 1980; but see below). In all species of *Sceloporus* that have been studied, males occupy and defend territories against other conspecific males. Behavioral and experimental studies have shown that males identify conspecifics with blue belly and throat patches as male, and those with white or less intrusive blue patches as female (Noble, 1934; Vinegar, 1972, 1975a; Cooper and Burns, 1987). Females hold separate territories within the territory of a male, often at a sex ratio biased toward several adult females to each territorial male (2–3 females per male in *S. jarrovi,* Ruby, 1981; and up to 4–6 females per male in *S. olivaceus,* Blair, 1960). Females are actively courted by the territorial male in which the male's courtship involves a shudder display and then, if a female exhibits a submissive posture, the male grasps her shoulder in his mouth and attempts copulation (Carpenter, 1962). Thus, male mating success may depend directly on the quality of the territory held, a male's ability to defend it from conspecific males, and his ability to court resident females within their territories. Variation in territory quality and number of females per territory in general contribute to the potential for substantial variance in male reproductive success in polygynous lizards (Stamps, 1983), and the expectation is that sexual selection may be intense (see below).

Given these general features of their biology, species of *Sceloporus* are ideally suited to comparative analyses of both patterns and processes of the evolution of social behavior and traits used in social communication, at both the proximate and ultimate levels. Like many other phrynosomatid lizards, species of *Sceloporus* have relatively stereotypic social displays that are amenable to rigorous quantitative description, and for some aspects, to experimental manipulation. The energetics of display behavior and costs of territoriality have been studied on individual species (e.g., in *S. jarrovi,* see Simon, 1975; and Marler and Moore, 1988), but comparative studies of these parameters in the appropriate phylogenetic context could yield unique insights into the evolution of the display. These and other possible causes and consequences of social behavior in *Sceloporus* are considered below.

Courtship and agonistic behavior. Other than active habitat selection by species that results in isolation, either on a micro- or macrogeographic scale, courtship and agonistic behaviors among individuals are potentially important mechanisms of species isolation and would be expected to be subject to sexual selection. Among squamates, behaviors of selected species in the genera *Anolis* and *Sceloporus* have been investigated in some detail. The first studies of courtship and agonistic behavior in *Sceloporus* were recorded by Newman and Patterson (1909), Speck (1924), Noble and Bradley (1933), Noble (1934), and Wood (1936). Carpenter and Grubitz (1961) and Carpenter (1962, 1963) originated time-motion analysis of agonistic male display behavior as plots of vertical body displacement against time. The two primary behavior types identified are courtship bobs and high-intensity encounter or agonistic displays that may be produced by individuals of either sex (Ruby, 1977a). Readers should realize that the distinction between the two behavior types was made from data collected largely before recognition of the degree and importance of individual and intraspecific variation (Leslie, 1988; see Ferguson, 1970, for comparative display data in *Uta*). Rothblum and Jenssen (1978) presented a sophisticated quantitative analysis and a refinement of intraspecific variation in a single species (*S. undulatus*). Duvall (1979, 1981) showed that glandular secretions of *S. occidentalis* males were important in eliciting species-typical displays in both sexes. The agonistic displays of these lizards are performed in a large number of contexts including encounters between males and, although intraspecific variation has not been interpreted consistently in most species, clear differences among species in the sequences have been interpreted in both phylogenetic and adaptational contexts (Carpenter, 1978).

Carpenter (1978) made an extensive series of subjective comparisons of male agonistic display behavior among species from both the large- and small-bodied species groups that bring into question the placement of certain taxa. Displays from a total of 44 species were analyzed in detail. Nine species were examined in the *spinosus* group, and most of these were broadly similar, although the groups of species that Carpenter considered to be most similar were not so considered by Smith (1939). Carpenter, for example, considered the display of *S. orcutti* to be "unique to the [*spinosus*] group" but not distinct enough to warrant its removal from this group. The displays of the two *pyrocephalus* species examined (*S. nelsoni* and *S. pyrocephalus*) were so different from each other that Carpenter suggested that they were not phylogenetically close. The display of *S. lundelli* was also very distinct from those of other species of the *spinosus* group, and was most similar to those of *S. asper* and *S. lunaei. Sceloporus acanthinus* and *S. lunaei,* originally placed by Smith (1939) in the *spinosus* group, had displays resembling several species of that group more than did *S. asper* and *S. formosus.* Carpenter also showed that two species of Smith's *megalepidurus* group, *S. cryptus* and *S. megalepidurus,* differed substantially, and suggested that their placement in this group needed reexamination. The display of *S. cryptus* was especially suggestive of displays of species in the *formosus* or *spinosus* groups recognized by Smith (1939). Four species examined within the *undulatus* group (*S. cautus, S. occidentalis, S. undulatus,* and *S. woodi*) were very similar to *S. graciosus,* and Carpenter suggested a close affinity of all of these species to each other, and then to the *formosus* and *spinosus* groups. Six species were examined from the *torquatus* group, and Carpenter considered the displays to share a common "jerkiness" although they otherwise differed substantially.

Within the small-bodied radiation, the five species of the *variabilis* group examined (*S. couchii, S. cozumelae, S. parvus, S. teapensis,* and *S. variabilis*) were all quite similar in sharing "repeated jerky sequences," but were otherwise distinctive. Carpenter found however, that males of *S. teapensis* and *S. variabilis* court females of each other's species. Female discrimination tests have not been carried out between these or most other closely related taxa. The displays of *S. chrysostictus* and *S. merriami* were found to resemble the displays of other species in the *variabilis* group, suggesting close relationships. The displays of *S. siniferus,* the only species examined from its group, and *S. utiformis* were found to differ from each other and from those of all other species recorded. Three species from Smith's *scalaris* group (*S. aeneus, S. jalapae,* and *S. scalaris*) revealed a strong similarity between the first and third of these to the exclusion of *S. jalapae,* partially corroborating the arrangement of Hall (fig. 19).

Leslie (1988) has reviewed both the empirical data base and theoretical context upon which inferences of functions of lizard display behavior have been made for the past 30 years, and found serious flaws in both. For example, many problems were identified in the experimental methods used by almost all earlier studies of lizard displays (use of tethered "invaders," laboratory set-ups devoid of the appropriate social milieu, etc.) because they rarely allowed the full range of behaviors to be expressed. Frequently displays elicited by these behaviors were filmed, and problems arose when essentially continuous displays were divided into distinct behavioral units. This occurred because no stringent criteria were ever agreed upon to define a complete display or its components, and different authors used different endpoints. Finally, the underlying paradigm for most work completed to date, and certainly for all work on *Sceloporus* summarized by Carpenter (1978), has been based on the concept of stereotyped display (see Leslie, 1988: 9). This is a term borrowed from classical ethology and applied directly to lizard displays without rigorous assessment or definition of its implications: (1) a virtually complete dismissal of the importance of variation; (2) little attention given to making distinctions between individual and species recognition; and (3) little statistical evaluation of data. Evidence of the species-specificity of displays is weak, for example, and based almost entirely on "visual statistics" (Leslie, 1988: 33). As an example, *S. undulatus hyacinthinus* performs two displays, the species "signature bob" and an agonistic display, and these two show different levels of variability (Rothblum and Jenssen, 1978). This signature display is constant across individuals, whereas the agonistic display is unique to individuals; so unique that a "species-typic DAP" could not be discerned. The traditional view of a display repertoire is one of two types—territorial or agonistic displays toward conspecific males, and courtship displays toward conspecific females. This view is likely simplistic, as several species of lizards are known to have larger display repertoires (Leslie, 1988: 34).

Since communication is the purpose of display behavior, it is very likely that both constant and flexible information is encoded into the display, depending on what kind of information needs to be sent. Lizards very likely alter length, number of units, and/or amplitude of a given display, or modulate a display with alterations in posture or accessory movements, as a function of the social environment of the moment (number and sex of conspecifics present, distance from signaler, etc.). All of these variables potentially contribute to display variation, as do possible ontogenetic shifts, and none has received adequate attention. A further potentially compounding factor is the possibility that distantly related species in the same habitat may converge upon similar displays due to selection driving head-bobbing patterns away from background motion in the environment, such as wind-driven movement of vegetation. Such a deviation was recently demonstrated by Fleishman (1988) in the tropical lizard *Anolis auratus,* and could be a factor in grassland or arboreal *Sceloporus.* Despite the critical tone of Leslie's review, many constructive suggestions are made, and most center on application of rigorous methods, realistic consideration of sources of variation, and development of a paradigm based on game theory and signal theory (Leslie, 1988: pp. 53 and 80, respectively) to clarify hypotheses. Once robust estimates of phylogeny are available for a radiation as diverse and accessible as *Sceloporus,* closely related species living in similar and different environments could be investigated with appropriate controls for intra- and interspecific variability. Such fine-scale analyses would eventually provide much insight into the conflicting selection pressures acting on display behaviors.

Sexual dichromatism. In the vast majority of species of *Sceloporus,* females are relatively drab, and typically have white or cream-colored bellies and throats. In contrast, males are usually brightly colored, having blue, green, black, yellow, orange, or pink belly and/or throat patches that may encompass the entire venter. Males of some species also have orange, green, or blue flecks in their dorsal coloration, but the exact nature of all of this dichromatism varies within and among species. In at least one species, *S. virgatus,* females exhibit more color than males, at least during the breeding season when female blue throat patches turn orange (Vinegar, 1972). Taxonomically, geographic variation in ventral and dorsal coloration has been used to diagnose and identify subspecies. For example, *S. occidentalis* includes four named subspecific taxa that are identified primarily on the basis of diagnostic color polymorphisms. A recent study (Gallant and Archie, unpubl.) showed that the subspecies boundary between *S. o. occidentalis* and *S. o. biseriatus* is coincident with substantial step-cline variation in virtually all colors evaluated. In fact, females from populations of *S. o. biseriatus* exhibit coloration characteristics that are more "malelike" than those of average males from populations of *S. o. occidentalis* less than 30 km away. As individuals from these populations can be expected to interbreed since they presumably are members of the same species, the function, genetic basis for, and evolution of such color polymorphisms could be readily investigated.

Color has been shown experimentally to identify reproductively mature males in several species of dichromatic lizards (reviewed by Cooper and Burns, 1987). Dewlap coloration in *Urosaurus ornatus* males, for example, is related to agonistic dominance and display frequency (Hover, 1985). In *Sceloporus,* male-male intraspecific aggression was positively correlated with the degree of dichromatism in a comparison made among *S. undulatus consobrinus, S. u. tristichus,* and *S. virgatus,* although the effects of dichromatism could not be separated from the effects of population density (Vinegar, 1975a). Cooper and Burns (1987) experimentally showed that the blue belly patches in *S. undulatus* identify males, while white bellies identify females to conspecific males.

Color may also play a major role in signaling reproductive conditions between the sexes, as it is under steroidal control in females of several species of iguanians. The acquisition of bright orange lateral spots in gravid female *Crotaphytus collaris* and *Gambelia wislizenii,* for example, is stimulated by progesterone and follicle-stimulating hormone, respectively, and both processes are accelerated by pretreatments with estrogen (Cooper and Ferguson, 1973; Medica et al., 1973; respectively). In *Sceloporus,* Kimball and Erpino (1971) demonstrated that the black component of male ventral pigmentation in *S. occidentalis* was enhanced by injection with androgen. Rand (1990) showed that the intensity of yellow or orange coloration on the face and chin in *S. undulatus erythrocheilus* followed a testicular cycle (in adult males) that tracked a seasonal cycle, suggesting androgen control.

However, Cooper and Burns (1987) have suggested that cues other than visual stimuli, most likely behavioral and/or chemical, are likely to be important in some aspects of lizard communication. Chemical communication, as measured by tongue-extrusion rates in response to odor stimuli from exudates from both male and female donors, has been shown to permit discrimination between sexes by male skinks (*Eumeces laticeps,* Cooper and Vitt, 1984). Earlier discrimination tests with *S. occidentalis* revealed significant lingual discrimination ability by both sexes to exudates from male and female conspecifics, suggesting that pheromonal markings may be important in sex recognition, spacing, and establishment or maintenance of territories (see Duvall, 1979, 1981, 1982). Some pheromones may also have a releasing or eliciting function in social encounters of close physical proximity, with cues likely detected by the tongue-vomeronasal system (Duvall, 1982). Extensive study is needed to determine the relative importance of these alternative modes of communication at intra- and interspecific levels.

An interesting twist to sexual selection theory was proffered by Hamilton and Zuk (1982), and incorporates the effects of parasites on their hosts into equations of mate choice. These authors proposed that sexually dimorphic traits, in which one sex (usually males) displays extravagant colors or structures, have evolved in part because they allow the other sex to evaluate the parasite loads of potential mates. Discriminating females would select male phenotypes that were expressing genotypes for high parasite resistance. Many interspecific comparisons have provided correlational support for this hypothesis, but few examples of the effects of parasites on sexually dimorphic traits of their hosts are available (reviewed by Read, 1988; Borgia and Collis, 1990; Boyce, 1990; Sullivan, 1991). Strong support for the Hamilton-Zuk hypothesis requires that four premises be met in intraspecific studies: (1) a negative relationship between an individual's fitness and its parasite load; (2) heritable variation in parasite resistance; (3) expression of one or more secondary sexual characters that vary with the parasite burden; and (4) preferred or "chosen" mates having fewer parasites than those chosen under a system of random mating. Positive evidence for (3) and (4) would support the Hamilton-Zuk hypothesis, but evidence for either is only conclusive for this view if (1) and (2) are true.

This hypothesis is difficult to test in its entirety, but a promising system is *S. occidentalis* and its malarial parasite *Plasmodium mexicanum.* Infection appears to be life-long in *S. occidentalis,* and the *Plasmodium*-induced pathology is substantial, affecting the hematological, physiological, behavioral, and reproductive processes of the host (Schall et al., 1982; Schall, 1983a, 1983b; Bromwich and Schall, 1986; Schall and Sarni, 1987; Schall and Dearing, 1987). Ressel and Schall (1988) recently demonstrated *Plasmodium*-induced variation in *S. occidentalis* male color pattern; malaria-infected individuals exhibited significantly more black and less paleness on their ventral surfaces than did noninfected males of similar body size. However, regression analysis showed that females using male ventral color pattern alone as the gauge of infection would only marginally improve their chances of selecting a noninfected lizard over random selection of mates. Female choice was not empirically tested however, and females of other species of vertebrates (fishes) have been shown to choose healthy or lightly-parasitized males at statistically higher frequencies than males with high parasite loads (Kennedy et al., 1987; Milinski and Bakker, 1990). These findings suggest that further work is needed on *S. occidentalis* and other species of *Sceloporus.*

Of equal interest for ecological and evolutionary studies is the fact that males in several lineages of *Sceloporus* have completely lost the colored display patches, including *S. chrysostictus, S. cozumelae, S. exsul, S. horridus albiventris, S. siniferus, S. squamosus, S. utiformis,* and *S. virgatus.* Each of these instances appears to be an independent loss of dichromatism, and may be ecologically extremely significant. This variation in sexual dichromatism provides a substantial opportunity to examine the function of display behaviors, visual or chemical communication, and sexual selection in these species, particularly if sister taxa are characterized by pronounced differences in dichromatism.

Sexual size dimorphism. In addition to dichromatism, substantial intersexual differences have been documented in body size (sexual size dimorphism, SSD) in *Sceloporus* (Fitch, 1978). In 25 of 53 populations (23 species) examined by Fitch (1978), males were significantly larger (in snout–vent length, SVL) than females, while the reverse was true in 17 populations representing 9 species. Females were larger than males in samples of *S. cyanogenys, S. graciosus, S. lundelli, S. occidentalis, S. olivaceus, S. scalaris, S. undulatus, S. virgatus,* and *S. woodi.* In nearly all cases, species or subspecies thought to be closely related to these taxa have larger males than females (Fitch, 1978; see also table 9.1 in Stamps, 1983). For example, both *S. mucronatus* and *S. poinsetti* males are significantly larger than females, and one or both are likely very closely related to *S. cyanogenys.*

Classic sexual selection theory holds that intraspecific sexual dimorphism evolves when characters that confer an advantage in either competition for mates, or female mate choice, are selected within one sex (reviewed by Maynard-Smith, 1991). General body size may be one such trait (Harvey, 1990; Shine, 1990), and because male lizards frequently use jaws in combat (Carpenter and Ferguson, 1977), selection may favor elaboration of overall head size or selected head dimensions (width, depth, etc.) related to combat and/or acquisition of food resources (see examples in lizards in Carothers, 1984; Cooper and Vitt, 1989; Anderson and Vitt, 1990; and Hews, 1990a, 1990b). Others have recognized, however, that sexual dimorphism may also evolve when niches are dimorphic, such as when competition exists between the sexes for a limited resource. Further, the degree of dimorphism possible between the sexes may be constrained by the extent of intersexual genetic correlation in the trait(s) potentially influenced by the three factors listed above. Slatkin (1984), for example, has modeled ecological conditions under which sexual dimorphism can evolve, and showed that it is possible if either a dimorphic niche exists or between-sex competition is high, as long as genetic correlations are less than 1.0. These alternatives are, however, potentially difficult to test in nature (Shine, 1989).

The combination of selective regimes (any of the above possibilities) and differential constraints on the sexes can produce the same outcome in SSD, but for a multitude of reasons. If females are larger than males, the standard explanation is that selection has favored large females because they can produce larger clutches (the size-fecundity advantage; see below), since male gamete production is not likely constrained by size. Alternatively, if males are larger than females, the standard explanation has been sexual selection, as defined above. Harvey (1990) pointed out that these explanations are too general in the sense that they are more inclusive than the patterns they seek to explain. For example, fecundity increases with female body size in many species in which males are larger than females, and in other cases, increased body size confers mating advantages to males even though the sexes are of equal size or the females larger. It is more realistic to consider body size as a phenotypic trait, the expression of which is a compromise or equilibrium between one set of selective forces favoring large size, and another set of forces penalizing large size, coupled with the genetic or energetic constraints imposed on the system. Sexual dimorphism evolves when: (1) the intensities of the selective forces favoring or penalizing large size *differ* between the sexes, thus leading to different equilibria; and (2) there are sexual differences in constraints in responses to selection (see Snell et al., 1988, for a field study of the tradeoffs between natural and sexual selection in males of the Galapagos lava lizard *Tropidurus albemarlensis*).

The above summaries of species-specific display patterns, sexual dichromatism, and sexual size dimorphisms among species of *Sceloporus* reveal levels of within- and between-species variation extremely well suited for more synthetic studies of the evolutionary causes and consequences of sexual selection, and more fundamentally, of the variation in behavior. However, as Cooper and Vitt (1989) have recently pointed out, problems associated with attributing such features as body size dimorphism to sexual selection are frequently based only on comparisons between the sexes. Yet clear evidence for the role of sexual selection derives most convincingly from studies of differential reproductive success among individuals within the competing sex; attributing SSD to the direct consequences of sexual selection without proper comparisons among all age and sex classes to determine the pattern of development of such differences, and without extensive behavioral observations and/or experimental studies implicating the importance of the trait(s) for reproductive success, is unjustified (e.g., Cooper and Vitt, 1989: 733; see also King, 1989; Shine, 1989, 1990; Anderson and Vitt, 1990; Hews, 1990a, 1990b). As an example, Cooper and Vitt (1989) showed that head size dimorphism in *S. undulatus* (males have heads larger than females of equivalent body size) is due to reduction in rate of head growth relative to body size growth in females, rather than strictly by an increase in male head size. Presumably, females invest mostly in body growth and reproduction at the expense of an increased head size once sexual maturity is reached. If this interpretation is correct, it is possible that many other examples of sexual dimorphism/dichromatism in *Sceloporus* represent compromises between opposing forces of sexual and natural selection, but this can only be verified by field observations or experiments (see also Vitt and Cooper, 1985). A detailed study of resource defense and sexual selection in a related territorial phrynosomatid, *Uta palmeri,* by Hews (1990a) revealed that differences in quality of male territories translated into differential male mating success (female mate choice based on male traits is limited in this species, as female distribution is determined by food distribution).

Territory quality in *U. palmeri* appears to act as a proximate mechanism of selection working indirectly on male morphology, with the exception of male head depth. Hews (1990a) showed that this single morphological trait was a direct target of selection, probably due to the biomechanical advantage that increased head depths conveyed for grasping other individuals (i.e., females during copulation). Hews (1990b) also studied patterns of allometry in *U. palmeri* adults and juveniles of both sexes, and showed that the observed patterns of differential growth are consistent with her interpretations of direct selection on adult male head depth. Hews (1990b) pointed out that additional information on such patterns in closely related species is necessary to determine if the patterns in *U. palmeri* represent a derived condition that developed in response to the currently observed patterns of selection. Detailed developmental and ecological studies cannot answer questions about evolutionary changes outside the proper phylogenetic context.

Stamps (1983) developed a general model of polygyny for territory-holding species of lizards, which are similar in overall pattern to, though not as thoroughly documented as, the *Uta palmeri* breeding structure described by Hews (1990a, 1990b). The general attributes of territorial lizards are: (1) single males cannot sequester and defend large "harems" of females; (2) females do not congregate in leks to actively choose suitable males; and (3) females must be actively courted—often repeatedly—within their own home ranges before they will mate with any male. These attributes limit male options to increase reproductive success, and Stamps argued (1983: 182) that insectivorous lizards can only evolve polygynous mating systems if: (1) males arrange their home ranges to overlap female home ranges; and (2) males must increase their home range sizes so as to encompass more than one female home range. A third mechanism must insure that there is greater variance in mating success for males than for females, and one obvious mechanism is territoriality. If some males defend enlarged home ranges against other males, and thereby gain exclusive breeding rights over females in their territories (relative to subordinate males with smaller territories with fewer or no females) then a polygynous mating system would result.

A similar mating system could evolve in a nonterritorial species if males had enlarged home ranges that extensively overlapped female home ranges. The result would be a wider choice of males per female, and if females make choices on the basis of certain male traits—large size, bright colors, enticing scents, flamboyant courtship displays, etc.—sufficient between-male variability in these traits would increase variance in male reproductive success. This model assumes active female choice on the basis of one or more of these traits, but it would lead to sexual selection and polygyny. While this remains a theoretical possibility, there is little direct support for active female choice in *Sceloporus* or related genera.

A third alternative to the hypothesis of territoriality for reproductive purposes is the trophic hypothesis, which suggests that male home range size is determined by trophic requirements (Stamps, 1983: 184). These two hypotheses make different predictions about male : female home range ratios. If males defend oversized home ranges in order to increase reproductive success, then male : female home range ratios should be higher in breeding territorial lizards than in breeding nonterritorial lizards. Home range ratios are predicted to be similar between territorial and nonterritorial species if home ranges are determined by male trophic requirements. A related pair of predictions is that, under the reproductive success hypothesis, home range ratios should increase in breeding territorial *individuals* relative to nonbreeding individuals within a species, while home range ratios should be similar under the trophic hypothesis. Provisional support for the reproductive success hypothesis is summarized by Stamps (1983: 187): *S. jarrovi* female home range sizes are the same in breeding and nonbreeding seasons, while male territory sizes increase in the breeding season; and *S. virgatus* male territory sizes increase while female territories decrease during the breeding season. Recent experimental studies of *S. graciosus* have shown that manipulation of female densities does not influence male territory size, perhaps because long-term maintenance of a stable territory size maximizes male reproductive success in this relatively long-lived species (Deslippe and M'Closkey, 1991).

Mating systems in territorial species may also be influenced by selection for avoidance of competition between sexes, which predicts that the most pronounced sexual-size dimorphism (SSD) will occur in monogamous species (Stamps, 1983: 189–190). The alternative is that SSD is due to intrasexual selection for mates among males, in which case polygynous species should show the most pronounced sexual dimorphism.

As we discuss below, other selective forces can influence body size ratios, and frequently may conflict with sexual selection when it is present. The hypotheses of Stamps and others, however, coupled with the large base of preliminary data already available for *Sceloporus,* provide conceptual structure and guidelines for future research efforts. A deeper understanding of the evolution of social behavior and territoriality in lizards will likely require integration of studies of energetic and physiological aspects of displays, chemical nature of color pigments and their hormonal and neural control, functional significance of the different modes of communication, and sources of variation, with robust estimates of phylogenies. The genus *Sceloporus* however, is amenable to both rigorous quantitative field and experimental studies of all of these phenomena, and should be a high-priority group for more sophisticated study.

VI. ECOLOGY AND THE EVOLUTION OF LIFE-HISTORY STRATEGIES

Certain species of *Sceloporus* have been used extensively for investigating patterns of life-history evolution, and various aspects of population, physiological, and community ecology. Tinkle et al. (1970) and Dunham et al. (1988b) presented extensive analyses of lizard reproductive strategies, including data from up to 25 populations of various species of *Sceloporus* (over 20% of records of Dunham et al.), and formulated hypotheses regarding the evolution of life-history strategies. *Sceloporus* has figured prominently in these studies for reasons mentioned in the Introduction, but also because most species have relatively short generation times and ecological and reproductive characteristics that are reasonably easy to evaluate. For similar reasons, they have been used in detailed studies of physiological ecology (Sinervo and Adolph, 1989; Adolph, 1990; Grant, 1990; Sinervo, 1990; Sinervo and Huey, 1990), interspecific competition (Dunham, 1980), and community structure (Pianka, 1986: ch. 5, 8).

Demography. The first comparative life-history studies, including reproductive anatomy, courtship, and territoriality, date back to Woodbury and Woodbury (1945) and Blair (1960), while Tinkle (1967, 1969, 1972, 1973), Tinkle et al. (1970), and Tinkle and Ballinger (1972), Vinegar (1975b), Tinkle and Dunham (1986), and Dunham (1981) demonstrated the importance of long-term ecological studies in *Sceloporus, Urosaurus,* and *Uta.* Virtually all measured life-history traits, such as timing of reproduction, number of offspring per clutch, number of clutches per season, age to first reproduction, and size of offspring, have been shown to vary geographically within species (see also Grant and Dunham, 1990; Benabib, 1991).

The most extensively studied oviparous species has been *S. undulatus.* Ferguson et al. (1990) summarized the information derived from a large number of geographic studies for 10 populations of *S. undulatus* from diverse habitats and scattered geographic regions. These populations were characterized by variation in virtually all demographic and life-history parameters measured, including: number of clutches per year (2–4), mean clutch size (6.3–11.8), minimum SVL of adult females (52–66 mm), mean SVL of adult females (57–75 mm), mean age at first reproduction (1 or 2 years), and both juvenile and adult survivorship. In spite of the wealth of information derived from this single species, Ferguson et al. (1990) argued for long-term, in-depth studies not only of population demographic parameters, but also of the genetics of intra- and interpopulation variability. As an extension of these earlier studies, Ferguson and Snell (1986) used intraspecific variation in basic life-history characteristics to formulate and test a series of hypotheses concerning tradeoffs and evolution of reproductive traits (number of eggs, and egg and hatchling size).

Sceloporus merriami has been studied extensively by Dunham (1978, 1981) and colleagues (Ruby and Dunham, 1984; Grant and Dunham, 1988, 1990; Grant, 1990; see also W. P. Porter, 1989) in west Texas. These studies show that, as in *S. undulatus,* age-specific survival, age-specific fecundity, age-specific body size and growth rate, individual home range size and foraging success, and prehibernation lipid levels all vary significantly among seasons and among years. This is due to seasonal and annual variation in the arthropod prey base, which itself varies as a function of precipitation (Dunham, 1978). Three populations of *S. merriami* have been extensively studied along an elevational gradient which spans the full elevation range of the species in west Texas (560 to 1609 m, see Ruby and Dunham, 1984). These studies are discussed in more detail below, but in summary they reveal many of the proximate factors acting on life-history traits within a species.

Similar studies were carried out by Benabib (1991) for the tropical species *S. variabilis* at two sites separated by an elevation of almost 1000 m, in a tropical area of the Mexican state of Veracruz. The high-elevation site was distinctly more seasonal than the low-elevation locality, even though both were in close geographic proximity (within 20 km), and shifted life-history traits in different directions. *Sceloporus variabilis* at high elevations had shorter growing seasons, delayed maturity, smaller egg size, and shorter total reproductive season relative to low-elevation conspecifics.

Another reasonably well-studied oviparous species is *S. scalaris.* Ortega and Barbault (1984), Newlin (1976), and Ballinger and Congdon (1981) examined geographically separated populations of *S. scalaris,* and showed that males in northern populations reach a reproductive maximum in February (based on testicular weight; Ballinger and Congdon, 1981; Newlin, 1976), while males in Mexican populations (Durango) reach a reproductive maximum in April (Ortega and Barbault, 1984). In addition, while females are singly brooded in Arizona, they are doubly brooded in Durango (Ortega and Barbault, 1984).

Sceloporus jarrovi has provided a wealth of data on geographic variation in life-history parameters in a viviparous species (Ballinger, 1973, 1979; Ruby, 1976, 1977a, 1977b, 1978; Ruby and Dunham, 1984; Beuchat, 1986; Beuchat and Ellner, 1987). Ballinger (1973, 1979) found substantial life-history differences between high (2542 m) and low (1675 m) elevation populations in Arizona, in that survivorship was consistently higher (although not significantly so for any single year class except neonates) at the high-elevation site. Similarly, although the size-fecundity relationships were the same at both elevations, the average size of mature females at high elevations was greater and, as a result, the mean number of offspring per female was also greater at high elevations. The most striking difference in life histories, however, was the age of first reproduction. Up to 84 percent of females from the low-elevation population (range 41–84% in different years) bred in the fall of their first year (when they were only 4–5 months old), while none of the high-elevation females bred in their first year. As a result, the estimated average generation time differed by 0.74 year (1.86 vs. 2.60 years). A further aspect of the life history of *S. jarrovi* is that they are active all year, but abandon warm-weather territories and form winter aggregations (Ruby, 1977b) in which gravid females regulate their body temperatures at lower levels than males and nongravid females (Beuchat, 1986; Beuchat and Ellner, 1987).

The detail with which these data represent natural variation in life-history traits has been a critical source of quantitative information for testing hypotheses of the evolution of life-history strategies. Beuchat and Ellner (1987) used *S. jarrovi* to develop and test a two-component model of the thermoregulatory biology of live-bearing lizards, including demographic and physiological models. Their model isolates the tradeoffs in gravid females necessary to maximize fitness and survival, in contrast to the behavior and thermal selection displayed by males and nongravid females.

Ferguson et al. (1990) outlined general requirements for testing the genetic basis of other life-history phenomena such as growth rate, adult body size, clutch size, and weight. Although this study used *Uta stansburiana* as a model, similar studies have been or could be carried out within *Sceloporus.* For example, recent studies have shown that patterns of geographic variation and the genetics of life-history characteristics can be effectively studied in *Sceloporus* by experimental manipulation. Sinervo (1990) and Sinervo and Huey (1990) investigated tradeoffs among offspring number, size, and performance traits by manipulating offspring size through removal of yolk materials from fertilized eggs taken from populations along elevational and latitudinal gradients. These workers demonstrated both geographic variability and among-family variability in growth rates, egg weights, and hatchling sizes in *S. occidentalis,* verifying a genetic basis for those traits, and thus a potential for selection to modify them.

Along different lines of inquiry, Ruby and Dunham (1984), Grant (1990), and Grant and Dunham (1988, 1990) investigated the influence of the interactions of food abundance and operative environmental temperatures (thermal microhabitats amenable to lizard activity) along an elevational gradient, on several life-history traits in *S. merriami.* They showed a number of complex between-sex and between-population differences in daily activity schedules, home range sizes, growth rates, and the size at first reproduction, presumably reflecting different constraints and tradeoffs to elevational shifts in selective forces along this transect. For example, the high-elevation (1609 m) site was characterized by more rain, higher food availability, and cooler temperatures relative to mid- and low-elevation sites (1036 and 560 m, respectively). At the high site, *S. merriami* was active throughout the day, while lizard body temperatures (T_b) were higher during inactivity and late-afternoon activity at the lower sites. At the lowest site, low food availability, reduced foraging time, and higher T_b constrained energy budgets and resulted in lower individual activity and growth rates. Paradoxically, lizards at the highest site, which was the most food-rich, also exhibited low daily growth rates. This likely resulted from increased energy expenditures, the longer activity period, and lower food processing rates (lower inactive T_b). These and other important differences among populations in life-history characteristics are influenced by interactions between resource levels and biophysical constraints, which act as proximate environmental factors. However, the resulting differences in age-specific resource allocation to growth, storage, and reproduction may significantly affect fitness.

Sinervo and Adolph (1989) studied the thermal sensitivity of *S. graciosus* and *S. occidentalis* hatchlings, and showed that variation in the thermal environment could cause phenotypic variation in growth rate, and hence hatchling size. These species differed in both the magnitude and thermal sensitivity of growth rate, due to interspecific differences in behavioral thermoregulation. Further, these authors also found evidence of among-family variation in growth rates in *S. occidentalis,* suggesting a partial genetic basis to growth rates (in addition to the behavioral and physiological components). Hatchling size is positively correlated with sprint speed in *S. occidentalis,* and may therefore have important fitness consequences. (Sprint speed is a commonly used estimate of performance because it is constant and repeatable in individuals; see Huey and Dunham, 1987.) These kinds of detailed field and experimental studies (see also Sinervo and Losos, 1991) provide the basis for establishing a theoretical framework within which to examine intra- and interspecific variation in characters related to age-specific resource allocation to growth and reproduction, and the physiological and genetic constraints of the evolution of life-history traits.

Although interspecific comparisons of life-history traits are accumulating (e.g., Ballinger [1973] compared allopatric populations of *S. jarrovi* and *S. poinsetti*; Derickson [1976] compared reproductive traits of sympatric populations of *S. graciosus* and *S. undulatus*; Tinkle and Dunham [1986] compared life history and demographic variation in sympatric populations of *S. clarki* and *S. undulatus*; and Adolph [1990] compared the influence of behavioral thermoregulation on microhabitat use in areas of sympatry between *S. graciosus* and *S. occidentalis*), few of these studies have been carried out in a phylogenetic framework. This is unfortunate in that a recovered phylogenetic history could refine our interpretations, and lead to development of more explicit hypotheses of the evolution of life-history traits.

Reproductive cycles. Seasonal reproductive cycles have been documented in a variety of temperate and tropical-montane species of *Sceloporus*, including both oviparous and viviparous species. Altlund (1941) and Woodbury and Woodbury (1945) were the first to document seasonal reproductive cycles in oviparous species (*S. graciosus* and *S. undulatus*). Since then, most research has centered on only six species representing three species groups, including: *S. graciosus* (Goldberg, 1975a), *S. occidentalis* (Jameson and Allison, 1976; Goldberg, 1973, 1974, 1975b), and *S. undulatus* (McKinney and Marion, 1985) of the *undulatus* group and *S. cyanogenys* (Crisp, 1964), *S. jarrovi* (Goldberg, 1970, 1971; Beuchat, 1986), and *S. poinsetti* (Ballinger, 1973) of the *torquatus* group. Additional species studied in some detail include the oviparous taxa *S. orcutti* (Mayhew, 1963), *S. scalaris* (Newlin, 1976), and *S. virgatus* (Ballinger and Ketels, 1983); and the viviparous taxa *S. formosus* (Guillette and Sullivan, 1985), *S. grammicus* (Guillette and Casas-Andreu, 1980, 1981; Ortega, 1986), *S. malachiticus* (Marion and Sexton, 1971), and *S. mucronatus* (Mendez de la Cruz et al., 1988). Vitt (1977) summarized data for several southwestern U.S. species of both parity types, and Benabib's (1991) recent work provides detailed data on seasonal reproductive cycles in two populations of *S. variabilis* in tropical environments.

The choice of species in the majority of these studies appears to have been based primarily on availability, i.e., most have included species that are primarily temperate in spite of the fact that over 75 percent of all species are subtropical or tropical in distribution. Nevertheless, two significant contrasting patterns have emerged. First, in oviparous species gonadal development begins in late summer before hibernation, while gonadal maturation, ovulation, and mating occurs in early spring, and hatching occurs in late summer. The exception is the tropical *S. variabilis*, which responds primarily to seasonal rainfall patterns (Benabib, 1991). Viviparous species, in contrast, breed in the fall, with embryonic development occurring during the winter months. In at least one species (*S. grammicus*), maximal male and female gonadal development are out of phase, with male reproductive activity being initiated in the spring (February) while female reproductive activity begins in mid-summer (July) near the end of the male cycle. *Sceloporus malachiticus*, a tropical viviparous species, is characterized by coordinated development of male and female reproductive activity (summer and fall in both, with young born in January). The second contrast in reproductive patterns is that oviparous species tend to be multiply brooded and to produce relatively small clutches, while the viviparous species appear to all be singly brooded, but produce relatively large clutches.

The ecological significance of oviparity versus viviparity in different species of *Sceloporus*, as well as the factors that influence reproductive cycles, have been extensively investigated. The contrast in behavior between species exhibiting these reproductive modes is substantial, but because the taxa that have been studied represent a more-or-less arbitrary assemblage of species, answers to critical questions on the significance of these ecological and behavioral differences are difficult to provide.

Observations on life-history strategies, reproductive cycles, and SSD suggest that additional comparative studies could be proposed to explicitly address the relationship between female body size and fecundity. Conventional life-history theory hypothesizes that increased female body size allows for increased production of ova (see above section on Sexual Size Dimorphism), which has been invoked to explain why females are usually larger than males across broad groups of organisms (zooplankton, insects, fishes, amphibians, reptiles, and birds; see Shine, 1988). It is important to emphasize that selection is predicted to favor the evolution of traits that maximize *lifetime* reproductive success, rather than instantaneous reproductive success in any single breeding season. As Shine (1988) pointed out, however, a female's particular clutch size reflects a tradeoff between her own growth and reproduction, so that the fecundity advantage model should apply mainly to species that are not energy-limited. In such species, female body size should evolve to be larger, relative to males, than it does in energy-limited species. Determination of energy limitation is difficult, but Shine (1988) produced correlational evidence that appeared to refute this prediction of the size-fecundity model. He compared female : male size ratios in closely related groups of lizards differing in fecundity (invariant vs. variable clutch sizes, as in *Anolis* vs. other iguanians, for example), and showed that the proportion of species in which females were larger than males was similar in both fecundity types. Shine's comparisons were limited to higher taxonomic categories (geckos/pygopodids, iguanians, skinks, teiids, etc.), and he recognized that factors such as offspring size, frequency of clutches, and other possibilities could have confounded his results. However, the diversity of fecundity levels, reproductive cycles, and female : male body size ratios present in *Sceloporus* make it ideal for high resolution, "close in" phylogenetically structured studies of life-history theory.

Further, recent advances in theory suggest new approaches. For example, Congdon (1989) has identified four classes of proximate constraints acting on the life histories of desert lizards, including: (1) absolute resource availability; (2) harvest rate limitations; (3) process limitations (mediated by basking behavior and thermal constraints); and (4) limitations on resource harvest or processing imposed by risk of predation. These factors collectively determine the total amount of energy ultimately captured by individual lizards. Given this total budget, a female must then allocate portions to reproductive effort, optimal egg size, paternal investment, and her own growth and maintenance. These factors interact with others to influence birth and death rates, and rates of emigration and immigration in populations, and effectively couple the biophysical and physiological ecology of individuals with population-level processes and patterns (Dunham et al., 1989). A life history can be defined as the set of interactions whereby variation in environmental factors is transduced into age- or size-specific birth rates and probabilities of mortality and migration, and it can be thought of as a time-ordered sequence of age-specific allocation decisions that are subject to the above-mentioned tradeoffs, constraints, and environmental influences. Selection should favor those life histories (heritable sets of allocation rules) that result in greatest expected lifetime reproductive success (fitness) over the spectrum of environmental variation experienced by individuals in the population in question (Dunham et al., 1989: 336–337). Dunham et al. then presented a model attempting to make explicit the interaction of environmental variation with the set of important tradeoffs and constraints acting within any system to produce variation within and among populations in life-history phenotypes, demography, and emergent population properties (1989: 338). Dunham et al. then used *S. merriami* as a model system for these kinds of investigations, and suggested additional linkages between daily time budgets and integrated seasonal energy-mass budgets and critically unexplored aspects of life-history evolution.

The success of these kinds of studies, coupled with the amenability of *Sceloporus* to experimental testing (Tsuji et al., 1989; van Berkum and Tsuji, 1987; Sinervo and Losos, 1991) and manipulation of important life-history parameters (Dunham, 1980; Sinervo, 1990; Sinvervo and Adolph, 1989; Sinervo and Huey, 1990; see also Sinervo and Licht, 1991), implies that species of this genus will continue to figure prominently in future long-term ecological research.

VII. OTHER ISSUES

There are many other research possibilities for the genus *Sceloporus* that are not discussed in this review, but two others deserve at least brief mention. First, *Sceloporus* is one of only a very few reptilian squamate genera known in which isozyme data strongly suggest evidence for independent regional gene duplications. Extensive population surveys have revealed "fixed heterozygosity" in *S. graciosus* and some populations of *S. grammicus* for the enzyme glycerol-3-phosphate dehydrogenase (G3PDH, E.C. 1.1.1.8). In both cases, independent electromorphic heterozygosity at each homodimer isozyme, and consistently strong expression of interlocus heterodimer isozymes have been demonstrated in both liver and muscle extracts (Sites and Murphy, 1991). The first two observations constitute the strongest evidence for two loci (fixed heterozygosity and independently segregating electromorphs at each of the two homodimer isozymes) that can be collected in the absence of breeding studies, and the third observation suggests that the duplication of G3PDH has occurred relatively recently in *Sceloporus* (see details in Sites and Murphy, 1991). Additional species will need to be surveyed for patterns of isozyme expression at this enzyme to determine the phylogenetic distribution of this duplication, and molecular approaches will be needed to identify the number and distribution of functional loci and pseudogenes in the genome of species suspected of having duplicate loci, but *Sceloporus* offers an accessible vertebrate system likely to yield much new information about patterns and processes of gene duplication and silencing.

Second, a recent study by Gadsden (1988) reported some interesting relationships between ectoparasites (mites) and *Sceloporus* along an elevational transect in the Sierra de Tepoztlan south of Mexico City. Gadsden sampled several populations in the *S. grammicus* complex at elevations of 1950 m (the "low-elevation" 2n = 32 race, at Municipio de Tlalnepantla, Morelos), 2400 m (2n = 34 [F6], part of *S. palaciosi* as described by Lara-Gongora, 1983; at Felipe Neri, Morelos), and at 3050 m (the "high-elevation" 2n = 32 race, *S. anahuacus* as described by Lara-Gongora, 1983; at CICYTEC, see table 2 of Gadsden, 1988, for exact localities). A total of 133 lizards were examined for their mite faunas, with the following results: the mite *Eutrombicula alfreddugesi* (Trombiculidae) occurred on lizards at all three localities, while a second species, *Geckobiella texana* (Pterygosomatidae), occurred only on the "high" 2n = 32 lizards, and a third species, *Hirstiella pelaezi* (Pterygosomatidae), was confined to the "low" 2n = 32 lizards. These data are insufficient to permit any kind of generalization for *Sceloporus,* but the apparent host specificity shown by *Eutrombicula* and *Geckobiella* suggests that *Sceloporus* offers interesting possibilities for cospeciation studies of host-parasite assemblages. Empirical methods of investigating these kinds of coevolutionary questions have become increasingly rigorous (Brooks, 1987, 1990; Hafner and Nadler, 1990), and *Sceloporus* is amenable to any of these approaches for studies of either ectoparasite or endoparasite faunas.

SUMMARY

This review summarizes alternative ideas of the phylogenetic history of the genus *Sceloporus,* beginning with the morphologically based studies of H. M. Smith. Smith's phylogenetic hypotheses are summarized for species-group relationships within the genus, and for species relationships within species groups, insofar as these could be determined. The phylogenetic hypotheses of K. R. Larsen and W. W. Tanner, which were based on phenetic analyses of cranial osteology and combinations of morphological, karyotypic, behavioral, and distributional data, were then summarized in the same manner. We also present tabular summaries of the osteological characters and ratios used by Larsen and Tanner. We then review and update the largely unpublished chromosomal data set of W. P. Hall, incorporate many unpublished data of C. J. Cole, and summarize the cytogenetically based phylogenetic hypotheses of Hall in the same manner as for the Smith and Larsen-Tanner hypotheses. Distributional maps are presented for all species groups recognized by Hall, and the three sets of hypotheses are compared to emphasize areas of congruence and disagreement.

The second section of the review summarizes much of the recent work on *Sceloporus* for various ecological and evolutionary issues, and highlights the value of this genus in such studies if in the future they can be placed within a comparative (i.e., phylogenetic) context. Specific discussions focus on questions in: (1) historical biogeography; (2) the evolution of viviparity; (3) the evolution of heteromorphic sex chromosomes; (4) speciation and hybridization issues; (5) social behavior and sexual selection; (6) ecology and life-history studies; and (7) gene duplication and host-parasite coevolution. We summarize the data available for *Sceloporus* under each of these themes, and argue that all of these issues could continue to be profitably studied in *Sceloporus.* In the introduction of the paper, we quote H. M. Smith's 1939 opinions regarding the many "attractive problems" he saw in *Sceloporus* at that time. We can only add here that, given our rich contemporary theoretical vantage point and the technology available for both data collection and analysis, Smith's earlier pronouncement is more true today than ever before.

REFERENCES

Adkins, R. M., K. McBee, C. A. Porter, and R. J. Baker
1991. Hybrid breakdown in *Peromyscus leucopus* and examination of the recombination breakdown model. J. Mammal. 72: 535–541.

Adolph, S. C.
1990. Influence of behavioral thermoregulation on microhabitat use by two *Sceloporus* lizards. Ecology 71: 315–327.

Ajioka, J. W., and W. Eanes
1989. The accumulation of P elements on the tip of the X chromosome in populations of *Drosophila melanogaster.* Genet. Res. 53: 1–6.

Altlund, P. D.
1941. Annual reproductive cycle of the male fence lizard. J. Elisha Mitchell Sci. Soc. 57: 73–83.

Alvarez-C., S., C. P. Gallina-T., A. Gonzales-R., and A. Ortega
1988. Herpetofauna. *In* L. Arriaga and A. Ortega (eds.), La Sierra de la Laguna de Baja California Sur, pp. 167–184. Centro de Investigaciones Biologícas de Baja California Sur. A.C. Pub. No. 1. La Paz, B.C.S., Mexico.

Anderson, R. A., and L. J. Vitt
1990. Sexual selection versus alternative causes of sexual dimorphism in teiid lizards. Oecologia 84: 145–157.

Arevalo, E., C. A. Porter, A. Gonzales, F. Mendoza, J. L. Camarillo, and J. W. Sites, Jr.
1991. Population cytogenetics and evolution of the *Sceloporus grammicus* complex (Iguanidae) in central Mexico. Herpetol. Monogr. 5: 79–115.

Arnold, S. J.
1983. Sexual selection: the interface of theory and empiricism. *In* P. G. Bateson (ed.), Mate choice, pp. 67–107. New York: Cambridge Univ. Press.

Asmussen, M. A., J. Arnold, and J. C. Avise
1989. The effects of assortative mating and migration on cytonuclear associations in hybrid zones. Genetics 122: 923–934.

Atchley, W. R., C. T. Gaskins, and D. Anderson
1974. Statistical properties of ratios. I. Empirical results. Syst. Zool. 25: 137–148.

Atwater, T.
1970. Implications of plate tectonics for the Cenozoic tectonic evolution of western North America. Geol. Soc. Am. Bull. 81: 3513–3536.

Avise, J. C.
1977. Is evolution gradual or rectangular? Evidence from living fishes. Proc. Nat. Acad. Sci. USA 74: 5083–5087.

Avise, J. C., and F. J. Ayala
1975. Genetic change and rates of cladogenesis. Genetics 81: 757–773.
1976. Genetic differentiation in speciose versus depauperate phylads: evidence from the California minnows. Evolution 30: 46–58.

Axtell, R. W.
1956. A solution to the long-neglected *Holbrookia lacerata* problem and the description of two new subspecies of *Holbrookia.* Bull. Chicago Acad. Sci. 10: 163–179.

Axtell, R. W., and C. A. Axtell
1971. A new lizard (*Sceloporus jarrovi cyanostictus*) from the Sierra Madre of Coahuila, Mexico. Copeia 1971: 89–98.

Baker, R. H., M. W. Baker, J. D. Johnson, and R. G. Webb
1981. New records of mammals and reptiles from northwestern Zacatecas, Mexico. Southwest. Nat. 25: 568–569.

Baker, R. J., M. B. Qumsiyeh, and C. S. Hood

1987. Role of chromosome banding patterns in understanding mammalian evolution. Pp. 67–96, *In* H. H. Genoways (ed.), Current mammalogy. New York: Plenum.

Ballinger, R. E.
1973. Comparative demography of two viviparous iguanid lizards (*Sceloporus jarrovi* and *Sceloporus poinsetti*). Ecology 54: 269–283.
1979. Intraspecific variation in demography and life history of the lizard, *Sceloporus jarrovi* along an altitudinal gradient. Ecology 60: 901–909.

Ballinger, R. E., and J. D. Congdon
1981. Population ecology and life history strategy of a montane lizard (*Sceloporus scalaris*) in southeastern Arizona. J. Nat. Hist. 15: 213–222.

Ballinger, R. E., and D. J. Ketels
1983. Male reproductive cycle in the lizard *Sceloporus virgatus*. J. Herpetol. 17: 99–102.

Barton, N. H., and G. M. Hewitt
1985. Analysis of hybrid zones. Ann. Rev. Ecol. Syst. 16: 113–158.
1989. Adaptation, speciation and hybrid zones. Nature 341: 497–503.

Bell, G.
1989. A comparative method. Am. Nat. 133: 553–571.

Benabib, M.
1991. Life history and ecology of *Sceloporus variabilis* in Los Tuxtlas, Veracruz, Mexico. Ph.D. diss., Univ. Georgia, Athens.

Beuchat, C. A.
1986. Reproductive influence on the thermoregulatory behavior of a live-bearing lizard. Copeia 1986: 971–979.

Beuchat, C. A., and S. Ellner
1987. A quantitative test of life history theory: thermoregulation by a viviparous lizard. Ecol. Monogr. 57: 45–60.

Blackburn, D. G.
1982. Evolutionary origins of viviparity in the Reptilia. I. Sauria. Amphibia–Reptilia 3: 185–205.

Blair, W. F.
1960. The rusty lizard. A population study. Austin: Univ. Texas Press.

Borgia, G., and K. Collis
1990. Parasites and bright male plumage in the satin bowerbird (*Ptilonorhynchus violaceus*). Am. Zool. 30: 279–285.

Boulenger, G. A.
1897. A revision of the lizards of the genus *Sceloporus*. Proc. Zool. Soc. London 1897: 474–522.

Boyce, M. S.
1990. The Red Queen visits sage grouse leks. Am. Zool. 30: 263–270.

Boyer, T. H., H. M. Smith, and G. Casas-Andreu
1982. The taxonomic relationships of the Mexican lizard species *Sceloporus horridus*. Bull. Maryland Herpetol. Soc. 18: 189–191.

Bradbury, J. W., and M. B. Anderson
1987. (Eds.). Sexual selection: testing the alternatives. Dahlem Konferenzen. Chichester, U.K.: John Wiley.

Bromwich, C. R., and J. J. Schall
1986. Infection dynamics of *Plasmodium mexicanum*, a malarial parasite of lizards. Ecology 67: 1227–1235.

Brooks, D. R.
1985. Historical ecology: a new approach to studying the evolution of ecological associations. Ann. Missouri Bot. Gard. 72: 660–680.
1987. Analysis of host-parasite coevolution. Int. J. Parasitol. 17: 291–297.
1990. Parsimony analysis in historical biogeography and coevolution: methodological and theoretical update. Syst. Zool. 39: 14–30.

Brooks, D. R., and D. A. McLennan
1991. Phylogeny, ecology, and behavior. A research program in comparative biology. Chicago: Univ. Chicago Press.

Brown, W. L., Jr.
1957. Centrifugal speciation. Q. Rev. Biol. 32: 247–277.

Bull, J. J.
1980. Sex determination in reptiles. Q. Rev. Biol. 55: 3–21.
1983. Evolution of sex-determining mechanisms. Menlo Park, CA: Benjamin/Cummings.

Bull, J. J., and E. L. Charnov
1985. On irreversible evolution. Evolution 39: 1149–1155.

Bull, J. J., W. H. N. Gutzke, and M. G. Bulmer
1988. Nest choice in a captive lizard with temperature-dependent sex determination. J. Evol. Biol. 2: 177–184.

Burt, C. E.
1935. Notes on a collection of lizards from western Mexico and America. Trans. Am. Microsc. Soc. 54: 167–178.

Bussjaeger, L. J.
1971. Phylogenetic significance of the comparative ethology of the *spinosus* group of *Sceloporus*. Ph.D. diss., Norman: Univ. Oklahoma.

Carothers, J. H.
1984. Sexual selection and sexual dimorphism in some herbivorous lizards. Am. Nat. 124: 244–254.

Carpenter, C. C.
1962. Patterns of behavior in two Oklahoma lizards. Am. Midl. Nat. 67: 132–151.
1963. Patterns of behavior in three forms of the fringe-toed lizards (*Uma*—Iguanidae). Copeia 1963: 406–412.
1978. Comparative display behavior in the genus *Sceloporus* (Iguanidae). Milwaukee Publ. Mus. Contrib. Biol. Geol. 18: 1–71.

Carpenter, C. C., and G. W. Ferguson
1977. Variation and evolution of stereotyped behavior in reptiles. *In* C. Gans and D. W. Tinkle (eds.), Biology of the Reptilia 7: 335–554. London: Academic Press.

Carpenter, C. C., and G. Grubitz
1961. Time-motion study of a lizard. Ecology 42: 199–200.

Carpenter, J. M.
1989. Testing scenarios: wasp social behavior. Cladistics 5: 131–144.

Charlesworth, B.
1991. The evolution of sex chromosomes. Science 251: 1030–1033.

Charlesworth, D., and B. Charlesworth
1980. Sex differences in fitness and selection for centric fusions between sex chromosomes and autosomes. Genet. Res. 35: 205–214.

Charlesworth, B., J. A. Coyne, and N. H. Barton
1987. The relative rates of evolution of sex chromosomes and autosomes. Am. Nat. 130: 113–146.

Coates, D. J., and D. D. Shaw
1985. The chromosomal complement of reproductive isolation in the grasshopper *Caledia captiva*. III. Chiasma distribution patterns in a new chromosomal taxon. Heredity 53: 85–110.

Coddington, J. A.
1988. Cladistic tests of adaptational hypotheses. Cladistics 4: 3–22.

Cole, C. J.
1963. Variation, distribution, and taxonomic status of the lizard, *Sceloporus undulatus virgatus* Smith. Copeia 1963: 413–425.
1970. Karyotypes and evolution of the *spinosus* group of lizards in the genus *Sceloporus*. Am. Mus. Novitates 2431: 47 pp.
1971a. Karyotypes and relationships of the *pyrocephalus* group of lizards in the genus *Sceloporus*. Herpetologica 27: 1–8.
1971b. Karyotypes of five monotypic species groups of lizards of the genus *Sceloporus*. Am. Mus. Novitates 2450: 17 pp.
1972. Chromosomal variation in North American fence lizards (genus *Sceloporus*; *undulatus* species group). Syst. Zool. 21: 357–362.
1974. Chromosome evolution in selected treefrogs, including casque-headed species (*Pternohyla, Triprion, Hyla,* and *Smilisca*). Am. Mus. Novitates 2541: 10 pp.
1975. Karyotype and systematic status of the sand dune lizard (*Sceloporus graciosus arenicolous*) of the American Southwest. Herpetologica 31: 288–293.
1977. Chromosomal aberration and chromatid exchange in the North American fence lizard, *Sceloporus undulatus* (Reptilia: Iguanidae). Copeia 1977: 53–59.
1978. Karyotypes and systematics of the lizards in the *variabilis, jalapae,* and *scalaris* species groups of the genus *Sceloporus*. Am. Mus. Novitates 2653: 13 pp.
1983. Specific status of North American fence lizards, *Sceloporus undulatus* and *Sceloporus occidentalis,* with comments on chromosome variation. Am. Mus. Novitates 2768: 13 pp.

Cole, C. J., and C. H. Lowe
1968. The karyotype of a lizard (*Sceloporus virgatus*) and description of a spontaneous chromosomal aberration. J. Arizona Acad. Sci. 5: 128–130.

Cole, C. J., and T. R. Van Devender
1976. Surface structure of fossil and Recent epidermal scales from North American lizards of the genus *Sceloporus* (Reptilia, Iguanidae). Bull. Am. Mus. Nat. Hist. 156: 451–513.

Cole, C. J., C. H. Lowe, and J. W. Wright
1967. Sex chromosomes in lizards. Science 155: 1028–1029.

Collins, J. T.
1991. Viewpoint: a new taxonomic arrangement for some North American amphibians and reptiles. Herpetol. Rev. 22: 42–43.

Congdon, J. D.
1989. Proximate and evolutionary constraints on energy relations of reptiles. Physiol. Zool. 62: 356–373.

Cooper, W. E., Jr., and N. Burns
1987. Social significance of ventrolateral coloration in the fence lizards (*Sceloporus undulatus*). Anim. Behav. 35: 526–532.

Cooper, W. E., Jr., and G. W. Ferguson
1973. Estrogenic priming of color change induced by progesterone in the collared

lizard, *Crotaphytus collaris*. Herpetologica 29: 107–110.

Cooper, W. E., Jr., and L. J. Vitt

1984. Conspecific odor detection by the male broad-headed skink, *Eumeces laticeps*: effects of sex and site odor source and of male reproductive condition. J. Exp. Zool. 230: 199–209.

1989. Sexual dimorphism of head and body size in an iguanid lizard: paradoxical results. Am. Nat. 133: 729–735.

Cope, E. D.

1888. Catalogue of batrachians and reptiles of Central America and Mexico. Bull. U.S. Nat. Mus. 32: 1–98.

Cracraft, J.

1987. Species concepts and the ontology of evolution. Biol. Phil. 2: 329–346.

1988. Deep-history biogeography: retrieving the historical patterns of evolving continental biotas. Syst. Zool. 37: 221–238.

Cracraft, J., and R. O. Prum

1988. Patterns and processes of diversification: speciation and historical congruence in some Neotropical birds. Evolution 42: 603–620.

Crisp, T. M.

1964. Studies of reproduction in the female ovoviviparous lizard *Sceloporus cyanogenys* (Cope). Texas J. Sci. 16: 481.

Crother, B. I.

1990. Is "some better than none" or do allele frequencies contain phylogenetically useful information? Cladistics 6: 277–281.

Dasmann, M. M., and H. M. Smith

1974. A new sceloporine lizard from Oaxaca, Mexico. Great Basin Nat. 34: 231–237.

Davis, W. B., and H. M. Smith

1953. Lizards and turtles of the Mexican state of Morelos. Herpetologica 9: 100–108.

de Boer, P.

1986. Chromosomal causes for fertility reduction in mammals. *In* F. J. de Serres (ed.), Chemical mutagens 10: 427–467. New York: Plenum Press.

de Queiroz, K., and M. J. Donoghue

1988. Phylogenetic semantics and the species problem. Cladistics 4: 317–338.

1990. Phylogenetic systematics or Nelson's version of cladistics? Cladistics 6: 61–75.

Derickson, W. K.

1976. Ecological and physiological aspects of reproductive strategies in two lizards. Ecology 57: 445–458.

Deslippe, R. J., and R. T. M'Closkey

1991. An experimental test of mate defense in an iguanid lizard (*Sceloporus graciosus*). Ecology 72: 1218–1224.

Dickerson, M. C.

1919. Diagnoses of twenty-three new species and a new genus of lizards from Lower California. Bull. Am. Mus. Nat. Hist. 42: 461–477.

Dixon, J. R., C. A. Ketchersid, and C. S. Lieb

1972. A new species of *Sceloporus* (*undulatus* group; Sauria, Iguanidae) from Mexico. Proc. Biol. Soc. Washington 84: 307–312.

Dobson, F. S.

1985. The use of phylogeny in behavior and ecology. Evolution 39: 1384–1388.

Donoghue, M. J.

1989. Phylogenies and the analysis of evolutionary sequences, with examples from seed plants. Evolution 43: 137–156.

Douglas, M. E., and J. C. Avise

1982. Speciation rates and morphological divergence in fishes: tests of gradual versus rectangular modes of evolutionary change. Evolution 25: 156–167.

Dunham, A. E.

1978. Food availability as a proximate factor influencing individual growth rates in the iguanid lizard *Sceloporus merriami*. Ecology 59: 770–778.

1980. An experimental study of interspecific competition between the iguanid lizards *Sceloporus merriami* and *Urosaurus ornatus*. Ecol. Monogr. 50: 309–330.

1981. Populations in a fluctuating environment: the comparative population ecology of the iguanid lizards *Sceloporus merriami* and *Urosaurus ornatus*. Misc. Publ. Mus. Zool. Univ. Michigan (158): 1–62.

Dunham, A. E., B. W. Grant, and K. L. Overall

1989. Interfaces between biophysical and physiological ecology and the population ecology of terrestrial vertebrate ectotherms. Physiol. Zool. 62: 335–355.

Dunham, A. E., P. J. Morin, and H. M. Wilbur

1988a. Methods for the study of reptile populations. *In* C. Gans and R. Huey (eds.), Biology of the Reptilia 16: 331–386. New York: A. R. Liss.

Dunham, A. E., D. B. Miles, and D. N. Reznick

1988b. Life history patterns in squamate reptiles. *In* C. Gans and R. Huey (eds.), Biology of the Reptilia 16: 441–511. New York: A. R. Liss.

Duvall, D.

1979. Western fence lizard, *Sceloporus occidentalis*, chemical signals. I. Conspecific discrimination and release of a species-typical display. J. Exp. Zool. 210: 331–326.

1981. Western fence lizard (*Sceloporus occidentalis*) chemical signals. II. A replication with naturally breeding adults and a test of the Cowles-Phelan hypothesis of rattlesnake olfaction. J. Exp. Zool. 218: 351–361.

1982. Western fence lizard (*Sceloporus occidentalis*) chemical signals. III. An experimental ethogram of conspecific body licking. J. Exp. Zool., 221: 23–26.

Eldredge, N., and S. J. Gould
1972. Punctuated equilibria: an alternative to phyletic gradualism. *In* T. J. Schopf (ed.), Models in paleobiology, pp. 82–155. San Francisco: Freeman.

Ellis-Quinn, B. A., and C. A. Simon
1991. Lizard homing behavior: the role of the parietal eye during displacement and radio-tracking, and time-compensated celestial orientation in the lizard *Sceloporus jarrovi*. Behav. Biol. Sociobiol. 28: 397–407.

Endler, J. A.
1982. Problems in distinguishing historical from ecological factors in biogeography. Am. Zool. 22: 441–452.

1986. Natural selection in the wild. Monogr. Pop. Biol. 21. Princeton, NJ: Princeton Univ. Press.

Etheridge, R.
1964. The skeletal morphology and systematic relationships of sceloporine lizards. Copeia 1964: 610–631.

Etheridge, R., and K. de Queiroz
1988. A phylogeny of Iguanidae. *In* R. Estes and G. Pregill (eds.), Phylogenetic relationships of lizard families: essays commemorating Charles L. Camp, pp. 283–368. Stanford, CA: Stanford Univ. Press.

Felsenstein, J.
1974. The evolutionary advantage of recombination. Genetics 78: 737–756.

1985. Phylogenies and the comparative method. Am. Nat. 125: 1–15.

Ferguson, G. W.
1970. Variation and evolution of the push-up displays of the side-blotched lizard genus *Uta* (Iguindae). Syst. Zool. 19: 79–101.

Ferguson, G. W., and H. L. Snell
1986. Endogenous control of seasonal change of egg, hatchling, and clutch sizes of the lizard *Sceloporus undulatus garmani*. Herpetologica 42: 185–191.

Ferguson, G. W., H. L. Snell, and A. J. Landwer
1990. Proximate control of variation of clutch, egg, and body size in a west-Texas population of *Uta stansburiana stejnegeri* (Sauria: Iguanidae). Herpetologica 46: 227–244.

Ferris, V. R., and J. M. Ferris
1989. Why ecologists need systematists: the importance of systematics to ecological research. J. Nematol. 21: 308–314.

Fitch, H. S.
1978. Sexual size differences in the genus *Sceloporus*. Univ. Kansas Sci. Bull. 51: 441–461.

Fleishman, L. J.
1988. Sensory and environmental influences on display form in *Anolis auratus*, a grass anole from Panama. Behav. Ecol. Sociobiol. 22: 309–316.

Flores-Villela, O.
1992. Herpetofauna of Mexico: distribution and endemism. *In* T. Ramamoorthy, R. Bye, A. Lot, and J. Fa (eds.), Biological diversity of Mexico: origins and distributions, in press. New York: Oxford Univ. Press.

Frost, D. R., and R. Etheridge
1989. A phylogenetic analysis and taxonomy of iguanian lizards (Reptilia: Squamata). Occas. Pap. Mus. Nat. Hist. Univ. Kansas 81: 65 pp.

Frost, D. R., and D. M. Hillis
1990. Species in concept and practice: herpetological applications. Herpetologica 46: 87–104.

Gadsden-E., H.
1988. Comparacion altitudinal de ectoparasitos de lagartijas del complejo *Sceloporus grammicus* (Reptilia, Iguanidae) en la Sierra de Tepoztlan, Morelos, Mexico. Acta Zool. Mexicana 30: 21–31.

Gadsden-E., H., G. Casas-A., and J. W. Sites, Jr.
1989. Comparacion altitudinal morphologica entre poblaciones de dos citotipos cromosomicos del complejo *Sceloporus grammicus* (Sauria, Iguanidae) en la Sierra de Tepoztlan, Morelos, Mexico. Acta Zool. Mexicana 31: 3–25.

Gittleman, J. L., and M. Kot
1990. Adaptation: statistics and a null model for estimating phylogenetic effects. Syst. Zool. 39: 227–241.

Goldberg, S. R.
1970. Seasonal ovarian histology of the ovoviviparous iguanid lizard *Sceloporus jarrovi* Cope. J. Morphol. 132: 265–276.

1971. Reproductive cycle of the ovoviviparous iguanid lizard *Sceloporus jarrovi* Cope. Herpetologica 27: 123–131.

1973. Ovarian cycle of the western fence lizard *Sceloporus occidentalis*. Herpetologica 29: 284–289.

1974. Reproduction in mountain and lowland populations of the lizard *Sceloporus occidentalis*. Copeia 1974: 176–182.

1975a. Reproduction in the sagebrush lizard, *Sceloporus graciosus*. Am. Midl. Nat. 93: 177–187.

1975b. Yearly variations in the cycles of the lizard *Sceloporus occidentalis*. J. Herpetol. 9: 187–189.

Gorman, G. C.

1973. The chromosomes of the Reptilia, a cytotaxonomic interpretation. *In* A. B. Chiarelli and E. Capanna (eds.), Cytotaxonomy and vertebrate evolution, pp. 347–424. New York: Academic Press.

Gould, S. J., and N. Eldredge

1977. Punctuated equilibria: the tempo and mode of evolution reconsidered. Paleobiology 3: 115–151.

Gould, S. J., N. L. Gilinsky, and R. Z. German

1987. Asymmetry of lineages and the direction of evolutionary time. Science 236: 1437–1441.

Grant, B. W.

1990. Trade-offs in activity time and physiological performance for thermoregulatory desert lizards, *Sceloporus merriami*. Ecology 71: 2323–2333.

Grant, B. W., and A. E. Dunham

1988. Thermally imposed time constraints on the activity of the desert lizard *Sceloporus merriami*. Ecology 69: 167–176.

1990. Elevational covariation in environmental constraints and life histories of the desert lizard *Sceloporus merriami*. Ecology 71: 1765–1776.

Greene, H. W.

1986. Diet and arboreality in the emerald monitor, *Varanus prasinus*, with comments on the study of adaptation. Fieldiana, Zool. 31: 1–12.

Guillette, L. J., Jr.

1981. On the occurrence of oviparous and viviparous forms of the Mexican lizard *Sceloporus aeneus*. Herpetologica 37: 11–15.

1982. The evolution of viviparity and placentation in the high elevation, Mexican lizard *Sceloporus aeneus*. Herpetologica 38: 94–103.

1985. The evolution of egg retention in lizards. *In* G. Grigg, R. Shine, and H. Ehmann (eds.), The biology of Australian frogs and reptiles, pp. 379–386. Sydney: Surrey Beatty.

Guillette, L. J., Jr., and G. Casas-Andreu

1980. Fall reproductive activity in the high altitude Mexican lizard, *Sceloporus grammicus microlepidotus*. J. Herpetol. 14: 143–147.

1981. Seasonal variation in fat body weights of the Mexican high elevation lizard *Sceloporus grammicus microlepidotus*. J. Herpetol. 15: 366–371.

Guillette, L. J., Jr., and G. Lara

1986. Notes on the oviposition and nesting in the high-elevation lizard, *Sceloporus aeneus*. Copeia 1986: 232–233.

Guillette, L. J., Jr., and H. M. Smith

1985. Cryptic species in the Mexican lizard complex, *Sceloporus aeneus*. Bull. Maryland Herpetol. Soc. 21: 1–15.

Guillette, L. J., Jr., and W. P. Sullivan

1985. Reproductive and fat body cycles of the lizard, *Sceloporus formosus*. J. Herpetol. 19: 474–480.

Guillette, L. J., Jr., R. E. Jones, K. T. Fitzgerald, and H. M. Smith

1980. Evolution of viviparity in the lizard genus *Sceloporus*. Herpetologica 36: 1–15.

Guyer, C., and J. B. Slowinski

1991. Comparisons of observed phylogenetic topologies with null expectations among three monophyletic lineages. Evolution 45: 340–350.

Hafner, M. S., and S. A. Nadler

1990. Cospeciation in host-parasite assemblages: comparative analysis of rates of evolution and timing of cospeciation events. Syst. Zool. 39: 192–204.

Hagele, K.

1984. Different hybrid effects in reciprocal crosses between *Chironomus thummi thummi* and *Ch. th. piger* including spontaneous chromosome aberrations and sterility. Genetica 63: 105–111.

Hall, W. P.

1973. Comparative population cytogenetics, speciation, and evolution of the crevice-using species of *Sceloporus* (Sauria, Iguanidae). Ph.D. diss., Harvard Univ., Cambridge.

1977. Cascading chromosomal speciation and the paradoxical role of contact hybridization as a barrier to gene flow. Informally published, 91 pp. [cited by author's permission, see Hall, 1983, Modes of speciation and evolution in the sceloporine iguanid lizards. *In* Advances in herpetology and evolutionary biology, A. G. J. Rhodin and K. Miyata (eds.). Mus. Comp. Zool. Harvard Univ., Cambridge].

1980. Chromosomes, speciation, and evolution of Mexican iguanid lizards. Nat. Geog. Soc. Res. Rep. 12: 309–329.

1983. Modes of speciation and evolution in the sceloporine iguanid lizards. I. Epistemology of the comparative approach and introduction to the problem. *In* A. G. J. Rhodin and K. Miyata (eds.), Advances in herpetology and evolutionary biology, pp. 643–679. Cambridge, MA: Mus. Comp. Zool., Harvard Univ.

Hall, W. P., and R. K. Selander
1973. Hybridization of karyotypically differentiated populations in the *Sceloporus grammicus* complex (Iguanidae). Evolution 27: 226–242.

Hall, W. P., and H. M. Smith
1979. Lizards of the *Sceloporus orcutti* complex of the Cape region of Baja California. Breviora 452: 1–26.

Hamilton, W. D., and M. Zuk
1982. Heritable true fitness and bright birds: a role for parasites. Science 218: 384–387.

Harrison, R. G.
1991. Hybrid zones: windows on evolutionary process. *In* D. Futuyma and J. Antonovics (eds.), Oxford surveys in evolutionary biology 7: 69–128. London: Oxford Univ. Press.

Harvey, A. W.
1990. Sexual differences in contemporary selection acting on size in the hermit crab *Clibanarius digueti*. Am. Nat. 136: 292–304.

Harvey, P. H., and M. D. Pagel
1991. The comparative method in evolutionary biology. New York: Oxford Univ. Press.

Harvey, P. H., and A. Purvis
1991. Comparative methods for explaining adaptations. Nature 351: 619–624.

Hedin, M. C., P. D. Sudman, I. F. Greenbaum, and J. W. Sites, Jr.
1990. Synaptonemal complex analysis of sex chromosome pairing in the common ground skink, *Scincella lateralis*. Copeia 1990: 1114–1122.

Hewitt, G. M.
1988. Hybrid zones—natural laboratories for evolutionary studies. Trends Ecol. Evol. 3: 158–167.
1989. The subdivision of species by hybrid zones. *In* D. Otte and J. A. Endler (eds.), Speciation and its consequences, pp. 85–110. Sunderland, MA: Sinauer.

Hews, D. K.
1990a. Examining hypotheses generated by field measures of sexual selection on male lizards, *Uta palmeri*. Evolution 44: 1956–1966.
1990b. Resource defense, sexual selection and sexual dimorphism in the lizard *Uta palmeri*. Ph.D. diss., Univ. Texas, Austin.

Hillis, D. M., and C. Moritz (eds.)
1990. Molecular systematics. Sunderland, MA: Sinauer.

Hover, E. L.
1985. Differences in aggressive behavior between two throat color morphs in a lizard, *Urosaurus ornatus*. Copeia 1985: 933–940.

Huey, R. B.
1987. Phylogeny, history, and the comparative method. *In* M. E. Feder et al. (eds.), New directions in ecological physiology, pp. 76–98. New York: Cambridge Univ. Press.

Huey, R. B., and A. F. Bennett
1987. Phylogenetic studies of coadaptation: preferred temperatures versus optimal performance temperatures of lizards. Evolution 41: 1098–1115.

Huey, R. B., and A. E. Dunham
1987. Repeatability of locomotor performance in natural populations of the lizard *Sceloporus merriami*. Evolution 41: 1116–1120.

Huey, R. B., E. R. Pianka, and T. W. Schoener, (eds.).
1983. Lizard ecology: studies of a model organism. Cambridge: Harvard Univ. Press.

Imai, H. T., T. Maruyama, T. Gojobori, Y. Inoue, and R. Crozier
1986. Theoretical bases for karyotype evolution. 1. The minimum-interaction hypothesis. Am. Nat. 128: 900–920.

Jablonski, D.
1987. Heritability at the species level: analysis of geographic ranges of Cretaceous mollusks. Science 238: 360–363.

Jackson, J. F.
1973a. The phenetics and ecology of a narrow hybrid zone. Evolution 27: 58–68.
1973b. Distribution and population phenetics of the Florida scrub lizard, *Sceloporus woodi*. Copeia 1973: 746–761.

Jackson, L., and D. Hunsaker
1970. Chromosome morphology of sceloporine lizards (*Sceloporus occidentalis* and *S. graciosus*). Experientia 26: 198–199.

Jameson, E. W., Jr., and A. Allison
1976. Fat and breeding cycles in two montane populations of *Sceloporus occidentalis* (Reptilia, Lacertilia, Iguanidae). J. Herpetol. 10: 211–220.

John, B.
1981. Chromosome change and evolutionary change: a critique. *In* W. R. Atchley and

D. Woodruff (eds.), Evolution and speciation, pp. 23–51. London: Cambridge Univ. Press.

1983. The role of chromosome change in the evolution of orthopteroid insects. *In* A. K. Sharma and A. S. Sharma (eds.), Chromosomes in the evolution of eukaryotes, pp. 1–110. Boca Raton, FL: CRC Press.

John, B., D. C. Lightfoot, and D. B. Weissman

1983. The meiotic behavior of natural F1 hybrids between *Trimerotropis suffusa* Scudder and *T. cyaneipennis* Bruner (Orthoptera: Oedipodinae). Can. J. Gen. Cytol. 25: 467–477.

Jones, K. W.

1984. The evolution of sex chromosomes and chromosomal inactivation in reptiles and mammals. *In* M. W. J. Ferguson (ed.), The structure, development, and evolution of reptiles, pp. 305–316. New York, NY: Academic Press.

Kennedy, C. E., J. A. Endler, S. L. Poynton, and H. McMinn

1987. Parasite load predicts mate choice in guppies. Behav. Ecol. Sociobiol. 21: 291–295.

Kidwell, M. G.

1990. Evolutionary aspects of hybrid dysgenesis in *Drosophila*. Can. J. Zool. 68: 1716–1726.

Kimball, F. A., and M. J. Erpino

1971. Hormonal control of pigmentary sexual dimorphism in *Sceloporus occidentalis*. Gen. Comp. Endocrinol. 16: 375–384.

King, R. B.

1989. Sexual dimorphism in snake tail length: sexual selection, natural selection, or morphological constraint? Biol. J. Linn. Soc. 38: 133–154.

Kluge, A. G.

1988. Parsimony in vicariance biogeography: a quantitative method and a Greater Antillean example. Syst. Zool. 37: 315–328.

Kourani, M., C. W. Meyers, and C. R. Schneider

1970. Panamanian amphibians and reptiles as carriers of *Salmonella*. Am. J. Trop. Med. Hyg. 19: 632–638.

Lande, R.

1989. Fisherian and Wrightian theories of speciation. Genome 31: 221–227.

Lande, R., and S. J. Arnold

1985. Evolution of mating preference and sexual dimorphism. J. Theoret. Biol. 117: 651–644.

Langebartel, D. A.

1959. A new lizard (*Sceloporus*) from the Sierra Madre Occidental of Mexico. Herpetologica 15: 25–27.

Lara-Gongora, G.

1983. Two new species of the lizard genus *Sceloporus* (Reptilia, Sauria, Iguanidae) from the Ajusco and Ocuilan Sierras, Mexico. Bull. Maryland Herpetol. Soc. 19: 1–14.

Larsen, K. R.

1973. Speciation in the genus *Sceloporus* (Sauria, Iguanidae) as determined by cranial osteology and other characters. Ph.D. diss., Brigham Young Univ., Provo.

Larsen, K. R., and W. W. Tanner

1974. Numeric analysis of the lizard genus *Sceloporus* with special reference to cranial osteology. Great Basin Nat. 34: 1–41.

1975. Evolution of the sceloporine lizards (Iguanidae). Great Basin Nat. 35: 1–20.

Larson, R. L., H. W. Menard, and S. M. Smith

1968. Gulf of California: a result of ocean-floor spreading and transform faulting. Science 161: 781–784.

Lauder, G. V.

1981. Form and function: structural analysis in evolutionary morphology. Paleobiology 7: 430–442.

1982. Historical biology and the problem of design. J. Theoret. Biol. 97: 57–67.

Leslie, M. A.

1988. The evolutionary omission: lizard displays and evolution. M.S. thesis, Univ. Texas, Austin.

Linsdale, J. M.

1932. Amphibians and reptiles from Lower California. Univ. California Publ. Zool. 38: 345–386.

Losos, J. B.

1990a. Ecomorphology, performance capability, and scaling of West Indian *Anolis* lizards: an evolutionary analysis. Ecol. Monogr. 60: 369–388.

1990b. A phylogenetic analysis of character displacement in Caribbean *Anolis* lizards. Evolution 44: 558–569.

1990c. The evolution of form and function: morphology and locomotor performance in West Indian *Anolis* lizards. Evolution 44: 1189–1203.

1990d. Concordant evolution of locomotor behavior, display rate and morphology in *Anolis* lizards. Anim. Behav. 39: 879–890.

Lowe, C. H., and M. D. Robinson

1971. The chromosome pattern in *Sator grandaevus* (Reptilia: Iguanidae), Baja California, Mexico. J. Arizona Acad. Sci. 6: 282.

Lowe, C. H., C. J. Cole, and J. L. Patton
1967. Karyotype evolution and speciation in lizards (genus *Sceloporus*) during evolution of the North American desert. Syst. Zool. 16: 269–300.

Lucchesi, J. C.
1978. Gene dosage compensation and the evolution of sex chromosomes. Science 202: 711–716.

Lynch, J. D.
1989. The gauge of speciation: on the frequencies of modes of speciation. *In* D. Otte and J. A. Endler (eds.), Speciation and its consequences, pp. 527–552. Sunderland, MA: Sinauer.

Lynch, J. D., and H. M. Smith
1965. New or unusual amphibians and reptiles from Oaxaca, Mexico. I. Herpetologica 21: 168–177.

Lynch, M.
1991. Methods for the analysis of comparative data in evolutionary biology. Evolution 45: 1065–1080.

Maddison, W. P.
1989. Reconstructing character evolution on polytomous cladograms. Cladistics 5: 365–377.
1990. A method for testing the correlated evolution of two binary characters: are gains or losses concentrated on certain branches of a phylogenetic tree? Evolution 44: 539–557.

Maddison, W. P., and M. Slatkin
1991. Null models for the number of evolutionary steps in a character on a phylogenetic tree. Evolution 45: 1184–1197.

Marion, K. R., and O. J. Sexton
1971. The reproductive cycle of the lizard *Sceloporus malachiticus* in Costa Rica. Copeia 1971: 517–526.

Marler, C. A., and M. C. Moore
1988. Evolutionary costs of aggression revealed by testosterone manipulation in free-living male lizards. Behav. Ecol. Sociobiol. 23: 21–26.

Martin, P. S.
1958. A biogeography of reptiles and amphibians in the Gomez Farias region, Tamaulipas, Mexico. Misc. Pub. Mus. Zool. Univ. Michigan 101: 1–102.

Martins, E. P., and T. Garland, Jr.
1991. Phylogenetic analyses of the correlated evolution of continuous characters: a simulation study. Evolution 45: 534–557.

Mayden, R. L.
1986. Species and depauperate phylads and tests of punctuated and gradual evolution: fact or artifact? Syst. Zool. 35: 591–602.
1988. Vicariance biogeography, parsimony, and evolution in North American freshwater fishes. Syst. Zool. 37: 329–355.

Mayhew, W. W.
1963. Biology of the granite spiny lizard, *Sceloporus orcutti.* Am. Midl. Nat. 69: 310–327.

Maynard-Smith, J.
1991. Theories of sexual selection. Trends Ecol. Evol. 6: 146–151.

Maynard-Smith, J., and J. Haigh
1974. The hitch-hiking effect of a favorable gene. Genet. Res. 23: 23–35.

Mayr, E.
1963. Animal species and evolution. Cambridge: Belknap Press, Harvard Univ.

McKinney, R. B., and K. R. Marion
1985. Reproductive and fat body cycles in the male lizard, *Sceloporus undulatus,* from Alabama, with comparisons of geographic variation. J. Herpetol. 19: 208–217.

McLennan, D. A.
1991. Integrating phylogeny and experimental ethology: from pattern to process. Evolution 45: 1773–1789.

McLennan, D. A., D. R. Brooks, and J. D. McPhail
1988. The benefits of communication between comparative ethology and phylogenetic systematics: a case study using gasterosteid fishes. Can. J. Zool. 66: 2177–2190.

Medica, P. A., F. B. Turner, and D. D. Smith
1973. Hormonal induction of color change in female leopard lizards, *Crotaphytus wislizenii.* Copeia 1973: 658–661.

Mendez de la Cruz, F. R., L. J. Guillette, Jr., M. Villagram Santa Cruz, and G. Casas-Andreu
1988. Reproductive and fat body cycles of the viviparous lizard, *Sceloporus mucronatus* (Sauria: Iguanidae). J. Herpetol. 22: 1–12.

Meyne, J., R. J. Baker, H. H. Hobart, T. C. Hsu, O. A. Ryder, O. G. Ward, J. E. Wiley, D. H. Wurster-Hill, T. L. Yates, and R. K. Moyzis
1990. Distribution of non-telomeric sites of the (TTAGGG)n telomeric sequence in vertebrate chromosomes. Chromosoma 99: 3–10.

Milinski, M., and T. C. M. Bakker
1990. Female sticklebacks use male coloration

in mate choice and hence avoid parasitized males. Nature 344: 330–333.

Milstead, W. W. (ed.).
1967. Lizard ecology. A symposium. Columbia, MO: Univ. Missouri Press.

Mindell, D. P., J. W. Sites, Jr., and D. Graur
1989. Speciational evolution: a phylogenetic test with allozymes and *Sceloporus* (Reptilia). Cladistics 5: 49–61.
1990a. Mode of allozyme evolution: increased genetic distance associated with speciation events. J. Evol. Biol. 3: 125–131.
1990b. Assessing the relationship between speciation and evolutionary change. Cladistics 6: 393–398.

Mittleman, M. B.
1942. A summary of the iguanid genus *Urosaurus*. Bull. Mus. Comp. Zool. 91: 105–181.

Morafka, D. J.
1977. A biogeographic analysis of the Chihuahuan Desert through its herpetofauna. The Hague, Netherlands: W. Junk.

Muller, H. J.
1914. A gene for the fourth chromosome of *Drosophila*. J. Exp. Zool. 17: 325–336.

Murphy, R. W.
1975. Two new blind snakes (Serpentes: Leptotyphlopidae) from Baja California, Mexico with a contribution to the biogeography of peninsular and insular herpetofauna. Proc. California Acad. Sci. 40: 87–92.
1983a. Paleobiogeography and genetic differentiation of the Baja California herpetofauna. Occas. Pap. California Acad. Sci. 137: 1–48.
1983b. The reptiles: origin and evolution. *In* T. J. Case and M. L. Cody (eds.), Island biogeography in the Sea of Cortez, pp. 130–158. Univ. California Press, Berkeley, CA.

Murphy, R. W., and J. R. Ottley
1984. Distribution of amphibians and reptiles on islands in the Gulf of California. Ann. Carnegie Mus. 53: 207–230.

Naviera, H., and A. Fontdevila
1985. The evolutionary history of *Drosophila buzzatii*. IX. High frequencies of new chromosome rearrangements induced by introgressive hybridization. Chromosoma 91: 87–94.

Neill, W. T.
1957. Historical biogeography of present day Florida. Bull. Florida State Mus. 2: 175–220.

Nelson, G., and N. I. Platnick
1981. Systematics and biogeography, cladistics and vicariance. New York: Columbia Univ. Press.

Newlin, M. E.
1976. Reproduction in the bunch grass lizard, *Sceloporus scalaris*. Herpetologica 32: 171–184.

Newman, H. H., and J. T. Patterson
1909. Field studies of the behavior of the lizard *Sceloporus spinosus floridanus*. Bull. Univ. Texas Sci. Ser. 15: 1–24.

Nixon, K. C., and Q. D. Wheeler
1990. An amplification of the phylogenetic species concept. Cladistics 6: 211–233.

Noble, G. K.
1934. Experimenting with courtship in lizards. Nat. Hist. 34: 3–15.

Noble, G. K., and H. T. Bradley
1933. The mating behavior of lizards: its bearing on the theory of sexual selection. Ann. New York Acad. Sci. 35: 25–100.

Noonan, G. R.
1988. Biogeography of North American and Mexican insects, and a critique of vicariance biogeography. Syst. Zool. 37: 366–384.

O'Donald, P.
1980. Genetic models of sexual selection. London: Cambridge Univ. Press.

O'Hara, R. J.
1988. Homage to Clio, or, toward an historical philosophy for evolutionary biology. Syst. Zool. 37: 142–155.

Ohno, S.
1967. Sex chromosomes and sex-linked genes. Berlin, Springer-Verlag.

Olson, R. E.
1987. Taxonomic revision of the lizards *Sceloporus serrifer* and *cyanogenys* of the Gulf Coastal Plain. Bull. Maryland Herpetol. Soc. 23: 158–167.

Ortega, A.
1986. Fat body cycles in a montane population of *Sceloporus grammicus*. J. Herpetol. 20: 104–108.

Ortega, A., and R. Barbault
1984. Reproductive cycles in the mesquite lizard, *Sceloporus scalaris*. J. Herpetol. 18: 168–173.

Otte, D., and J. A. Endler (eds.).
1989. Speciation and its consequences. Sunderland, MA: Sinauer.

Packard, G. C., C. R. Tracy, and J. J. Roth
1977. The physiological ecology of reptilian eggs and embryos, and the evolution of viviparity within the class Reptilia. Biol. Rev. 52: 71–105.

Page, R. D. M.

1988. Quantitative cladistic biogeography: constructing and comparing area cladograms. Syst. Zool. 37: 254–270.

Pagel, M. D., and P. H. Harvey
1988. Recent developments in the analysis of comparative data. Q. Rev. Biol. 63: 413–440.

Paterson, H. E. H.
1985. The recognition concept of species. *In* E. S. Vrba (ed.), Species and speciation 4: 21–29. Pretoria: Transvaal Mus. Monogr.

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.

Pearson, D. L., M. S. Blum, T. H. Jones, H. M. Fales, E. Gonda, and B. R. White
1988. Historical perspective and the interpretation of ecological patterns: defensive compounds of tiger beetles (Coleoptera: Cicindelidae). Am. Nat. 132: 404–416.

Pennock, L. A., D. W. Tinkle, and M. W. Shaw
1969. Minute Y chromosome in the lizard genus *Uta* (family Iguanidae). Cytogenetics 8: 9–19.

Peters, G. B.
1982. The recurrence of chromosome fusion in interpopulation hybrids of the grasshopper *Atractomorpha similis*. Chromosoma 85: 323–347.

Pianka, E. R.
1986. Ecology and natural history of desert lizards. Princeton, NJ: Princeton Univ. Press.

Platnick, N. I., and G. Nelson
1978. A method of analysis for historical biogeography. Syst. Zool. 27: 1–16.

Poglayen, I., and H. M. Smith
1958. Noteworthy herptiles from Mexico. Herpetologica 14: 11–15.

Porter, C. A.
1988. Triploidy in the lizard, *Sceloporus grammicus*. J. Herpetol. 22: 112–115.

Porter, C. A., and J. W. Sites, Jr.
1985. Normal disjunction in Robertsonian heterozygotes from a highly polymorphic lizard population. Cytogenet. Cell Genet. 39: 250–257.
1986. Evolution of *Sceloporus grammicus* complex (Sauria: Iguanidae) in central Mexico: Population cytogenetics. Syst. Zool. 35: 362–386.
1987. Evolution of *Sceloporus grammicus* complex in central Mexico. II. Studies on rates of nondisjunction and the occurrence of spontaneous chromosomal mutations. Genetica 75: 137–152.

Porter, C. A., M. J. Hamilton, J. W. Sites, Jr., and R. J. Baker
1991. Distribution of ribosomal DNA in reptilian chromosomes: systematic and evolutionary implications. Herpetologica 47: 271–280.

Porter, W. P.
1989. New animal models and experiments for calculating growth potential at different elevations. Physiol. Zool. 62: 286–313.

Pounds, J. A., and J. F. Jackson
1981. Riverine barriers to gene flow and the differentiation of fence lizard populations. Evolution 35: 516–528.

Presch, W.
1969. Evolutionary osteology and relationships of the horned lizard genus *Phrynosoma* (family Iguanidae). Copeia 1969: 250–275.

Purdue, J. D., and C. C. Carpenter
1972a. A comparative study of the body movements of displaying males of the lizard genus *Sceloporus* (Iguanidae). Behavior 41: 68–81.
1972b. A comparative study of the display motion in the iguanid genera *Sceloporus, Uta,* and *Urosaurus*. Herpetologica 28: 137–140.

Raikow, R. J.
1988. The analysis of evolutionary success. Syst. Zool. 37: 76–79.

Rand, M. S.
1990. Polymorphic sexual coloration in the lizard *Sceloporus undulatus erythrocheilus*. Am. Midl. Nat. 124: 352–359.

Read, A. F.
1988. Sexual selection and the role of parasites. Trends Ecol. Evol. 3: 97–101.

Reed, K. M., P. D. Sudman, J. W. Sites, Jr., and I. F. Greenbaum
1990. Synaptonemal complex analysis of sex chromosomes in two species of *Sceloporus*. Copeia 1990: 1122–1129.

Ressel, S., and J. J. Schall
1988. Parasites and showy males: malarial infection and color variation in fence lizards. Oecologia 78: 158–164.

Rice, W. R.
1987. Genetic hitchhiking and the evolution of reduced gene activity of the Y sex chromosome. Genetics 116: 161–167.

Ricklefs, R. E.
1987. Community diversity: relative roles of local and regional processes. Science 235: 167–171.
1989. Speciation and diversity: the integration of local and regional processes. *In* D.

Otte and J. A. Endler (eds.), Speciation and its consequences, pp. 599–622. Sunderland, MA: Sinauer.

Ridley, M.
1989. Why not use species in comparative tests? J. Theoret. Biol. 131: 361–364.

Robinson, M. D.
1973. Chromosomes and systematics of the Baja California whiptail lizards *Cnemidophorus hyperythrus* and *C. ceralbensis* (Reptilia: Teiidae). Syst. Zool. 22: 30–35.

Ronquist, F., and S. Nylin
1990. Process and pattern in the evolution of species associations. Syst. Zool. 39: 323–344.

Rosen, D. E.
1978. Vicariant patterns and historical explanation in biogeography. Syst. Zool. 27: 159–188.

Rothblum, L., and T. A. Jenssen
1978. Display repertoire analysis of *Sceloporus undulatus hyacinthinus* (Sauria: Iguanidae) from southwestern Virginia. Anim. Behav. 26: 130–137.

Rowell, D. M.
1990. Fixed fusion heterozygosity in *Delena cancerides* Walck. (Araneae: Sparassidae): an alternative to speciation by monobrachial fusion. Genetica 80: 139–157.

Ruby, D. E.
1976. The behavioral ecology of the viviparous lizard, *Sceloporus jarrovi*. Ph.D. diss., Univ. Michigan, Ann Arbor.
1977a. The function of shudder displays in the lizard *Sceloporus jarrovi*. Copeia 1977: 110–114.
1977b. Winter activity in Yarrow's spiny lizard. Herpetologica 33: 322–333.
1978. Seasonal changes in the territorial behavior of the iguanid lizard *Sceloporus jarrovi*. Copeia 1978: 430–438.
1981. Phenotypic correlates of male reproductive success in the lizard *Sceloporus jarrovi*. *In* R. D. Alexander and D. W. Tinkle (eds.), Natural selection and social behavior, pp. 96–107. New York: Chiron Press.

Ruby, D. E., and A. E. Dunham
1984. A population analysis of the ovoviviparous lizard *Sceloporus jarrovi* in the Pinaleno Mountains of southeastern Arizona. Herpetologica 40: 425–436.

Sanderson, M. J.
1990. Estimating rates of speciation and evolution: a bias due to homoplasy. Cladistics 6: 387–391.

Savage, J. M.
1958. The iguanid lizard genera *Urosaurus* and *Uta*, with remarks on related groups. Zoologica 43: 41–54.
1982. The enigma of the Central American herpetofauna: dispersals or vicariance? Ann. Missouri Bot. Gard. 69: 464–597.

Schall, J. J.
1983a. Lizard malaria: parasite-host ecology. *In* R. B. Huey, T. W. Schoener, and E. R. Pianka (eds.), Lizard ecology: studies on a model organism, pp. 84–100. Cambridge: Harvard Univ. Press.
1983b. Lizard malaria: cost to vertebrate host's reproductive success. Parasitology 87: 1–6.

Schall, J. J., and M. D. Dearing
1987. Malarial parasitism and male competition for mates in the western fence lizard, *Sceloporus occidentalis*. Oecologia 73: 389–392.

Schall, J. J., and G. A. Sarni
1987. Malarial parasitism and the behavior of the lizard, *Sceloporus occidentalis*. Copeia 1987: 84–93.

Schall, J. J., A. F. Bennett, and R. W. Putnam
1982. Lizards infected with malaria: physiological and behavioral consequences. Science 217: 1057–1059.

Schmidt, K. P.
1922. The amphibians and reptiles of lower California and the neighboring islands. Bull. Am. Mus. Nat. Hist. 46: 607–707.

Searle, J. B.
1988. Selection and Robertsonian variation in nature: the case of the common shrew. *In* A. Daniel (ed.), The cytogenetics of mammalian autosomal rearrangements, pp. 507–531. New York: A. R. Liss.

Seib, R. L.
1980. Baja California: a peninsula for rodents but not for reptiles. Am. Nat. 115: 613–620.

Sessions, S. K., and A. Larson
1987. Developmental correlates of genome size in plethodontid salamanders: their implications for genome evolution. Evolution 41: 1239–1251.

Shaw, D. D., and D. J. Coates
1983. Chromosomal variation and the concept of the coadapted genome—a direct cytological assessment. *In* P. E. Brandham and M. D. Bennett (eds.), Kew chromosome conference, pp. 207–216. London: G. Allen and Unwin.

Shaw, D. D., P. Wilkinson, and D. J. Coates
1983. Increased chromosomal mutation rate

after hybridization between two subspecies of grasshoppers. Science 220: 1165–1167.

Shaw, D. D., D. J. Coates, and P. Wilkinson
1986. Estimating the genic and chromosomal components of reproductive isolation within and between subspecies of the grasshopper *Caledia captiva.* Can. J. Genet. Cytol. 28: 686–695.

Shaw, D. D., A. D. Marchant, M. L. Arnold, N. Contreras, and B. Kohlmann
1990. The control of gene flow across a hybrid zone: a selective role for chromosomal rearrangement? Can. J. Zool. 68: 1761–1769.

Shine, R.
1983a. Reptilian reproductive modes: the oviparity-viviparity continuum. Herpetologica 39: 1–8.
1983b. Reptilian viviparity in cold climates: testing the assumptions of an evolutionary hypothesis. Oecologia 57: 397–405.
1985. The evolution of viviparity in reptiles: an ecological analysis. *In* C. Gans and F. Billet (eds.), Biology of the Reptilia, 15: 605–694. New York: Academic Press.
1988. The evolution of body size in females: a critique of Darwin's fecundity advantage model. Am. Nat. 131: 124–131.
1989. Ecological causes for the evolution of sexual dimorphism: a review of the evidence. Q. Rev. Biol. 64: 419–461.
1990. Proximate determinants of sexual size differences in adult body size. Am. Nat. 135: 278–283.

Shine, R., and J. J. Bull
1979. The evolution of live-bearing in lizards and snakes. Am. Nat. 113: 905–923.

Shine, R., and L. J. Guillette, Jr.
1988. The evolution of viviparity in reptiles: a physiological model and its ecological consequences. J. Theoret. Biol. 132: 43–50.

Simon, C. A.
1975. The influence of food abundance on territory size in the iguanid lizard *Sceloporus jarrovi.* Ecology 56: 993–998.

Sinervo, B.
1990. The evolution of maternal investment in lizards: an experimental and comparative analysis of egg size and its effects on offspring performance. Evolution 44: 279–294.

Sinervo, B., and S. C. Adolph
1989. Thermal sensitivity of growth rate in hatching *Sceloporus* lizards: environmental, behavioral, and genetic aspects. Oecologia 78: 411–419.

Sinervo, B., and R. B. Huey
1990. Allometric engineering: an experimental test of the causes of interpopulational differences in performance. Science 248: 1106–1109.

Sinervo, B., and P. A. Licht
1991. Proximate constraints on the evolution of egg size, number, and total clutch mass in lizards. Science 252: 1300–1302.

Sinervo, B., and J. B. Losos
1991. Walking the tight rope: arboreal sprint performance among *Sceloporus occidentalis* populations. Ecology 72: 1225–1233.

Singh, L., I. F. Purdom, and K. W. Jones
1976. Satellite DNA and evolution of sex chromosomes. Chromosoma 59: 43–62.
1980. Sex chromosome associated satellite DNA: evolution and conservation. Chromosoma 79: 137–157.

Sites, J. W., Jr.
1983. Chromosome evolution in the iguanid lizard *Sceloporus grammicus.* I. Chromosome polymorphisms. Evolution 37: 38–53.

Sites, J. W., Jr., and S. K. Davis
1989. Phylogenetic relationships and variability within and among six chromosome races of *Sceloporus grammicus* (Sauria, Iguanidae) based on nuclear and mitochondrial markers. Evolution 43: 296–317.

Sites, J. W., Jr., and J. R. Dixon
1982. Geographic variation in *Sceloporus variabilis* and its relationship to *S. teapensis* (Sauria: Iguanidae). Copeia 1982: 14–27.

Sites, J. W., Jr., and M. W. Haiduk
1979. The karyotype of *Sceloporus exsul.* Southwest. Nat. 24: 393–395.

Sites, J. W., Jr., and C. Moritz
1987. Chromosomal evolution and speciation revisited. Syst. Zool. 36: 153–174.

Sites, J. W., Jr., and R. W. Murphy
1991. Isozyme evidence for independently derived, duplicate G3PDH loci in squamate reptiles. Can. J. Zool. 69: 2381–2396.

Sites, J. W., Jr., J. L. Camarillo, A. Gonzales, F. Mendoza, L. Javier, M. Mancilla, and G. Lara-Gongora
1988. Allozyme variation and genetic divergence within and between three cytotypes of the *Sceloporus grammicus* complex (Sauria, Iguanidae) in central Mexico. Herpetologica 44: 297–307.

Slatkin, M.

1984. Ecological causes of sexual dimorphism. Evolution 38: 622–630.

Slowinski, J. B.

1990. Probabilities of n-trees under two models: a demonstration that asymmetrical interior nodes are not improbable. Syst. Zool. 39: 89–94.

Slowinski, J. B., and C. Guyer

1989a. Testing null models in questions of evolutionary success. Syst. Zool. 38: 189–191.

1989b. Testing the stochasticity of patterns of organismal diversity: an improved null model. Am. Nat. 134: 907–921.

Smith, H. M.

1936 [38]. The lizards of the *torquatus* group of the genus *Sceloporus* Wiegmann, 1828. Univ. Kansas Sci. Bull. 24: 539–693.

1937a. A synopsis of the *Scalaris* group of the lizard genus *Sceloporus.* Occas. Pap. Mus. Zool. Univ. Michigan 361: 1–8.

1937b. A synopsis of the *Variabilis* group of the lizard genus *Sceloporus,* with descriptions of new subspecies. Occas. Pap. Mus. Zool. Univ. Michigan 358: 1–14.

1938. Remarks on the status of the subspecies of *Sceloporus undulatus,* with descriptions of new species and subspecies of the *undulatus* group. Occas. Pap. Mus. Zool. Univ. Michigan 387: 1–17.

1939. The Mexican and Central American lizards of the genus *Sceloporus.* Zool. Ser. Field Mus. Nat. Hist. 26: 1–397.

1941. An analysis of the Biotic Provinces of Mexico, as indicated by the distribution of the lizards of the genus *Sceloporus.* An. Esc. Nac. Cienc. Biol. Mex. 2: 95–102.

1942. Mexican herpetological miscellany. Proc. U.S. Natl. Mus. 92: 349–395.

1946. Handbook of lizards. Ithaca, NY: Comstock Pub.

1987. Current nomenclature for the names and material cited in Gunther's Reptilia and Batrachia volume of the *Biologia Centrali-Americana. In* Biologia Centrali-Americana, pp. XIII–LI. A. C. L. G. Gunther. SSAR facsimile reprint.

Smith, H. M., and R. A. Brandon

1971. A range extension for the Mexican lizard *Sceloporus a. aeneus.* J. Herpetol. 5: 60–61.

Smith, H. M., and C. B. Bumzahem

1953. A new lizard of the genus *Sceloporus* from the Isthmus of Tehuantepec. Herpetologica 9: 185–188.

1955. The identity of the transisthmic populations of the malachite tree-lizard (*Sceloporus malachiticus* Cope). Herpetologica 11: 118–1120.

Smith, H. M., and W. P. Hall

1974. Contributions to the concepts of reproductive cycles and the systematics of the *scalaris* group of the lizard genus *Sceloporus.* Great Basin Nat. 34: 97–104.

Smith, H. M., and K. R. Larsen

1975. A new species of the *formosus* group of the lizard genus *Sceloporus.* Copeia 1975: 47–50.

Smith, H. M., and J. D. Lynch

1967. A new cryptic lizard (Iguanidae: *Sceloporus*) with comments on other reptiles from Oaxaca, Mexico. Herpetologica 23: 18–29.

Smith, H. M., and A. H. Savitsky

1974. Another cryptic associate of the lizard *Sceloporus formosus* in Guerrero, Mexico. J. Herpetol. 8: 297–303.

Smith, H. M., and E. H. Taylor

1950. An annotated checklist and key to the reptiles of Mexico exclusive of the snakes. Bull. U.S. Natl. Mus. 199: 1–253.

Snell, H. L., R. D. Jennings, H. M. Snell, and S. Harcourt

1988. Intrapopulation variation in predator-avoidance performance of Galapagos lava lizards: the interaction of sexual and natural selection. Evol. Ecol. 2: 353–369.

Speck, F. C.

1924. A note on the breeding habits of *Sceloporus.* Copeia 1924: 35–36.

Stamps, J. A.

1983. Sexual selection, sexual dimorphism, and territoriality. *In* R. B. Huey et al. (eds.), Lizard ecology. Studies on a model organism, pp. 169–204. Cambridge: Harvard Univ. Press.

Stanley, S. M.

1979. Macroevolution: pattern and process. San Francisco: Freeman.

Strauss, R. E.

1987. The importance of phylogenetic constraints in comparisons of morphological structure among fish assemblages. *In* W. J. Matthews and D. C. Heins (eds.), Community and evolutionary ecology of North American stream fishes, pp. 136–143. Norman: Univ. Oklahoma Press.

Stuart, L. C.

1970. A brief review of the races of *Sceloporus serrifer* Cope with special reference to the *Sceloporus serrifer prezygus* Smith. Herpetologica 26: 141–149.

1971. Comments on the malachite *Sceloporus* (Reptilia: Sauria; Iguanidae) of southern Mexico and Guatemala. Herpetologica 27: 235–259.

Sullivan, B. K.
1991. Parasites and sexual selection: separating causes and effects. Herpetologica 47: 250–264.

Swofford, D. L., and S. H. Berlocher
1987. Inferring evolutionary trees from gene frequency data under the principle of maximum parsimony. Syst. Zool. 36: 293–325.

Templeton, A. R.
1989. The meaning of species and speciation: a genetic perspective. *In* D. Otte and J. A. Endler (eds.), Speciation and its consequences, pp. 3–27. Sunderland, MA: Sinauer.

Thomas, R. A., and J. R. Dixon
1976. A re-evaluation of the *Sceloporus scalaris* group (Sauria: Iguanidae). Southwest. Nat. 20: 523–536.

Thompson, P., and J. W. Sites, Jr.
1986a. Comparison of population structure in chromosomally polytypic and monotypic species of *Sceloporus* (Sauria: Iguanidae) in relation to chromosomally-mediated speciation. Evolution 40: 303–314.
1986b. Two aberrant karyotypes in the sagebrush lizard (*Sceloporus graciosus*): triploidy and a "supernumerary" oddity. Great Basin Nat. 46: 224–227.

Tinkle, D. W.
1967. The life and demography of the side-blotched lizard, *Uta stansburiana*. Misc. Publ. Mus. Zool. Univ. Michigan 132: 1–182.
1969. The concept of reproductive effort and its relation to the evolution of life-histories of lizards. Am. Nat. 103: 501–516.
1972. The dynamics of a Utah population of *Sceloporus undulatus*. Herpetologica 28: 351–359.
1973. A population analysis of the sagebrush lizard, *Sceloporus graciosus* in southern Utah. Copeia 1973: 284–296.

Tinkle, D. W., and R. E. Ballinger
1972. *Sceloporus undulatus*: a study of the intraspecific comparative demography of a lizard. Ecology 53: 570–584.

Tinkle, D. W., and A. E. Dunham
1986. Comparative life histories of two syntopic sceloporine lizards. Copeia 1986: 1–18.

Tinkle, D. W., and J. W. Gibbons
1977. The distribution and evolution of viviparity in reptiles. Misc. Publ. Univ. Michigan Mus. Zool. 154: 1–55.

Tinkle, D. W., H. Wilbur, and S. G. Tilley
1970. Evolutionary strategies in lizard reproduction. Evolution 24: 55–74.

Tsuji, J. S., R. B. Huey, F. H. van Berkum, T. Garland, Jr., and R. G. Shaw
1989. Locomotor performance of hatchling fence lizards (*Sceloporus occidentalis*): quantitative genetics and morphometric correlates. Evol. Ecol. 3: 240–252.

van Berkum, F. H., and J. S. Tsuji
1987. Interfamilial differences in sprint speed of hatchling lizards (*Sceloporus occidentalis*). J. Zool. (London) 212: 511–519.

Van Denburgh, J.
1896. Additional notes on the herpetology of Lower California. Proc. California Acad. Sci. 5: 1004–1008.
1922. The reptiles of western North America. Part I. Lizards. Occas. Pap. California Acad. Sci. 10: 1–611.

Vinegar, M. B.
1972. The function of breeding coloration in the lizard *Sceloporus virgatus*. Copeia 1972: 660–664.
1975a. Comparative aggression in *Sceloporus virgatus, S. undulatus consobrinus,* and *S. u. tristichus* (Sauria: Iguanidae). Anim. Behav. 23: 279–286.
1975b. Demography of the striped plateau lizard, *Sceloporus virgatus*. Ecology 56: 172–182.

Vitt, L. J.
1977. Observations on clutch and egg size and evidence for multiple clutches in some lizards of southwestern United States. Herpetologica 33: 333–338.

Vitt, L. J., and W. E. Cooper, Jr.
1985. The evolution of sexual dimorphism in the skink *Eumeces laticeps*: an example of sexual selection. Can. J. Zool. 63: 995–1002.

Wake, D. B., and A. Larson
1987. Multidimensional analysis of an evolving lineage. Science 238: 42–48.

Wanntorp, H.-E., D. R. Brooks, T. Nilsson, S. Nylin, F. Ronquist, S. C. Stearns, and N. Wedell
1990. Phylogenetic approaches in ecology. Oikos 57: 119–132.

Webb, R. G.
1967. Variation and distribution of the iguanid lizard *Sceloporus bulleri*, and the description of a related new species. Copeia 1967: 202–213.
1969. Variation, status, and relationships of the iguanid lizard *Sceloporus shannonorum*. Herpetologica 25: 300–307.

Webb, R. G., and M. Hensley
1959. Notes on reptiles from the Mexican state of Durango. Publ. Mus. Michigan State Univ. Biol. Ser. 1: 249–258.

Webster, T. P., W. P. Hall, and E. E. Williams.
1972. Fission in the evolution of a lizard karyotype. Science 177: 611–613.

White, M. J. D.
1957. Some general problems of chromosomal evolution and speciation in animals. Surv. Biol. Prog. 3: 109–147.
1973. Animal cytology and evolution. London: Cambridge Univ. Press.

Wiens, J. J.
1993. Phylogenetic relationships of phrynosomatid lizards and monophyly of the *Sceloporus* group. Copeia 1993 (in press).

Wiley, E. O.
1987. Methods in vicariance biogeography. *In* P. Hovenkamp (ed.), Systematics and evolution: a matter of diversity, pp. 283–306. Utrecht Univ., Utrecht: IPTS Faculty of Biology.
1988. Parsimony analysis and vicariance biogeography. Syst. Zool. 37: 271–290.

Wiley, E. O., and R. L. Mayden
1985. Species and speciation in phylogenetic systematics, with examples from the North American fish fauna. Ann. Missouri Bot. Gard. 72: 596–635.

Wood, S. F.
1936. Courtship and behavior of some western lizards. Copeia 1936: 177.

Woodbury, M., and A. M. Woodbury
1945. Life-history studies of the sagebrush lizard *Sceloporus g. graciosus* with special reference to cycles of reproduction. Herpetologica 2: 175–196.

Woodruff, D. S.
1973. Natural hybridization and hybrid zones. Syst. Zool. 22: 213–218.

Wyles, J. S.
1980. Phylogenetic studies of Iguanid lizards (Lacertilia, Iguanidae). Ph.D. diss., Los Angeles: Univ. California.

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.