KARYOTYPES AND EVOLUTION OF THE SPINOSUS GROUP OF LIZARDS IN THE GENUS SCELOPORUS

by

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SIGNED: Charles James Cole

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willingly performed many of the average "man's" household chores in addition to the others, to provide me with the necessary time for my academic endeavors. Furthermore, her tolerance for my extended absences during field trips and for many sudden, unanticipated, all-night experiments, writing sessions, etc., has been unlimited.

My parents also have made unusual contributions to my academic development. Though often disapproving of my sometimes absurd requests and "far out" actions during my upbringing, they never attempted to squelch an inquisitive look into any subject, and in many instances they encouraged, rather than simply tolerated, what most parents would have flatly banned. For this I am most grateful.

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ABSTRACT

Karyotypes in the nine species of the spinosus group of lizards were analyzed by means of the colchicine, hypotonic citrate, air-dried technique, employing both bone marrow and testicular tissues. The following cytogenetic phenomena were found within this species group: (1) interspecific variation in chromosome number and morphology, (2) intraspecific variation in chromosome number and morphology, (3) polymorphism within local populations, (4) sex chromosomes, and (5) natural chromosomal aberrations.

There are four basic karyotypes in the species group, though some exhibit relatively minor variations. Diploid chromosome numbers range from a high of 40 (with nearly all chromosomes telocentric) to a low of 22 (with all or nearly all chromosomes metacentric and submetacentric). The cytogenetic data, together with ecologic, behavioral, and zoogeographic data, indicate that speciation within the group includes two major phylads. Karyotypic evolution within each phylad primarily involved chromosomal centric fusion (whole-arm translocation). The phylogeny of the group is strongly compatible with the evidence that semi-arid to arid-adapted desert-dwelling species were eventually derived from humid to semi-humid, tropical to subtropical forest-dwelling ancestors.

INTRODUCTION

The lizard genus Sceloporus provides tremendous opportunities for investigations in evolutionary biology. This genus, which contains nearly 60 species and twice as many subspecies, is one of the largest in the family Iguanidae and is, indeed, one of the largest of all lizard genera in the New World. Moreover, the various species of Sceloporus exhibit a spectrum of morphologic, ecologic, and physiologic adaptations to an assortment of habitats and microhabitats geographically distributed from southern Canada southward throughout most of the vast territory comprised by the continental United States, Mexico, and Central America to western Panama.

With few exceptions, such as Smith's (1939) monographic treatment of the taxonomy of essentially the entire genus and Etheridge's (1964) consideration of osteological details in a large number of species, the potentials provided by Sceloporus have not been considerably exploited. As is the case with most reptiles, the cytogenetics of Sceloporus has hardly been touched.

The first consideration of Sceloporus chromosomes was provided by Painter (1921), who reported generalities on two species (in addition to other species in different genera). Such earlier investigations with reptilian karyotypes were generally hampered and partly inaccurate due to the lack of techniques and equipment that could provide adequate resolution. These problems have been greatly relieved and more recent

investigations have indicated the potential of cytogenetics for effectively probing into the evolutionary history of Sceloporus (see Lowe, Wright, and Cole, 1966; Cole, Lowe, and Wright, 1967; Lowe, Cole, and Patton, 1967; Cole and Lowe, 1968).

This paper considers the cytogenetics of the lizards in the spinosus group, which is one of the 15 species groups recognized as comprising the genus Sceloporus (see Smith, 1939). The spinosus group, which includes nine species (27 species and subspecies), is one of the largest and most diverse in the genus and geographically ranges from Guatemala northward to Nevada and Utah (Smith, 1939; Smith and Taylor, 1950; Smith and Smith, 1951; Shannon and Urbano, 1954; Phelan and Brattstrom, 1955; Tanner and Robison, 1959). Species within this group occupy various habitats ecologically ranging from the ancient neotropical rainforest or rainforest-edge in southern Mexico and northern Central America to the relatively recently derived deserts of North America. Furthermore, these species include primarily arboreal forms as well as primarily ground-dwelling forms. Thus this group constitutes a unit particularly fitting for evolutionary investigations.

The karyotype analyses reported herein reveal examples of the following cytogenetic phenomena within the nine species of the spinosus group: (1) interspecific variation in chromosome number and morphology, (2) intraspecific variation in chromosome number and morphology, (3) polymorphism within local populations, (4) sex chromosomes, and (5) natural chromosomal aberrations.

METHODS

This report is based on the examination of chromosomes in more than 2,170 cells from a total of 159 individual lizards (88 males and 71 females) representing each and all of the nine species in the spinosus group. Chromosomes were prepared for microscopic examination by means of the colchicine, hypotonic citrate, air-dried procedures used by Patton (1967), with slight modifications for lizards (Lowe, Wright, and Cole, 1966). Both bone marrow and testicular tissues were utilized.

I was fortunate to be able to obtain field experience with each of the species in the group while carrying on the field work to obtain freshly captured specimens for karyotypic analysis. Each lizard examined was preserved, and the sex of each individual was determined by dissection. All specimens are deposited in the herpetological collection of the Department of Biological Sciences at The University of Arizona (UAZ), as follows.

Specimens Examined

Sceloporus clarki (N = 81, with 46 males and 35 females). MEXICO: Sinaloa: 5 mi. (by Mex. 15) SE Rosario (UAZ Nos. 28305 and 28307); 6 mi. NW La Concha, 29 mi. (by Mex. 15) SE Escuinapa (UAZ Nos. 28308-28309); 1 mi. NW El Aguaje, 13 mi. (by Mex. 15) NW Río Elota (UAZ Nos. 28310-28311). Sonora: Alamos (UAZ No. 25685); abandoned tequila factory, 2 mi. W Alamos (UAZ Nos. 16237-16238); 7.5 mi.

(by Alamos Rd.) W Alamos (UAZ Nos. 25466 and 25472); La Aduana Watermine, ca. 1/2 mi. N La Aduana (UAZ No. 24211); along Río Mayo, Navojoa (UAZ Nos. 18127, 16221-16223, 25467, 25686-25688, and 25690-25691). UNITED STATES: Arizona: Coconino Co.: Verde Valley School, ca. 7 mi. S. Sedona (UAZ No. 21860). Pima Co.: Kitt Peak, Quinlan Mts. (UAZ No. 16228); Sycamore Canyon, ca. 3700 ft. elev., Baboquivari Mts. (UAZ No. 24222); Milagrosa Canyon, ca. 3000 ft. elev. (UAZ No. 16239). Santa Cruz Co.: Sycamore Canyon, 3800 ft. elev., Pajarito Mts. (UAZ Nos. 24186, 24195, 24206-24207, 24209, 24214, 24218, 24862-24867, 24869-24870, 24872-24873, 24876, 24878-24880, 24883, 24885, 24904, 24906, 25456, 25458, 25461, 25464, 25469-25470, and 25473); either Sycamore Canyon, ca. 3800 ft. elev., or 13.1 mi. (by Ruby Rd.) W of U.S. 89, vic. W. Peña Blanca Canyon, 4200 ft. elev., Pajarito Mts. (UAZ Nos. 25465, 25468, and 25471); White Cak Mine, Walker Canyon, 1.9 mi. (by rd.) SW of 7.7 mi. (by Ruby Rd.) W Nogales Hwy., ca. 4200 ft. elev., Pajarito Mts. (UAZ No. 19082); Walker Canyon, ca. 1/2 mi. (by rd.) SW of 7.7 mi. (by Ruby Rd.) W Nogales Hwy., ca. 3900 ft. elev., Pajarito Mts. (UAZ Nos. 24874, 25454-25455, 25457, 25459-25460, and 25462); vic. Peña Blanca Spring, Pajarito Mts. (UAZ No. 24187); Sycamore Canyon, ca. 7 mi. on Washington Camp Rd. E of jct. with Ariz. 82, ca. 4500 ft. elev., Patagonia Mts. (UAZ Nos. 24871, 24877, 24884, 24887, and 25463); Sycamore Canyon, Patagonia Mts. (UAZ No. 24896); Duquesne, 5100 ft. elev., Patagonia Mts. (UAZ No. 24875). New Mexico: Catron Co.: San Francisco (Frisco) Hot Springs, 4800 ft. elev. (UAZ Nos. 16218-16220). Grant Co.: ca. 2 mi. (by rd.) S Pinos Altos (UAZ No. 16226).

Sceloporus melanorhinus (N = 7, with 3 males and 4 females). MEXICO: Chiapas: Jardín Botánico, Tuxtla Gutiérrez (UAZ No. 28300). Colima: 2 mi. (by Mex. 110) E jct. to Colima (UAZ Nos. 28299 and 28303-28304). Guerrero: vic. Villa Treppiedi, Acapulco (UAZ Nos. 18548 and 28301-28302).

Sceloporus orcutti (N = 8, with 4 males and 4 females). MEXICO: Baja California Sur: Boca de la Sierra (UAZ No. 18550). UNITED STATES: California: Riverside Co.: ca. 9 mi. (by Calif. 74) SE Hemet, N Fork San Jacinto Creek, San Jacinto Mts. (UAZ Nos. 21669-21672); 2 mi. (by rd. to Idyllwild) S Banning, San Jacinto Mts. (UAZ No. 21674); 3 mi. (by rd. to Idyllwild) S Banning, San Jacinto Mts. (UAZ No. 21673). San Diego Co.: Calif. 78 crossing of San Felipe Creek, W Anza-Borrego Desert State Park (UAZ No. 21675).

Sceloporus magister (N = 16, with 9 males and 7 females). MEXICO: Sonora: 17.6 mi. S International Border (Lukeville, Pima Co., Arizona), on rd. to Puerto Peñasco (UAZ No. 16227); ca. 2 mi. (by rd.) N Desemboque del Río San Ignacio (UAZ No. 24197). UNITED STATES: Arizona: Mohave Co.: Alamo Crossing (UAZ Nos. 16215-16216 and 16231-16232). Pima Co.: N end Campbell Ave., N Tucson (UAZ No. 16225); 3 mi. N on Soldier's Trail from Reddington Rd., 2800 ft. elev. (UAZ No. 16235); 1/4 mi. S Ajo Rd., on Sierra Mt. Rd. (UAZ No. 16234); SE corner of Anklam and Greasewood, N Tumamoc Hill, W Tucson (UAZ No. 16236); Tanque Verde Creek, on N edge of Tanque Verde Country Club, NE Tucson (UAZ No. 16230). Pinal Co.: 11.9 mi. SE Mammoth on Mammoth to Reddington Rd., at San Pedro River crossing (UAZ Nos. 16229 and 16233).

Utah: Garfield Co.: Trachyte Creek, 8.1 mi. (by rd. to Bullfrog) S Utah 95, 4900 ft. elev., Henry Mts. (UAZ No. 16224). San Juan Co.: Rainbow Bridge National Monument (UAZ Nos. 21859 and 21867).

Sceloporus lundelli (N = 13, with 8 males and 5 females). MEXICO: Yucatan: Pisté (UAZ Nos. 28337, 28345-28346, and 28349-28350); Balneario Chicalá, ca. 2 Km. E Río Lagartos (UAZ Nos. 28339-28344 and 28347-28348).

Sceloporus edwardtaylori (N = 9, with 6 males and 3 females). MEXICO: Oaxaca: Juchitán (UAZ Nos. 28359 and 28365-28367); Puente Las Tejas, base of Cerro Quiengola, 7 mi. (by Mex. 190) NW Tehuantepec (UAZ Nos. 28368-28369, 28371-28372, and 28376).

Sceloporus olivaceus (N = 12, with 5 males and 7 females). UNITED STATES: Texas: Kendall Co.: 7 mi. (by Interstate 10) NW Boerne (UAZ No. 28335). Kerr Co.: Guadalupe River at 8 mi. S (by Texas 39) Camp Mystic (19 mi. S Ingram) (Uaz No. 28334). Travis Co.: Municipal Golf Course (Lake Austin and Exposition Dr.), Austin (UAZ Nos. 28326-28333). Val Verde Co.: 1 mi. N old Devil's River bridge, near Devil's River (UAZ No. 24199); Devil's River, near site of old Devil's River bridge (old U.S. 90), NW Del Río (UAZ No. 24205).

Sceloporus spinosus (N = 5, with 1 male and 4 females). MEXICO: Guanajuato: 3 mi. S. Cacalote, 14 mi. (by rd. to Salvatierra) S Celaya (UAZ Nos. 28353-28354). Oaxaca: 5 mi. (by Mex. 175) NW Miahuatlán (UAZ No. 28355); 8 mi. SE El Tule, 13 mi. (by Mex. 190) SE Oaxaca de Juárez (UAZ Nos. 28351-28352).

Sceloporus horridus (N = 8, with 6 males and 2 females).

MEXICO: Colima: 2 mi. (by Mex. 110) SSW jct. to Colima (UAZ No. 28324); vic. Tecuizitlán, 8 mi. (by Mex. 110) E jct. to Colima (UAZ No. 28312). Guerrero: ca. 2 Km. (by Mex. 95) S jct. to Iguala (UAZ No. 18119). Jalisco: 1 mi. (by Mex. 80) NE Autlán (UAZ No. 28319). Nayarit: vic. El Refugio, 8 mi. (by Mex. 15) SE Tepic (UAZ Nos. 28315 and 28317); 3 mi. (by rd.) NE Santa María del Oro (UAZ No. 28322). Puebla: 7 mi. (by rd.) NW Teotitlán del Camino (Oaxaca) (UAZ No. 28321).

RESULTS AND DISCUSSION

Karyotypes

Sceloporus clarki Baird and Girard

The karyotype of Clark's spiny lizard was previously described (Lowe, Cole, and Patton, 1967) on the basis of examining chromosomes in more than 106 mitotic cells from 11 individuals (7 males and 4 females) that represented localities covering more than the northern half of its geographic range in northern Mexico and the United States. On this basis the karyotype appeared monomorphic; there were apparent neither sex-correlated chromosomes nor geographic differences in the karyotype, as is considered typical for most species of lizards.

Extensive subsequent field and laboratory investigations, now involving analysis of more than 1,200 cells from 81 individuals (46 males and 35 females), reveal that in addition to the typical karyotype previously described, there are at least two similar, though clearly distinct and considerably rarer, atypical karyotypes. These occur as a local polymorphism in southern Arizona. The three karyotypes (Fig. 1) are described immediately below; they will be referred to hereafter as KA, KB, and KC, respectively.

KA. The typical karyotype of S. clarki has a diploid number of 40 chromosomes ($2n = 40$). These include 20 macrochromosomes (10 homomorphic pairs) and 20 microchromosomes (10 homomorphic pairs; Fig. 1A). The pairs are numbered in order of decreasing length for the purpose

Fig. 1. Karyotypes of *Sceloporus clarki*

A. Typical ($2n = 40$), with 20 macrochromosomes (10 pairs) and 20 microchromosomes (10 pairs). UAZ Number 25464, a female.
B. Atypical ($2n = 40$), with 20 macrochromosomes (10 pairs) + 1 intermediate-sized chromosome (arrow) + 19 microchromosomes (9 pairs + the 1 that synapses with the intermediate-sized chromosome). UAZ Number 24186, a female. Line represents 10 μ.
C. Atypical ($2n = 40$), with 20 macrochromosomes (10 pairs) + 20 microchromosomes (10 pairs). Note that pair number 5 is heteromorphic, with one telocentric and one subtelocentric element (arrow). UAZ Number 24904, a male.

All three specimens are from Sycamore Canyon, 3,800 ft. elev., Pajarito Mountains, Santa Cruz County, Arizona.

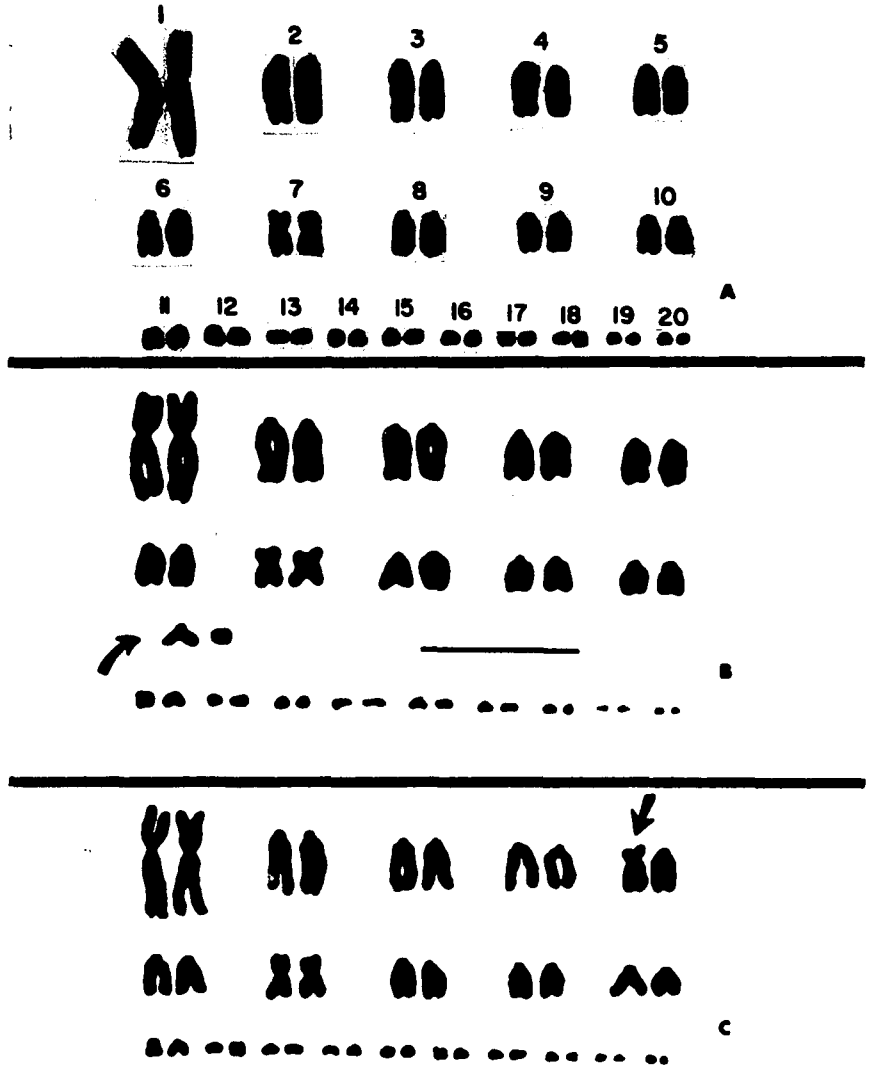

Fig. 1. Karyotypes of Sceloporus clarki

of describing the karyotype. Of the macrochromosomes, numbers 1 and 7 are submetacentric and no. 1 bears a terminal satellite on the long arm; the satellites, though consistently located here, are not conspicuous in many cells. The remaining macrochromosomes are telocentric and several are difficult or impossible to differentiate individually because of their general morphological similarities (size and shape); nos. 4, 5, and 6 are often particularly difficult to distinguish between, as are nos. 8, 9, and 10. Morphology of the microchromosomes is generally difficult to determine, particularly in this species, and cannot be considered definite because of their minute dimensions; nevertheless, in many cells it appears that no. 12 and another pair (ca. no. 14) are subtelocentric while the rest are telocentric. Most of the microchromosomes are exceedingly difficult, if not impossible, to differentiate in all cells examined.

KB. This atypical karyotype (Fig. 1B) is similar to the typical KA. The 20 macrochromosomes are the same as those in KA; the remaining 20 chromosomes consist of 19 typical microchromosomes plus a single telocentric chromosome intermediate in size between the macrochromosomes and microchromosomes ($2n = 40$). Thus it is abbreviated hereafter as 20 + 1 + 19 (the typical karyotype being represented by 20 + 0 + 20 chromosomes). In this 20 + 1 + 19 karyotype it appears as though the intermediate-sized element and one of the microchromosomes are unpaired. Actually, these two "odd" chromosomes constitute a heteromorphic pair (Figs. 1B; 2).

Examination of testicular tissue reveals that spermatogonia have the same karyotype as bone marrow cells. Furthermore, during meiosis I in primary spermatocytes (Fig. 2A), there are regularly formed 10 bivalents of macrochromosomes, 1 intermediate-sized bivalent, and 9 bivalents of microchromosomes (10 + 1 + 9). The intermediate bivalent is composed of the intermediate-sized chromosome and the "unpaired" microchromosome, which, therefore, clearly constitute a heteromorphic pair (size heteromorphism).

Analysis of 51 cells at prophase II and metaphase II (secondary spermatocytes) revealed normal chromosome segregation from the heteromorphic bivalent in anaphase I, since both expected types of secondary spermatocytes (10 + 1 + 9 and 10 + 0 + 10; Fig. 2B, C) occur in a frequency not significantly different from the hypothetical 1:1 (N = 20 cells having 10 + 1 + 9; N = 31 cells having 10 + 0 + 10; $\chi^2 = 2.38$; $0.20 > P > 0.10$). As meiosis proceeds normally it is reasonable to assume that both types of spermatozoa are generated in equal frequency.

Difficulty in analyzing the minute microchromosomes results in uncertainty as to precisely which pair of microchromosomes is involved. It appears to be one of the larger pairs, but not the largest; I suggest that it is *ca.* number 12 (Fig. 1B).

The exact mode of origin of the heteromorphic condition is likewise uncertain, although a reasonable explanation is available. Reciprocal translocation is not likely because polyvalents are not formed in meiosis I; the intermediate-sized bivalent is regularly

Fig. 2. Spermatocytes from an Individual of *Sceloporus clarki* with the Atypical 20 + 1 + 19 Karyotype

A. Primary spermatocyte (metaphase I), with 10 bivalents of macrochromosomes + 1 intermediate-sized bivalent + 9 bivalents of microchromosomes (n = 20). The intermediate bivalent represents the heteromorphic pair (arrow).
B. Secondary spermatocyte (metaphase II), with 10 + 0 + 10 constitution (n = 20).
C. Secondary spermatocyte (metaphase II), with 10 + 1 + 9 constitution (n = 20). Arrow indicates the intermediate-sized chromosome.

All three spermatocytes are from UAZ Number 24862, a male from the same locality as those illustrated in Fig. 1 (Sycamore Canyon).

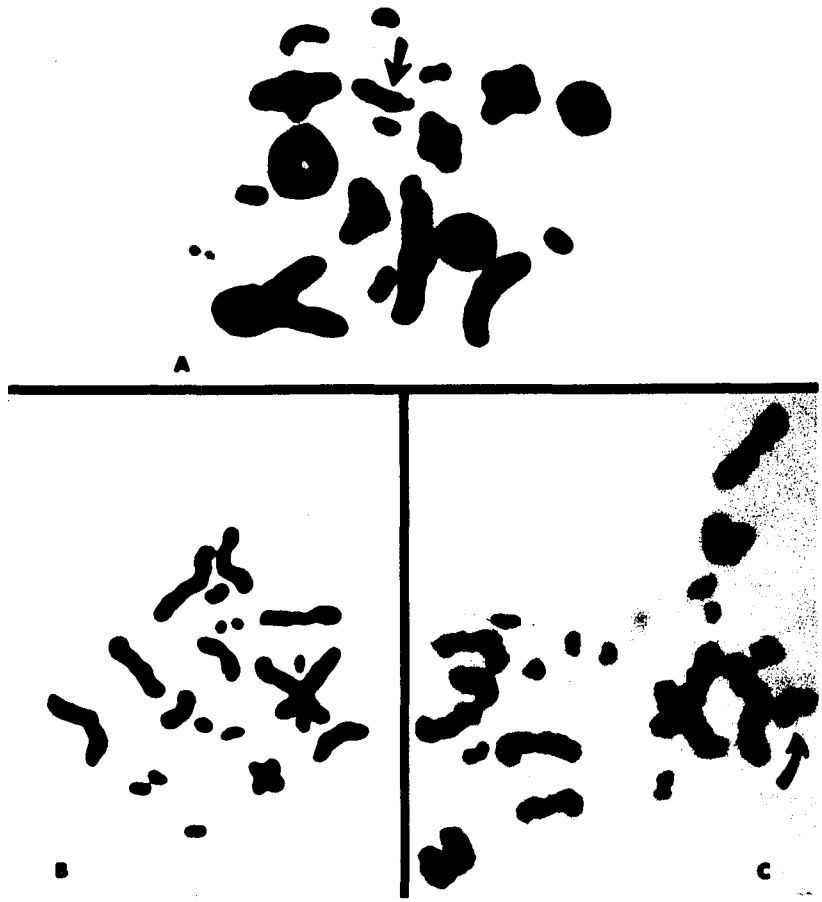

Fig. 2. Spermatocytes from an Individual of Sceloporus clarki with the Atypical 20 + 1 + 19 Karyotype

formed (N = 45 cells examined at diakinesis and metaphase I). Indeed, it cannot be known for sure whether the large member of the heteromorphic pair represents the derived condition (addition of chromatin) or whether the smaller member of the pair is derived (loss of chromatin). But a diploid bisexual species such as S. clarki is more likely to withstand addition of chromatin rather than loss of chromatin, so it is likely that the larger member of the heteromorphic pair has been evolutionarily enlarged. Such enlargement could result from duplication or a combination of duplication and unequal crossing over. For example, when two homologous chromosomes differ from the standard by two overlapping inversions (one each), a single crossover within the common inverted segment will result in an enlarged chromosome bearing a duplicated segment and no deficiencies.

Thus it appears that the only difference between the typical karyotype KA (20 + 0 + 20) and this KB (20 + 1 + 19) is that in the latter, one "microchromosome" is now considerably larger than its homologue (a true microchromosome; Fig. 1A, B). This karyotype is not sex-correlated (see below), as it is equally expressed in members of both sexes from the same locality.

KC. This atypical karyotype (Fig. 1C) is also similar to the typical one (KA) and differs from it in having one pair (ca. no. 5) that is heteromorphic. In this case, both members of the heteromorphic pair are the same size, though one is subtelocentric and one is telocentric (Fig. 1C). Again, there is no sex-correlation.

As with the first heteromorphism considered (KB), this one also is expressed equally in spermatogonia and bone marrow cells. At metaphase I in primary spermatocytes (Fig. 3A) there are regularly formed 10 bivalents of macrochromosomes and 10 of microchromosomes (10 + 0 + 10). Regular formation of these bivalents and the lack of polyvalents (N = 27 cells examined at diakinesis and metaphase I) clearly reveal that the chromosomes in question constitute a heteromorphic pair (shape heteromorphism).

Analysis of 100 secondary spermatocytes at prophase II and metaphase II (Fig. 3B, C) revealed normal chromosome segregation from the heteromorphic bivalent in anaphase I, since both expected types of secondary spermatocytes (one with the atypical subtelocentric no. 5 and one with the typical telocentric no. 5) occur in a frequency not significantly different from the hypothetical 1:1 (N = 59 cells having the subtelocentric no. 5; N = 41 cells having the telocentric no. 5; $\chi^2 = 3.24$; $0.10 > P > 0.05$). Thus, since meiosis proceeds normally, it is reasonable to assume that both types of spermatozoa are produced in equal frequency in these individuals.

Because of the similarities of the telocentric chromosomes in pairs 4 through 6 in the typical karyotype, I cannot be certain as to precisely which pair is involved; it is approximately no. 5 (Fig. 1C).

This heteromorphism apparently resulted from either an unequal pericentric inversion or a centromere shift (centric shift); inversion is more probable because it requires fewer breaks (two instead of three). Furthermore, I suggest that the telocentric condition is the

Fig. 3. Spermatocytes from an Individual of *Sceloporus clarki* having the Atypical Karyotype with the Heterozygous Subtelocentric Macrochromosome

A. Primary spermatocyte (diakinesis), with 10 bivalents of macrochromosomes + 10 of microchromosomes (n = 20).
B. Secondary spermatocyte (metaphase II), with 10 + 0 + 10 constitution (n = 20), and the macrochromosomes represented by the typical complement of 8 telocentric elements and 2 submetacentric elements.
C. Secondary spermatocyte (metaphase II), with 10 + 0 + 10 constitution (n = 20), and the macrochromosomes represented by the atypical complement of 7 telocentric elements, 1 subtelocentric element (atypical *ca.* no. 5; arrow), and 2 submetacentric elements.

All three spermatocytes are from UAZ Number 24904, the same male from Sycamore Canyon that is illustrated in Fig. 1C.

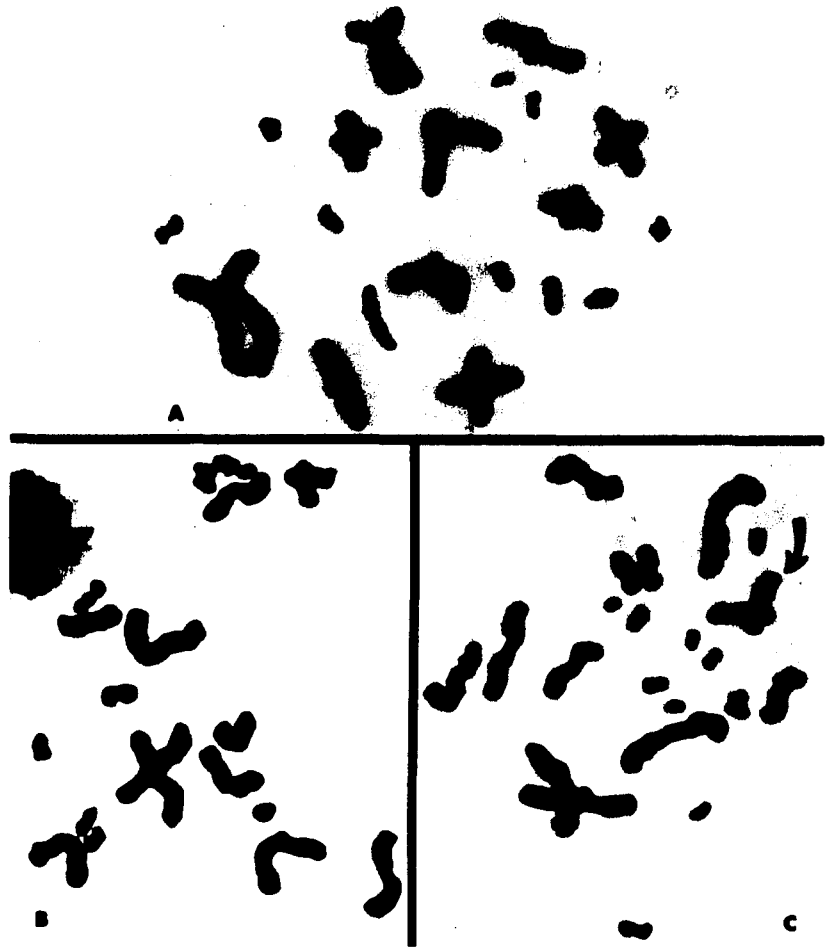

Fig. 3. Spermatocytes from an Individual of Sceloporus clarki having the Atypical Karyotype with the Heterozygous Subtelocentric Macrochromosome

ancestral one since it occurs throughout the species (the heteromorphism is known rarely from only one locality; see below) and particularly since S. melanorhinus, a species more primitive than S. clarki, possesses this same telocentric chromosome but not this same subtelocentric (see below).

Distribution and frequency. The typical karyotype (KA) of S. clarki occurs abundantly in both sexes from Arizona and New Mexico southward through Sinaloa (i.e., throughout the range of the species). The atypical karyotype having 20 + 1 + 19 chromosomes (KB) is known from only two localities: (1) 6 mi. NW la Concha, 29 mi. (by Mex. 15) SE Escuinapa, Sinaloa, Mexico, and (2) the Patagonia Mountains and Pajarito Mountains, Santa Cruz County, Arizona (these last populations are continuous through the vicinity of Nogales or a bit south thereof, and thus specimens from both mountains are treated as one population sample). The atypical karyotype with the heterozygous subtelocentric macrochromosome (KC) is known only from the locality in southern Arizona.

A sample of 51 lizards from the southern Arizona locality was examined in order to determine the frequency of occurrence of the three karyotypes. Of these 51 individuals (29 males and 22 females), 34 (23 males and 11 females; 66.66667 %) had the typical 20 + 0 + 20 karyotype (KA), 13 (4 males and 9 females; 25.49020 %) had the atypical 20 + 1 + 19 karyotype (KB), and 4 (2 males and 2 females; 7.84314 %) had the atypical karyotype with a heterozygous subtelocentric no. 5 chromosome (KC). A chi-square test for homogeneity

using a 2 X 3 contingency table (see Simpson, Roe, and Lewontin, 1960) indicates that there is no difference in the frequency distributions of these karyotypes in the two sexes ($\chi^2 = 5.438$; $0.10 > P > 0.05$); i.e., occurrence of these heteromorphic pairs of chromosomes is not sex-correlated.

It has been discussed and commented on above that (1) all three of the known karyotypes of S. clarki occur together at one locality (southern Arizona), (2) individual males of each of the two heteromorphic types carry on a normal meiosis and generate equal numbers of both types of spermatozoa, (3) the karyotypes occur in equal frequency in both sexes, and (4) the frequencies are as follows: (A) the typical karyotype = 0.6666667, (B) the 20 + 1 + 19 karyotype = 0.2549020, and (C) the karyotype with a heterozygous subtelocentric macrochromosome = 0.0784314. From this information, it follows that six additional karyotypes of S. clarki theoretically occur at the same locality; these are the homozygotes of each type thus far known only as heterozygotes, and the remaining various possible combinations of both. These occur in extremely low frequencies.

The Hardy-Weinberg formula and chi-square analysis were employed to determine whether the observed frequencies of the karyotypes differed significantly from what could be expected if the three karyotypes in southern Arizona presently occur at equilibrium. The expected frequency of each karyotype at equilibrium was determined from its observed frequency in the population sample at hand; all calculations were carried out to seven decimal places. At first,

since the atypical karyotypes (KB and KC) each varied from the typical one with respect to different individual chromosomes (ca. no. 12 and ca. no. 5, respectively), each was analyzed independently. In each case, three karyotypic conditions were possible: (1) homozygous typical, (2) heterozygous, and (3) homozygous atypical; only the first two were observed. Thus each case was individually treated in the manner of a Hardy-Weinberg problem involving one locus and two alleles. For the ca. no. 12 chromosomes (as in karyotype KB), chi-square analysis revealed no significant difference between the frequencies observed in the population sample and the hypothetical equilibrium frequencies ($\chi^2 = 1.088$; $0.70 > P > 0.50$). Likewise, there was no significant difference between the observed frequencies and the hypothetical equilibrium frequencies ($\chi^2 = 0.085$; $P > 0.95$) of the ca. no. 5 chromosomes (as in Karyotype KC). Next, chi-square analysis was performed after combining into one problem all of the karyotypic conditions; i.e., in the manner of a Hardy-Weinberg problem involving two loci, each with two alleles. Thus there were nine possible karyotypes; analysis was performed using as one class each the three karyotypes observed in the population sample, with the six remaining rare karyotypes pooled into another class. This test also revealed no significant difference between the frequencies in the observed sample and those in the hypothetical equilibrium ($\chi^2 = 2.860$; $0.50 > P > 0.30$). These analyses thus reveal that the various karyotypes of S. clarki could be in equilibrium in southern Arizona. The rarest expected karyotype is that which is homozygous

for both atypical conditions: $2n = 40$, composed of 20 (with a pair of the atypical subtelocentric ca. no. 5) + 2 + 18. Since its hypothetical frequency at equilibrium is 0.0000250, it is not astonishing that it was not encountered in the sample!

This same problem was also approached from another direction. Considering the population sample at hand as P_1, I determined the expected frequency of each karyotype in the next generation (F_1). Only six of the nine hypothetical karyotypes could be obtained in this F_1 since not all hypothetical types of gametes in the population could be produced by the sample observed (e.g., there could not be produced in the first generation any individual homozygous for both atypical chromosomal conditions). All hypothetical karyotypes first appeared in calculating the expected F_2 generation; their frequencies did not reach equilibrium until the hypothetical F_{21} generation (carried out to seven decimal places). The expected frequency of each karyotype in this hypothetical F_{21} generation was remarkably close to that which was predicted by means of the much shorter method discussed immediately above, considering the amount of rounding necessary in carrying out these extensive calculations. Chi-square analysis comparing the hypothetical F_{21} with the observed sample (P_1), using as one class each the three karyotypes observed in the sample and the six remaining rare karyotypes pooled into another class, produced the same results obtained in the earlier analysis ($\chi^2 = 2.860$; $0.50 > P > 0.30$), again indicating that these karyotypes could be in equilibrium in southern Arizona.

External morphology. Examination and analysis of characteristics of external morphology on the specimens comprising the sample from southern Arizona revealed no traits that were correlated with the occurrence of the atypical karyotypes. The following characteristics were analyzed: (1) total number of femoral pores, (2) number of scales medially separating the two series of femoral pores, (3) number of dorsal scales (occiput to rump), (4) number of scales around midbody, (5) body length (snout-vent), and (6) several characteristics of coloration and color pattern.

Several comparisons of the scale counts and length measurements were made with Student's t-tests. In one, all individuals possessing typical karyotypes were compared with those having atypical karyotypes; i.e., individuals with either atypical karyotype were pooled into one statistical sample. There was no significant difference between the samples for any of the characteristics examined (Table 1). Indeed, the lowest P value obtained was $0.20 > P > 0.10$, for body length; for each other trait, $P > 0.60$.

For another set of t-tests, all individuals with typical karyotypes were compared with those having 20 + 1 + 19 karyotypes. Again, there was no significant difference between the samples for any of the characteristics (Table 2). The lowest P value obtained was $0.10 > P > 0.05$, again for body length; for each other trait, $P > 0.20$. Reliable comparisons could not be made between the individuals possessing typical karyotypes and those exhibiting the

Table 1. Comparison of External Morphological Characteristics Exhibited in Specimens of S. clarki with Typical and Those with Atypical Karyotypes. - All lizards are from southern Arizona. No significant differences are indicated.

Ext. Charact. / Karyotype	Femoral Pores	Scales Between Pore Series	Dorsal Scales	Scales Around Midbody	Body Length
Typical	24.50 ± 0.32 (20-29) N = 34	8.88 ± 0.16 (7-11) N = 34	31.50 ± 0.26 (29-35) N = 34	38.06 ± 0.23 (35-40) N = 31	89.03 ± 3.14 (43-114) N = 34
Atypical	24.70 ± 0.46 (22-28) N = 17	8.94 ± 0.22 (8-11) N = 17	31.70 ± 0.46 (28-35 N = 17	38.12 ± 0.46 (35-42) N = 16	79.76 ± 4.97 (49-110) N = 17
Student's t-test	$t = 0.36$ $0.80 > P > 0.70$	$t = 0.22$ $0.90 > P > 0.80$	$t = 0.40$ $0.70 > P > 0.60$	$t = 0.13$ $0.90 > P > 0.80$	$t = 1.64$ $0.20 > P > 0.10$

Table 2. Comparison of External Morphological Characteristics Exhibited in Specimens of *S. clarki* with Typical and Those with Atypical 20 + 1 + 19 Karyotypes. - All lizards are from southern Arizona. No significant differences are indicated.

Karyotype \ Ext. Charact.	Femoral Pores	Scales Between Pore Series	Dorsal Scales	Scales Around Midbody	Body Length
Typical	24.50 ± 0.32 (20-29) N = 34	8.88 ± 0.16 (7-11) N = 34	31.50 ± 0.26 (29-35) N = 34	38.06 ± 0.23 (35-40) N = 31	89.03 ± 3.14 (43-114) N = 34
Atypical (20 + 1 + 19)	25.00 ± 0.54 (22-28) N = 13	8.92 ± 0.24 (8-11) N = 13	32.08 ± 0.55 (28-35) N = 13	38.08 ± 0.56 (35-42) N = 12	77.54 ± 5.69 (49-110) N = 13
Student's *t*-test	$t = 0.81$ $0.50 > P > 0.40$	$t = 0.013$ $P > 0.90$	$t = 1.06$ $0.30 > P > 0.20$	$t = 0.04$ $P > 0.90$	$t = 1.83$ $0.10 > P > 0.05$

atypical one having a heterozygous subtelocentric no. 5 chromosome because of the small number of lizards (N = 4) with the latter condition.

Of the characteristics analyzed, body length is the most likely candidate to have had disturbed analyses as a result of sexual dimorphism. Thus, body length was tested again, by comparing all of the females having normal karyotypes (N = 11) with all of the females having 20 + 1 + 19 karyotypes (N = 9); again, there was no significant difference between the samples ($\underline{t} = 1.24$); $0.30 > \underline{P} > 0.20$). This test was not repeated with the males because of their smaller numbers, but the above test reveals no difference within a sex in comparing lizards with typical and those with atypical (20 + 1 + 19) karyotypes.

The above analyses reveal no differences in external morphology between lizards with typical karyotypes and lizards with atypical ones. Surely this is not to say that there are no differences whatsoever; quite possibly some differences, physiological if not morphological, exist. At any rate, there are no present indications as to the adaptive significance of the various karyotypes.

Geographic variation and origin. The relative frequencies of the different karyotypes in S. clarki vary geographically. Although the atypical one with a heterozygous subtelocentric no. 5 is known only from southern Arizona, the atypical 20 + 1 + 19 karyotype is known from there and from southern Sinaloa, Mexico (of two males collected at this last locality, one had the typical 20 + 0 + 20 karyotype and one had the

20 + 1 + 19). All of the remaining 28 specimens of S. clarki examined had the typical karyotype. This includes a sample of 16 individuals from the Navojoa-Alamos area of southern Sonora, Mexico, and the remaining 12 lizards from seven other localities in Arizona, New Mexico, and Sinaloa. Thus, the atypical karyotypes are now known only from nearly the northern and southern extremes in the range, but not in a sizable population sample (N = 16) from in between (southern Sonora); and perhaps they occur in low frequencies elsewhere.

While it is most likely that each of the two different aberrations resulting in the two atypical karyotypes arose independently, it is unlikely that the same 20 + 1 + 19 karyotype evolved twice independently (once in the north and once in the south). Indeed, as this 20 + 1 + 19 karyotype occurs at the extremes of the range of S. clarki, and as a similar, if not identical, one occurs in Sceloporus melanorhinus (a more tropical species ancestral to S. clarki; see below), it is likely that it occurred as a karyotypic variant in the ancestral population from which S. clarki was derived. This conclusion is supported by the evidence (above) that the atypical and typical karyotypes may occur in an equilibrium, at least in particular places under particular circumstances. The atypical inversion (ca. no. 5) that occurs in S. clarki probably resulted from a more recent aberration (subsequent to derivation of the species), since the same inversion is not known in S. melanorhinus (though a similar one is!).

The specimens examined include representatives of the subspecies S. clarki clarki and S. c. boulengeri.

Sceloporus melanorhinus Bocourt

Analysis of chromosome complements in more than 143 mitotic bone marrow cells from seven individuals (3 males and 4 females) reveals the occurrence of three karyotypes in this species also. The three males had one karyotype while the other two karyotypes were equally distributed among the four females. These karyotypes are similar to those of Sceloporus clarki, as follows.

KA. This karyotype is extremely similar, if not identical, to the typical one (KA) of S. clarki (20 + 0 + 20); compare Figs. 1A and 4A). The secondary constriction also occurs on the tip of the long arm of chromosome no. 1. This karyotype occurred in a female from Tuxtla Gutiérrez, Chiapas, Mexico, and also in a female from near Colima, Colima, Mexico (only six cells were analyzable on the slides from this last individual; in each of these the macrochromosomes were clearly of this constitution, but the exact number of microchromosomes, about 20, could not be determined precisely).

KB. This karyotype is extremely similar, if not identical, to the atypical 20 + 1 + 19 one of S. clarki (compare Figs. 1B and 4B). It occurred in two females from Acapulco, Guerrero, Mexico.

KC. This karyotype is similar to the atypical one of S. clarki in which there is a heterozygous subtelocentric macrochromosome that pairs with a telocentric (compare Figs. 1C and 4C). In S. melanorhinus it also appears to involve pair ca. no. 5; however, the "odd" bi-armed macrochromosome is metacentric, rather than subtelocentric as in S. clarki. Another difference is that this atypical karyotype has only

Fig. 4. Karyotypes of Sceloporus melanorhinus

A. One having 2n = 40, with 20 macrochromosomes (10 pairs) and 20 microchromosomes (10 pairs). UAZ Number 28300, a female from Tuxtla Gutiérrez, Chiapas, Mexico.
B. One having 2n = 40, with 20 macrochromosomes (10 pairs) + 1 intermediate-sized chromosome (arrow) + 19 microchromosomes (interpreted as 9 pairs + the 1 that synapses with the intermediate-sized chromosome). UAZ Number 28302, a female from Acapulco, Guerrero, Mexico. Line represents 10 μ.
C. One having 2n = 39, with 20 macrochromosomes (interpreted as 10 pairs) and 19 microchromosomes. Note that pair number 5 is heteromorphic, with one telocentric and one metacentric element (arrow). UAZ Number 28299, a male from near Colima, Colima, Mexico.

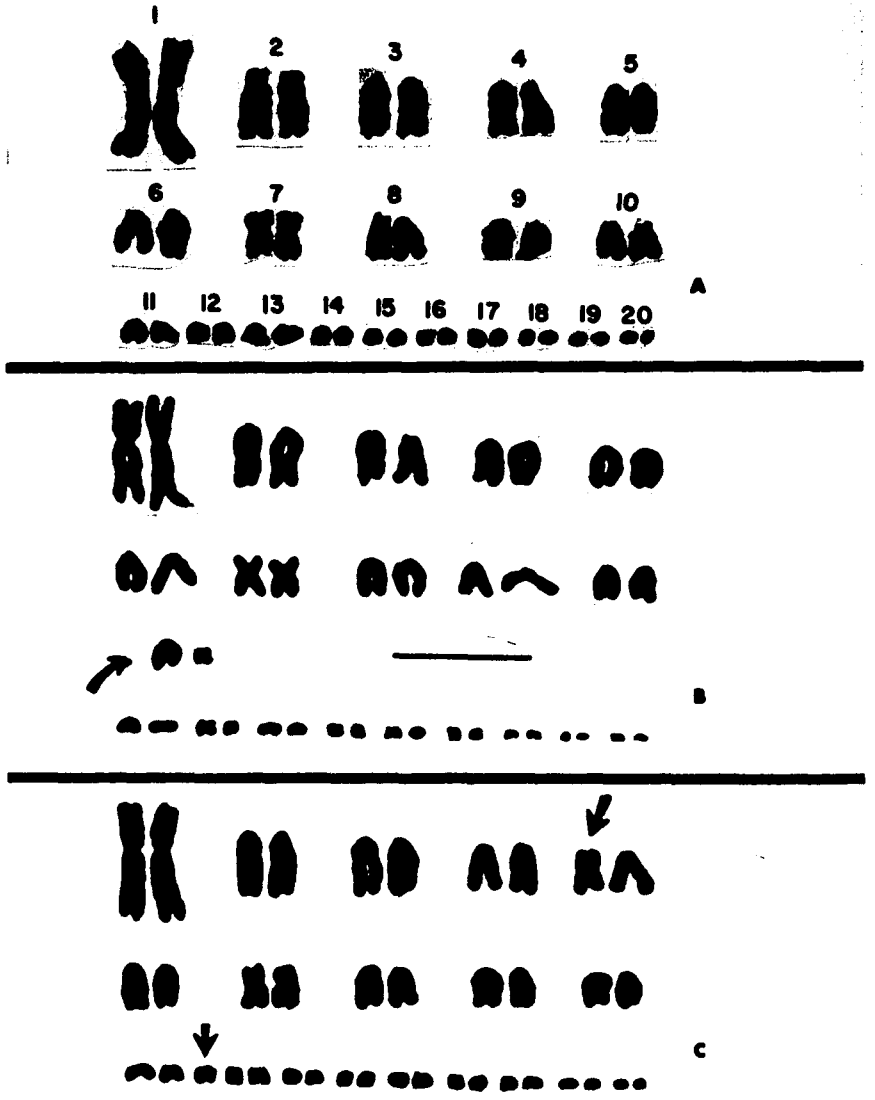

Fig. 4. Karyotypes of Sceloporus melanorhinus

19 microchromosomes instead of 20 and thus one appears unpaired. Three males (two from near Colima, Colima, Mexico, and one from Acapulco, Guerrero, Mexico) had this karyotype.

Presumably karyotypes KA and KB behave regularly in meiosis as in S. clarki; this may be generally so for karyotype KC also, but the fate of the "lost" microchromosome in this karyotype remains, for the present, unknown. Since the lizards were not collected during the breeding season and the peculiarities of their karyotypes were not known until after the animals were killed, additional field work is necessary to obtain meiotic material for analysis. More samples will also be necessary to determine local frequencies and distributions of the various karyotypes, and to determine for sure whether any of them are sex-correlated. Although individuals of both sexes of S. clarki can possess a karyotype generally similar to type KC of S. melanorhinus, it is indeed suspicious that the three males of S. melanorhinus all had that one karyotype, whereas none of the four females did.

Karyotypes KA and KB are presumably both very old and surely older than KC. Form KA evidently occurs throughout the range of the species, since it has been found in animals from Tuxtla Gutiérrez and from Colima. Form KB apparently was derived from KA and existed as a variant in the S. melanorhinus or melanorhinus-like populations from which Sceloporus clarki was derived (see above). Karyotype KC arose following more recent chromosomal aberrations.

The specimens examined include representatives of the subspecies S. melanorhinus calligaster, and S. m. stuarti.

Sceloporus orcutti Stejneger

Analysis of more than 73 mitotic bone marrow cells from eight individuals (four of each sex) reveals that $2n = 34$ chromosomes in S. orcutti, a considerably lower number than occurs in its southern relatives considered above. The karyotype (Fig. 5A) consists of 12 large, conspicuously bi-armed macrochromosomes (6 pairs) plus 22 microchromosomes (11 pairs). Of the macrochromosomes, nos. 1 and 5 are metacentric, while nos. 2 (most conspicuously), 3 (very less so), 4, and 6 (very less so) are submetacentric; there is a satellite on the tip of the long arm of no. 2. The microchromosomes are mostly telocentric, one larger pair rarely appearing subtelocentric. Excepting nos. 3 and 4, which often appear similar, the macrochromosome pairs are individually recognizable with high confidence in most cells, while the microchromosomes are not.

The specimens examined include representatives of both subspecies, S. orcutti orcutti, and S. o. licki.

Sceloporus magister Hallowell

This species has a diploid number of 26 chromosomes, which has been verified by examination of more than 142 cells from 16 lizards (9 males and 7 females). The karyotype (Fig. 5B), as earlier described (Lowe, Cole, and Patton, 1967), is comprised of 6 pairs of macrochromosomes and seven pairs of smaller elements; the latter include four pairs of smaller microchromosomes similar in size to those in S. clarki, and three larger pairs of metacentrics that are approximately twice as large.

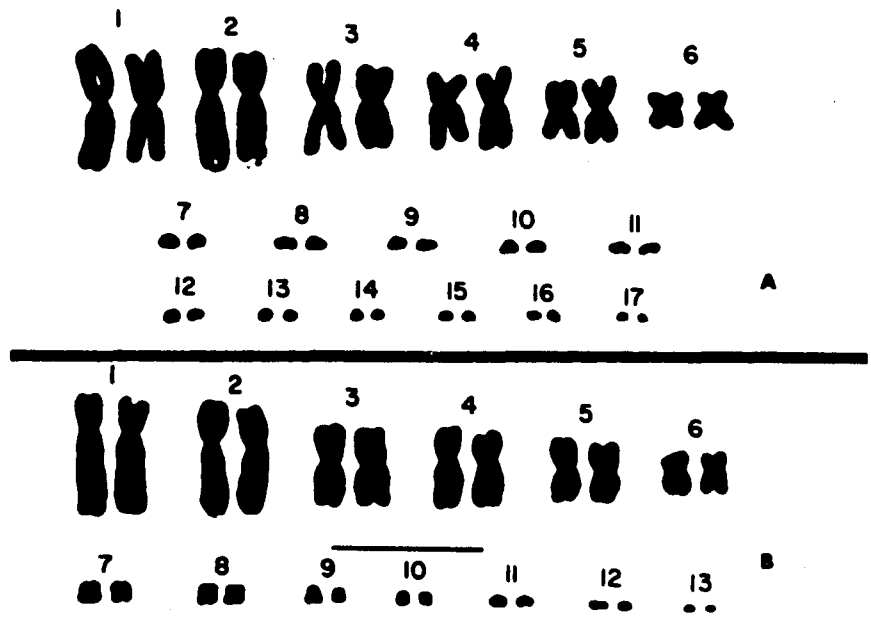

Fig. 5. Karyotypes of Sceloporus orcutti and Sceloporus magister

A. S. orcutti. UAZ Number 21674, a female from near Banning, San Jacinto Mountains, Riverside County, California.
B. S. magister. UAZ Number 24197, a male from near Desemboque del Río San Ignacio, Sonora, Mexico. Line represents 10 μ.

The macrochromosomes are similar to those of S. orcutti except that no. 1 is most conspicuously submetacentric and no. 3 is metacentric. Of the smaller pairs, 7, 8, and 9 are metacentric, 10 is subtelocentric, and the rest (11 through 13) are telocentric. In most cells all of the macrochromosomes are clearly recognized individually; the smaller chromosomes, particularly 7 and 8, and 11 and 12, cannot be labeled with certainty.

Specimens examined represent the subspecies S. magister magister, S. m. bimaculosus, and S. m. uniformis.

Sceloporus lundelli Smith

The karyotypes of S. lundelli were determined and verified by examination of at least 166 cells from 13 lizards (8 males and 5 females). These karyotypes have only 22 chromosomes, which is also the normal diploid number possessed by the remaining species in the spinosus group and is the lowest known chromosome number in the genus Sceloporus (see Lowe, Wright, and Cole, 1966). Unlike most species of the genus, however, including even the other members of the spinosus group, S. lundelli has conspicuous sex-correlated chromosomes of the X-Y type (Fig. 6).

The karyotypes (Fig. 6) are composed of six pairs of macrochromosomes and five pairs of smaller elements. Of the former, nos. 1, 3, 4, and 5 are metacentric, while nos. 2 (most conspicuously) and 6 (much less so) are submetacentric. Pair no. 2 bears a terminal satellite as in the other species considered immediately above. In females, both chromosomes of the largest pair in the smaller group (no. 7) are telocentric (X-X). Males, however, exhibit one individual

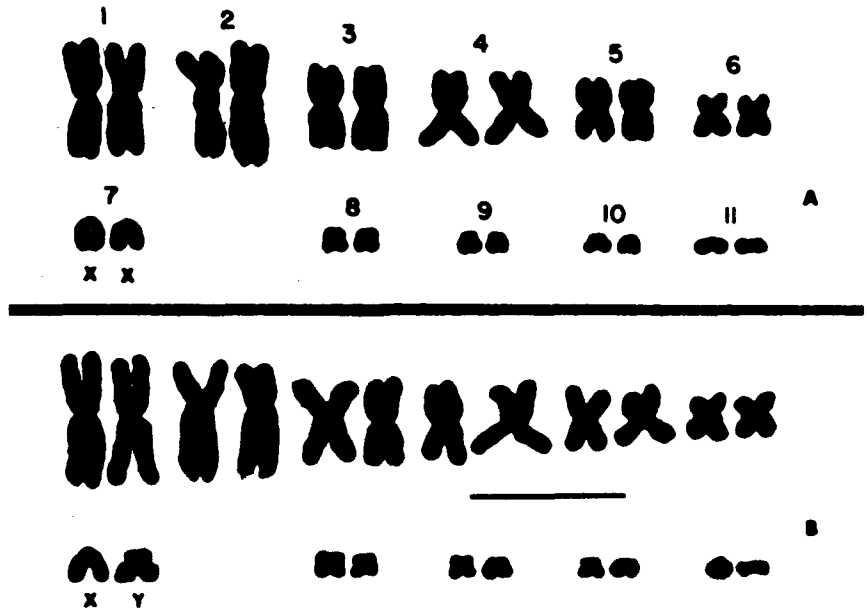

Fig. 6. Karyotypes of Sceloporus lundelli

A. Female, with two X chromosomes (no. 7). UAZ Number 28345, from Pisté, Yucatan, Mexico.
B. Male, with one X and one Y chromosome (no. 7). UAZ Number 28340, from near Río Lagartos, Yucatan, Mexico. Line represents 10 μ.

no. 7 that is telocentric and one that is subtelocentric (X-Y). The remaining chromosomes appear to be two pairs that are metacentric or nearly so (nos. 8 and 9), one pair that is subtelocentric (no. 10), and one pair of telocentrics (no. 11). Most of the chromosomes are readily recognized individually in most cells, excepting nos. 3 and 4, and nos. 8 and 9, which are most similar to one another.

The karyotypic sexual dimorphism in pair no. 7 was observed consistently; all eight males had the heteromorphic pair, whereas all five females had the homomorphic pair. Thus this is referred to as an X-Y sex chromosome system

Examination of testicular material demonstrates that there are six macrochromosome bivalents and five smaller bivalents in primary spermatocytes (Fig. 7A), and that segregation is regular and apparently undisturbed in the heteromorphic sex. Analysis of 50 secondary spermatocytes at metaphase II (Fig. 7B, C) revealed 30 containing the X chromosome and 20 containing the Y; as these frequencies are not significantly different from the hypothetical 1:1 ratio ($\chi^2 = 2.000$; $0.20 > P > 0.10$), I conclude that X-bearing and Y-bearing spermatozoa are produced in equal frequency.

Most species of Sceloporus do not exhibit morphologically recognizable sex chromosomes. Members of the torquatus species group, however, have been demonstrated as being exceptional in this regard (Cole, Lowe, and Wright, 1967). These have an $X_1X_2Y(\sigma):X_1X_1X_2X_2(\varphi)$ system rather than this simpler one of $XY(\sigma):XX(\varphi)$, and their Y chromosome is metacentric rather than

Fig. 7. Spermatocytes of Sceloporus lundelli

A. Primary spermatocyte (metaphase I), with 6 bivalents of macrochromosomes + 5 bivalents of smaller ones (n = 11). Arrow indicates the heteromorphic X-Y pair (no. 7). UAZ Number 28339, a male from near Río Lagartos, Yucatan, Mexico.
B. Secondary spermatocyte (metaphase II), with 6 + 5 constitution (n = 11), containing a telocentric X chromosome (no. 7; arrow). UAZ Number 28337, a male from Pisté, Yucatan, Mexico.
C. Secondary spermatocyte (metaphase II), with 6 + 5 constitution (n = 11), containing a subtelocentric Y chromosome (no. 7; arrow). UAZ Number 28340, a male from near Río Lagartos, Yucatan, Mexico (same individual illustrated in Fig. 6B).

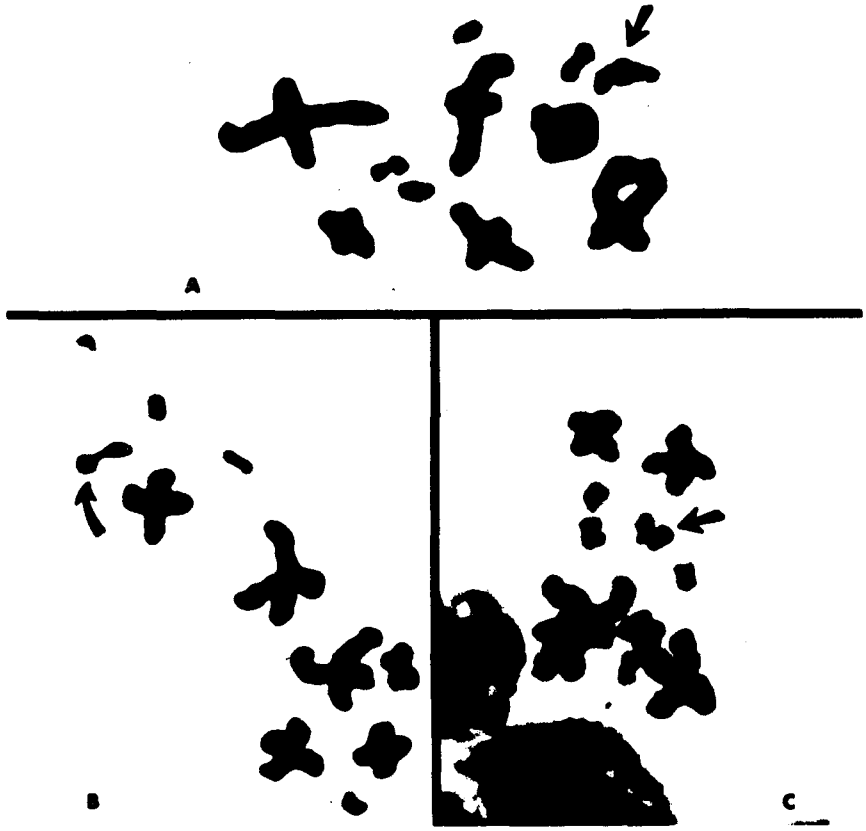

Fig. 7. Spermatocytes of Sceloporus lundelli

subtelocentric, suggesting that they evolved independently. It is particularly noteworthy nonetheless, that the Y chromosomes of both systems are approximately the same size and presumably they both evolved in part, at least, by means of centric fusion of microchromosomes (see below). Thus these particular independently evolved chromosomes may contain some historically identical gene loci that are directly concerned with the determination of the male sex. If this is so, a logical extension of this hyopthesis is that these particular sex-determining loci are still located today on microchromosomes of such species as Sceloporus melanorhinus and S. clarki, in which the microchromosomes have not undergone centric fusion, thus indicating a major role for at least some of these dot-like chromosomes that some investigators may be inclined to consider as insignificant merely because of their minute size.

All of the 13 specimens examined represent the subspecies S. lundelli gaigeae.

Sceloporus edwardtaylori Smith

The 83 cells analyzed from 9 individuals (6 males and 3 females) exhibited $2n = 22$ chromosomes generally similar to those of S. lundelli, but with heteromorphic sex chromosomes being conspicuously absent (Fig. 8A). The six pairs of macrochromosomes are nearly identical to those of S. lundelli, the most conspicuous difference being the lack of the satellites on no. 2 of S. edwardtaylori. Of the five pairs of smaller chromosomes, nos. 7, 8, 10, and 11 are metacentric or submetacentric,

Fig. 8. Karyotypes of Sceloporus edwardtaylori and Sceloporus olivaceus

A. S. edwardtaylori. UAZ Number 28371, a female from 7 mi. (by Hex. 190) NW Tehuantepec, Oaxaca, Mexico.
B. S. olivaceus. Typical, with pair no. 7 homomorphic, having two metacentric elements. UAZ Number 28328, a male from Austin, Travis County, Texas.
C. S. olivaceus. Atypical, with pair no. 7 heteromorphic, having one metacentric and one subtelocentric element (arrow). UAZ Number 24205, a male from along the Devil's River, NW of Del Rio, Val Verde County, Texas. Line represents 10 μ.
D. S. olivaceus. Aberrant cell from the same atypical individual illustrated in C. In addition to having pair no. 7 heteromorphic (arrow), there is a loop in one chromosome no. 1, which indicates a former break followed by sister chromatid fusion (arrow).

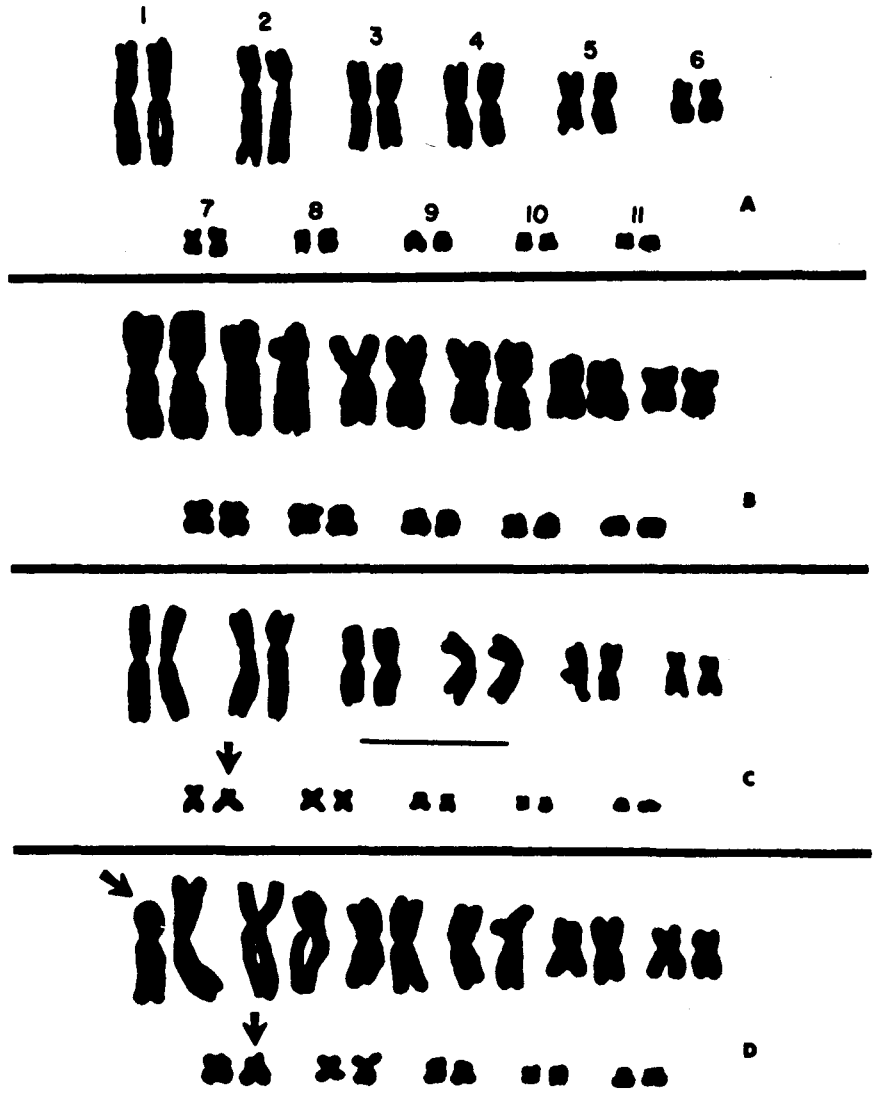

Fig. 8. Karyotypes of Sceloporus edwardtaylori and Sceloporus olivaceus

while no. 9 is subtelocentric. An inconspicuous satellite occurs terminally on one arm of pair no. 8.

As this is the only species in the group having the satellite on no. 8, and as all other species in the group, including more primitive and more derived forms (see below), have the satellite occurring terminally on no. 2, it is likely that the altered position in S. edwardtaylori resulted from a translocation of the satellite chromatin from no. 2, assuming that the satellite chromatin represents the same loci in these species. The translocated segment must be small since chromosome nos. 2 and 8 do not appear different in size from those in their related species and the centromere position in no. 2, in particular, appears the same. Thus, disregarding the satellite, chromosome no. 2 of S. edwardtaylori is morphologically similar to that of S. lundelli.

Sceloporus olivaceus Smith

This species also has $2n = 22$ chromosomes, which was determined and verified by analysis of more than 207 dividing cells from 12 individuals (5 males and 7 females). Normally the karyotype (Fig. 8B) is nearly identical to that of S. edwardtaylori (Fig. 8A). Their six pairs of macrochromosomes conspicuously differ only in the presence in S. olivaceus of the secondary constriction terminally on chromosome no. 2. In other words, the macrochromosomes of S. olivaceus are exceedingly similar, if not identical, to those of S. lundelli. The five pairs of microchromosomes include 4 (7 through 10) that are

metacentric or nearly so, and the fifth pair (no. 11), which is subtelocentric or submetacentric.

Two individuals were characterized by an atypical karyotype. In these (Fig. 8C), no. 7 is a heteromorphic pair having one metacentric element (typical) and one subtelocentric (atypical). Thus these individuals appear to be heterozygous for a pericentric inversion in pair no. 7. This is not a sex-correlated phenomenon since it occurred in one specimen of each sex. In the male, testicular tissues exhibited the same heteromorphism.

The aberration involved with this heteromorphic pair is of no greater magnitude than that in the apparent pericentric inversion heterozygotes in Sceloporus clarki (see above). Furthermore, the two specimens possessing it were from different localities; the male was from NW of Del Río, along the Devil's River, Val Verde County, Texas, and the female from Austin, Travis County, Texas. Thus it should not seem surprising that meiosis proceeded regularly in the heterozygous male, as it does also in the Sceloporus clarki heterozygotes (see above). Six bivalents of macrochromosomes and five of smaller chromosomes are regularly formed in meiosis I (Fig. 9A). Segregation is normal and produces both types of expected secondary spermatocytes (those with the atypical subtelocentric no. 7 and those with the typical metacentric one; Fig. 9B, C) with equal frequency, as determined by analysis of 50 cells at metaphase II (N = 21 typical; N = 29 atypical; $\chi^2 = 1.28$; $0.30 > P > 0.20$).

One other aberration was found in one bone marrow cell of the same aberrant male. This cell contained 12 macrochromosomes and 10

Fig. 9. Spermatocytes from an Individual of Sceloporus olivaceus with an Atypical Heteromorphic Pair of Chromosomes

A. Primary spermatocyte (metaphase I), with 6 bivalents of macrochromosomes + 5 smaller bivalents (n = 11).
B. Secondary spermatocyte (metaphase II), with 6 macrochromosomes and 5 microchromosomes (n = 11). Note that no. 7 (arrow) is the typical metacentric element.
C. Secondary spermatocyte (metaphase II), with 6 macrochromosomes and 5 microchromosomes (n = 11). Note that no. 7 (arrow) is the atypical subtelocentric element.

All three spermatocytes are from UAZ Number 24205, the same male illustrated in Fig. 8C and D.

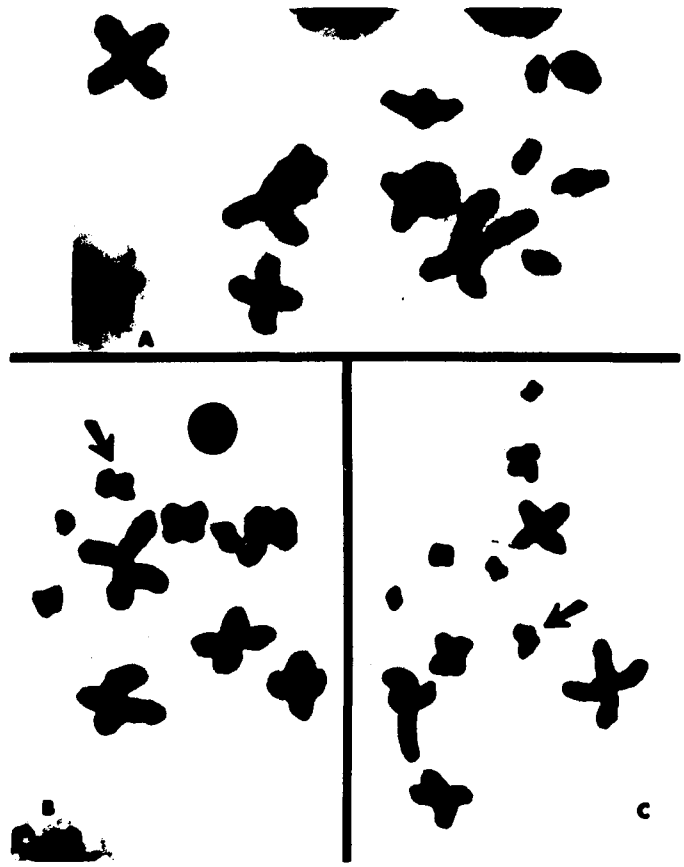

Fig. 9. Spermatocytes from an Individual of Sceloporus olivaceus with an Atypical Heteromorphic Pair of Chromosomes

smaller chromosomes as is typical, except that one macrochromosome had an unusually short arm that exhibited sister chromatid fusion, thus forming a loop (Fig. 8D). This is nearly identical to the chromosomal aberration in Sceloporus virgatus that was recently reported (Cole and Lowe, 1968). Indeed, even the same chromosome (one of the no. 1 homologues) is involved. Similarly, this presumably resulted from a break in the arm and was followed by sister chromatid fusion. But no acentric fragment occurred in this particular cell (Fig. 8D), suggesting that the aberration occurred in one of its ancestral cells and the fragment had since been lost (or passed into the other daughter cell). Thus it appears that at least certain types of bone marrow cells of S. olivaceus can survive the deletion of a sizable portion of a no. 1 chromosome, even while already supporting an atypical heteromorphic pair (no. 7).

Sceloporus spinosus Wiegmann

Examination of more than 65 mitotic bone marrow cells from 5 animals (1 male and 4 females) reveals two generally very similar but distinct karyotypes that appear to be geographically rather than sexually correlated, and neither of which has heteromorphic chromosomes. One of the karyotypic forms is from the vicinity of Miahuatlán and Oaxaca de Juárez, Oaxaca, Mexico (Fig. 10A; N = 3 females), and the other occurs in the specimens from the general vicinity of Celaya, Guanajuato, on the Mexican Plateau (Fig. 10B; N = 2 specimens, one of each sex).

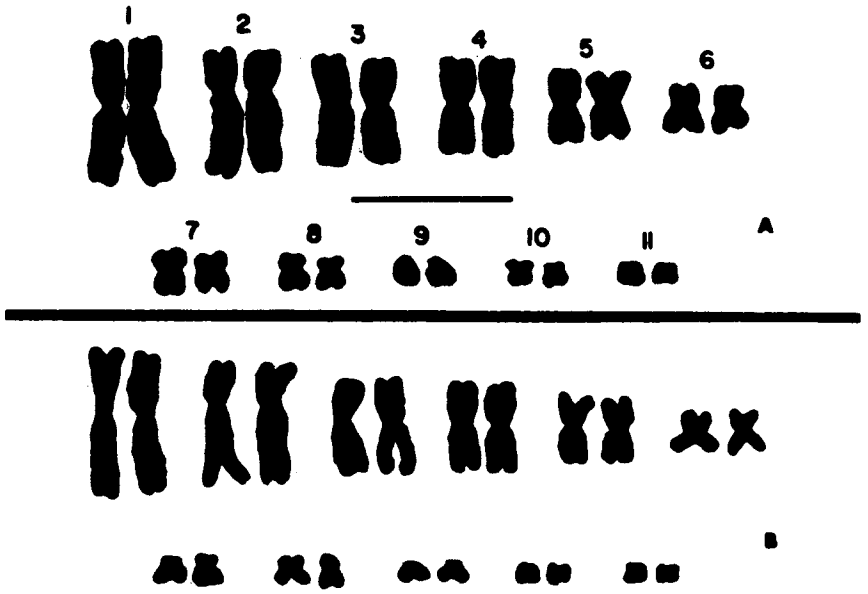

Fig. 10. Karyotypes of Sceloporus spinosus

A. Individual with pair no. 7 metacentric. UAZ Number 28355, a female from 5 mi. (by Mex. 175) NW Miahuatlán, Oaxaca, Mexico. Line represents 10 μ.
B. Individual with pair no. 7 subtelocentric. UAZ Number 28354, a female from near Celaya, Guanajuato, Mexico.

In both cases the diploid karyotype of 22 includes 6 pairs of macrochromosomes that are essentially indistinguishable from those of S. lundelli, S. edwardtaylori, and S. olivaceus (the satellite is on no. 2 as in S. lundelli and S. olivaceus) plus five pairs of smaller elements (Fig. 10A, B). The Miahuatlán and Oaxaca de Juárez animals (S. spinosus apicalis and S. spinosus caeruleopunctatus, respectively) have among the five pairs of smaller chromosomes four that are metacentric to submetacentric (nos. 7, 8, 10, and 11) and one that is subtelocentric (no. 9). In the specimens of S. spinosus from near Celaya (S. spinosus spinosus), pairs 8 through 11 are as just described but no. 7 is subtelocentric rather than metacentric (Fig. 10A, B). The subspecific difference in these karyotypes probably is the result of a pericentric inversion.

Specimens examined include representatives of the subspecies S. spinosus spinosus, S. s. apicalis, and S. s. caeruleopunctatus. Future collecting will be designed to determine whether the geographic distribution of the two karyotypic forms corresponds well with that of the subspecies, and the consequences when they approach one another or meet.

Sceloporus horridus Wiegmann

This species also has a diploid number of 22 composed of 6 pairs of macrochromosomes and five pairs of smaller ones, which was determined and verified by examination of nearly 100 mitotic bone marrow cells from eight individuals (6 males and 2 females). As in S. spinosus, there are two distinct though generally similar karyotypes (Fig. 11) that are

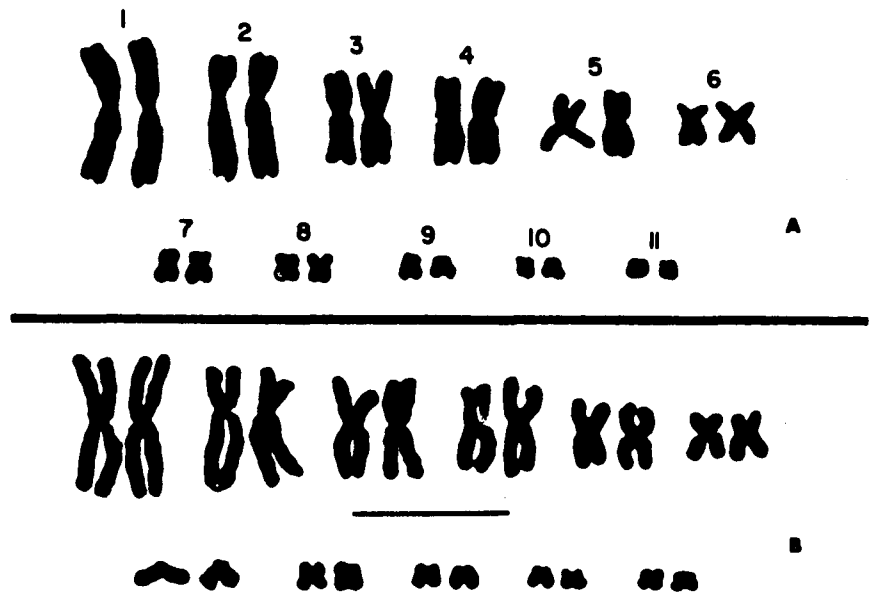

Fig. 11. Karyotypes of Sceloporus horridus

A. Individual with pair no. 7 metacentric. UAZ Number 28315, a male from 8 mi. (by Mex. 15) SE Tepic, Nayarit, Mexico.
B. Individual with pair no. 7 telocentric or essentially so. UAZ Number 28324, a male from near Colima, Colima, Mexico. Line represents 10 μ.

geographically rather than sexually correlated, and which do not involve heteromorphic pairs of chromosomes within individuals. One of the karyotypic forms is from two localities in Nayarit, Mexico, and the other occurs in specimens from four other widely scattered Mexican localities: (1) near Colima, Colima, (2) Autlán, Jalisco, (3) the vicinity of Iguala, Guerrero, and (4) 7 mi. (by rd.) NW Teotitlán del Camino (Oaxaca), Puebla, Mexico.

In both cases the 6 pairs of macrochromosomes are extremely similar to, if not identical with, those of S. spinosus, including even the terminal location of the satellites on chromosome no. 2. The Nayarit specimens (S. horridus albiventris) have all of the five smaller pairs (7 through 11) metacentric or nearly so (Fig. 11A). Karyotypes in animals (S. h. horridus and S. h. oligoporus) from the other localities are exceedingly similar, but chromosome no. 7 is clearly telocentric or essentially so, rather than metacentric (Fig. 11B). As in S. spinosus, it is most likely that this subspecific karyotypic difference results from a pericentric inversion.

Specimens examined include representatives of the three subspecies, S. horridus horridus, S. h. albiventris, and S. h. oligoporus. Future field and laboratory work is expected to determine the geographic and taxonomic relationships of these karyotypic forms. For the present, it appears that one chromosome form (metacentric no. 7) is restricted to S. h. albiventris, while the other form occurs in the remaining subspecies.

Evolution

Opening Remarks

Unabashedly I take up consideration of phylogenetic relationships within this group of lizards, fully aware that conclusions regarding phylogenies based only on traits of Recent species can be rather tenuous; nevertheless, the fossil record of Sceloporus is practically nonexistent. While many biologists feel that such endeavors are futile, there is no doubt that karyotypic data often provide tremendously functional tools for hypothesizing on evolutionary relationships (for reviews see Stebbins, 1950; Patterson and Stone, 1952; White, 1954), and more recently karyotypic analysis has revealed with virtual certainty the ancestry of particular species of lizards (Lowe and Wright, 1966).

I shall present the evolutionary relationships within the spinosus group as I see them, without a greatly detailed discussion and consideration of the numerous possible schemes that might be preferred by others. To provide "equal time" to all such alternatives would seriously cloud the story to be outlined below. I recognize that minor points may well be quibbled over interminably, and some investigators may even wish to twist the picture 180°. To the latter I bid good luck, for to convince me of a considerably different phylogeny within this group would necessitate educating me further in areas of which I am now ignorant, hopefully not to the point of hopelessness.

Characteristics

External morphology. Attempts at determining phylogenetic relationships between spinosus group species on the basis of classical characteristics of scutellation and color pattern are considerably frustrating. I have reviewed these characteristics in detail as presented by Smith (1939) for the various species, and I have re-examined most of them on series of specimens of each species. While these traits of external morphology generally serve in distinguishing between the species, most of them do not exhibit evolutionary trends or tendencies of conspicuous utility for phylogenetics. Indeed, in many cases the species must even be diagnosed on the basis of combinations of several detailed characteristics. Consideration of these external morphological characteristics follows.

A number of characteristics (e.g., number of canthal scales, number of loreals, and number of postrostrals) exhibit tremendous similarities in expression from species to species and are therefore useless for determining relationships within this group. Certain other traits are of little phylogenetic value because they characterize only one species, to which they may be particularly adaptive. For example, the general morphology of the scales at particular places on the body does not vary vastly from species to species in this group, one obvious exception being the reduced spines and keels on the dorsal body scales of Sceloporus orcutti; presumably this is an adaptive response to its petricolous mode of life, which is more highly developed than in any other species of the group. There are also traits with no apparent

adaptive significance that characterize only one species (e.g., the outer row of labiomentals regularly contacts the mental in S. magister but not in any of the other species); these likewise are of no direct use in reconstructing the phylogeny of this group.

Other specific characteristics more frequently used in saurian classification suffer from similar or additional deficiencies when examined with a view toward evolutionary relationships within the spinosus group. Number of dorsal scales, for example, varies from a mean as low as about 29 (e.g., in S. melanorhinus) to a mean as high as about 36 (e.g., in S. orcutti licki); and most of the species appear to exhibit little intraspecific variation in this characteristic. Nevertheless, different subspecies of Sceloporus magister reveal striking differences in dorsal scale counts, with population means from different localities varying from about 29 to about 34 (Smith, 1939; Phelan and Brattstrom, 1955), which encompasses nearly the entire range of variation for the species group and suggests that the trait may be relatively easily molded locally by selection and/or drift. Analysis of the number of scales around midbody, number of ventral scales, and number of femoral pores produces similar dilemmas.

The dilemmas just considered should not come as a surprise. After all, these species are considered as comprising a group of closely related forms precisely because of their similarities in external morphology and the scarcity of sharply demarcated differences between them. Thus, phylogenetic relationships within the group presently can

be best inferred primarily from cytogenetic, zoogeographic, ecologic, and behavioral characteristics.

Karyotypes. Basically there are four karyotypes represented by the nine species in the spinosus group (Table 3), disregarding for the moment the intraspecific variation, polymorphisms, and minor interspecific differences considered above. These four can be summarized as follows: (1) the melanorhinus-type, in which $2n = 40$, composed of 20 macrochromosomes (10 pairs, of which 2 are submetacentric and 8 are telocentric) + 20 microchromosomes (10 pairs); (2) the orcutti-type, in which $2n = 34$, composed of 12 macrochromosomes (6 pairs, of which 2 are metacentric and 4 are submetacentric) + 22 microchromosomes (11 pairs); (3) the magister-type, in which $2n = 26$, composed of 12 macrochromosomes (6 pairs, of which 2 are metacentric and 4 are submetacentric) + 14 smaller chromosomes (7 pairs, of which only 4 are really small enough to qualify as microchromosomes); and (4) the lundelli-type, where $2n = 22$, composed of 12 macrochromosomes (6 pairs, of which 4 are metacentric and 2 are submetacentric) + 10 smaller chromosomes (5 pairs, none of which is small enough to qualify as microchromosomes).

The nine spinosus group species are arranged into four subgroups of related forms on the basis of karyotypic similarities (Table 3). I do not doubt that this grouping reflects phylogenetic affinities, being based on cytogenetic characteristics of closely related populations. From the standpoint of karyotypic evolution by means of chromosomal centric fusions (whole-arm translocations; see Robertson, 1916; see White, 1954, for a review), which has been shown to be compatible with

Table 3. Occurrence of the Four Basic Karyotypes in the Nine Species of the Spinosus Group

Karyotype	melanorhinus-type ($2n = 40$)	orcutti-type ($2n = 34$)	magister-type ($2n = 26$)	lundelli-type ($2n = 22$)
Species	S. melanorhinus	S. orcutti	S. magister	S. lundelli
	S. clarki			S. edwardtaylori
				S. olivaceus
				S. spinosus
				S. horridus

hypotheses of amphibian and reptilian evolution both in a broad sense (e.g., Matthey, 1951) and at the specific level in some cases (e.g., Lowe, Cole, and Patton, 1967), two most likely phylogenies are suggested by the karyotypes occurring in the spinosus group (Table 3): (1) one general evolutionary line of centric fusions from the melanorhinus-type ($2n = 40$, with numerous telocentrics) through the orcutti- and magister-types, and terminating (today) in the lundelli-type ($2n = 22$, with nearly all, if not all, metacentrics and submetacentrics); or (2) two phylads, one of which involved a progression of centric fusions represented today by the sequence from the melanorhinus-type through the orcutti-type to the magister-type (referred to hereafter as the melanorhinus subgroup), and one of which also involved centric fusion and of which only the most advanced karyotypic forms (the lundelli-type) remain today (referred to hereafter as the lundelli subgroup). The latter hypothesis is most compatible by far with the ecologic and zoogeographic relations of these species (see below).

Ecology and zoogeography. The ecologic preferences of these species, together with their geographic distributions, are also strongly indicative of their phylogenetic relationships. The northernmost species (S. magister) is primarily a desert and desert-grassland form; the remaining species occur in similar habitats or generally in more southern, subtropical to tropical vegetative communities (thornscrub, short-tree forest, etc.), which are plant communities ancestral to those of the relatively recently derived deserts, and which evolved during the Tertiary Period largely in response

to gradually increasing aridity (Chaney, 1940, 1947; Axelrod, 1948, 1949, 1950a, b, 1958, 1960; Dorf, 1960; Turner, 1959). Furthermore, independent investigations with a variety of groups of amphibians and reptiles have demonstrated considerable compatibility with the evidence derived from the cited paleobotanical investigations, with occasional illustrative examples having been selected from desert and desert-edge-dwelling pairs of spinosus group species of Sceloporus (Lowe, 1950, 1959; Lowe, Cole, and Patton, 1967; Norris, 1958; Savage, 1960, 1966; Auffenberg, 1963; Brame and Wake, 1963; Tihen, 1964; Wake, 1966; Asplund, 1967). The evidence is overwhelmingly indicative that the southern, tropical, arboreal, humid to semi-humid forest-inhabiting species of the spinosus group are ancestral to the more northern, subtropical, semi-arboreal to terrestrial, semi-arid to arid scrub or desert-inhabiting species.

Ecologic generalizations about the individual species (Table 4) reveal that there are both southern, arboreal, tropical forest-dwelling forms and northern, terrestrial, subtropical scrub- to desert-dwelling forms in each karyotypic subgroup (the melanorhinus subgroup and the lundelli subgroup), strongly supporting the recognition of the two phylads suggested above. Furthermore, the general geographic distributions of these species (Fig. 12), together with their cytogenetic and ecologic attributes (Tables 3, 4), support the two phylad hypothesis most attractively; one phylad occurs primarily along the Pacific Coast lowlands of Mexico, the southwestern United States, Baja California, and nearby mountains, and the other phylad occurs to the east. In a broad sense and in a strongly suggestive fashion,

Table 4. General Habitat and Behavioral Preferences of the Nine Spinosus Group Species of Sceloporus

Species	Habitat	Behavior
	(A) melanorhinus subgroup	
S. melanorhinus	Semi-humid; tropical deciduous forest	Highly arboreal
S. clarki	Semi-arid; tropical deciduous forest, subtropical thorn forest, oak-pine woodland	Arboreal
S. orcutti	Semi-arid to arid; rocks in subtropical thorn forest, oak-pine woodland, chaparral, desert	Terrestrial (highly petricolous)
S. magister	Semi-arid to arid; subtropical thornscrub, desert-grassland, desertscrub	Terrestrial, with arboreal tendencies (shelters are in the ground)
	(B) lundelli subgroup	
S. lundelli	Humid to semi-humid; rainforest, tropical deciduous forest, thorn forest	Highly arboreal
S. edwardtaylori	Semi-humid to semi-arid; tropical deciduous forest, savanna	Arboreal
S. olivaceus	Semi-arid; subtropical thorn forest, live-oak woodland, riparian woodland in subtropical thornscrub and desert-grassland	Arboreal, with terrestrial tendencies
S. spinosus	Semi-arid to arid; subtropical savanna, thornscrub	Terrestrial, with arboreal tendencies (shelters are in the ground)
S. horridus	Semi-arid to arid; tropical deciduous forest, subtropical savanna, thornscrub	Terrestrial, with arboreal tendencies (shelters are in the ground)

Fig. 12. General Geographic Distributions of the Nine *Spinosus* Group Species of *Sceloporus*

A. The *melanorhinus* subgroup ($2n$ = 40, 34, 26; western phylad).
B. The *lundelli* subgroup ($2n$ = 22; eastern phylad).
Heavy branching lines represent geographic and phylogenetic affinities. Light latitudinal lines represent the Tropic of Cancer. Data from Smith (1939) and Stebbins (1966).

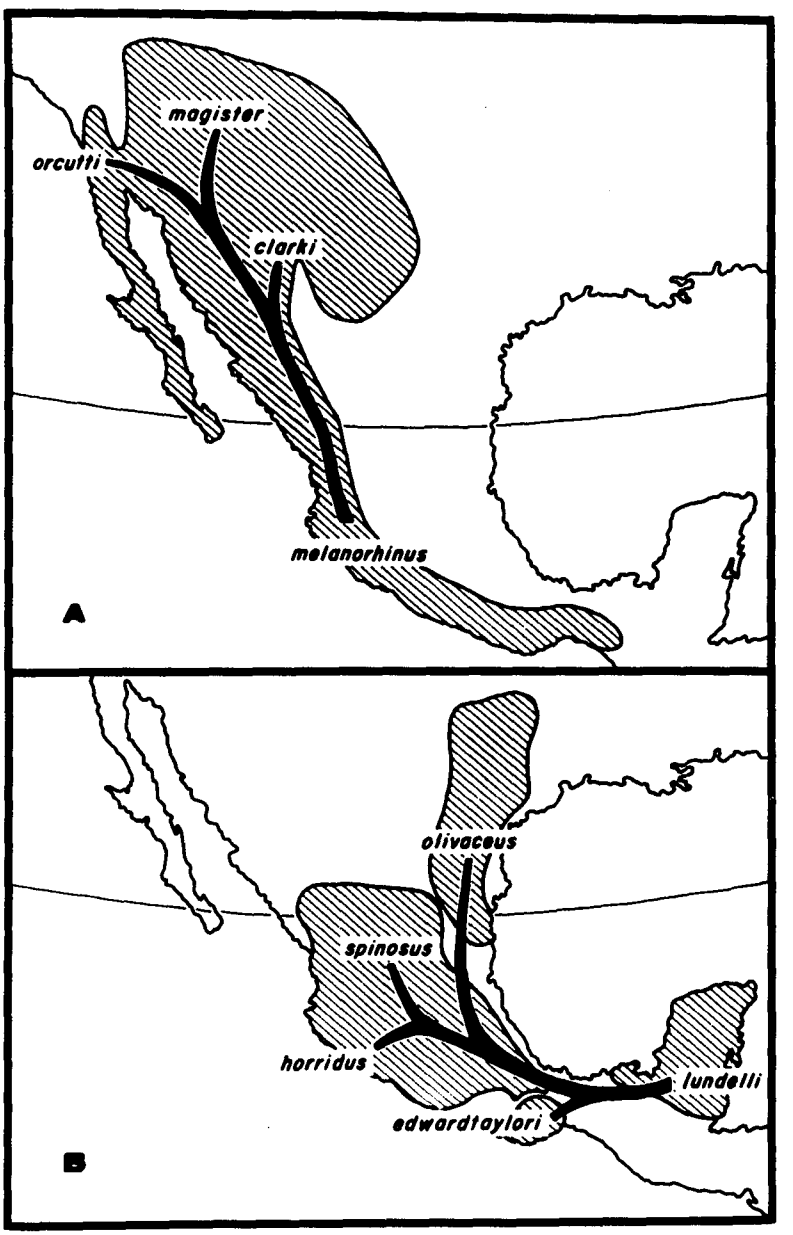

Fig. 12. General Geographic Distributions of the Nine Spinosus Group Species of Sceloporus

these phylads are mostly separated today by the massive Sierra Madre Occidental and the Sierra Madre del Sur, which presumably provided geographical isolation during their essentially independent evolution.

Phylogenetic Relationships

My interpretation of the specific relationships within this group is in the form, hopefully, of a non-deciduous phylogenetic tree (Fig. 13). Inappropriate as it first appears, I have followed the classical procedure of illustrating the most derived species at the upper reaches of the branches, although this schematically situates the most terrestrial forms in the phylogenetic treetops, and the most ancestral, highly arboreal forms at the base of the tree!

The position of S. magister in this phylogeny (Fig. 13) may seem to be most readily questioned. Sceloporus magister, in overall general morphological appearance, deceptively appears closely related to S. horridus and S. spinosus; ecologically and behaviorally it is similar to these species also. The similarities result from convergence, as these outwardly similar forms constitute the present terminal (most recently derived) species in their respective phylads and the trend in each has been adaptive response to increasing aridity and occupation of desert and subdesert communities. In addition to the zoogeographic and karyotypic indicators, some details of scutellation are also suggestive of the illustrated relationship (Fig. 13); for example, Sceloporus orcutti and S. magister are the only two species

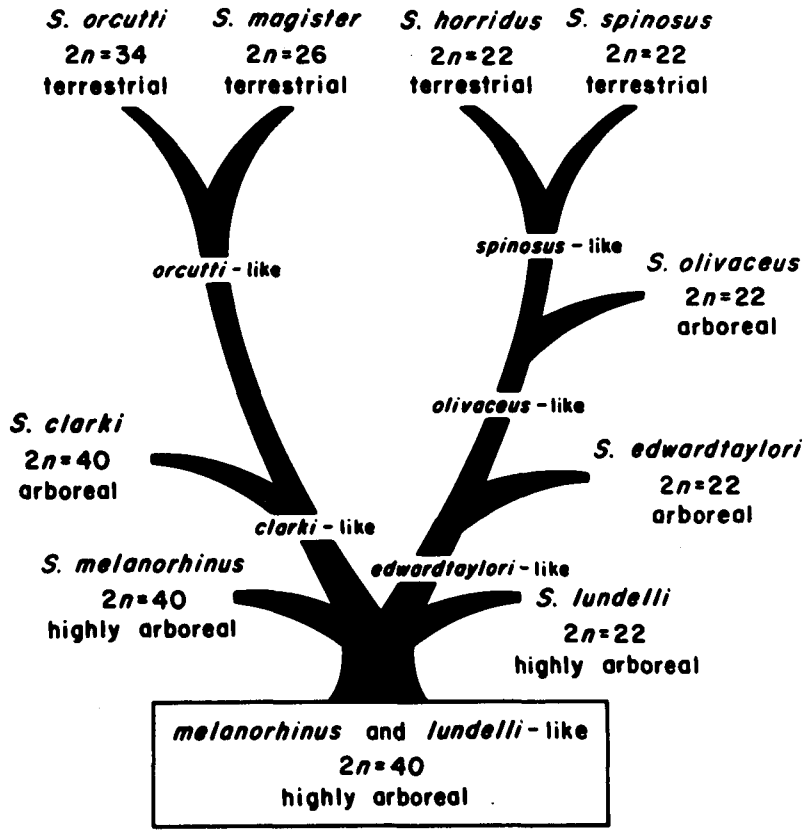

Fig. 13. Phylogeny of the Spinosus Group of Lizards in the Genus Sceloporus

in the entire group in which the first canthal scale is regularly vertically elongated with the consequence that it is in contact with the lorilabials in nearly all specimens.

Smith (1939: 59) presented a phylogeny of the spinosus group in his taxonomic monograph, without specifically discussing the criteria on which it was based. While our proposed phylogenies differ significantly, there are some striking similarities. Without explanatory discussion, Smith recognized the western phylad progression represented by S. melanorhinus, S. clarki, and S. orcutti. Furthermore, he generally recognized the more tropical and more arboreal forms as more ancestral in the phylogeny than the more terrestrial forms.

Smith considered Sceloporus magister to be a derivative of the same stock giving rise to S. horridus, S. olivaceus, and S. spinosus, with the last three species being the most recently derived. It is interesting that this particular relationship is in part what would be suggested by those who are inclined to infer phylogenetic relationships solely on the basis of karyotypic information, without regard to other equally important biological criteria (see above). Strictly cytogenetically oriented investigators probably would envision one phylad beginning with a melanorhinus-type of chromosomal constitution ($2n = 40$), evolution by means of centric fusion progressively through the northern terrestrial orcutti- and magister-types (my western phylad) and continuation of this fusion trend directly on to S. horridus or S. spinosus ($2n = 22$) in the same phylad, which would require, because of the karyotypic similarities, following through in a geographic circle to the southern arboreal

S. edwardtaylori and S. lundelli as the most recently derived forms, which is morphologically, ecologically, and zoogeographically untenable.

The majority of the speciation in the spinosus group occurred in the upper middle to late Tertiary Period, particularly in association with the elevation of mountains and plateaus, generally increasing aridity, and the restriction and evolution of vegetative communities (see paleobotanical and herpetological references cited above). The dates involved with this evolution cannot by hypothesized in detail, however, since the Tertiary and Quaternary history of Mexico would have to be known in unreasonably precise detail in order to be accurately correlated with speciation within such a species group. Nevertheless, the Miocene and Pliocene epochs are attractive as the general time span encompassing most, if not all, of the speciation in this group, considering in particular the paleobotanical information presented by Axelrod (1948, 1949, 1950a, b, 1958, 1960), the paleoherpetological information presented by Tihen (1964), and the present habitat preferences and behaviors exhibited by the extant forms. Thus, speciation within the spinosus group appears to have involved faunal restrictions as well as derivation in situ approximately as described below.

The prototype was a highly arboreal form occupying widespread portions of the Neotropical-Tertiary Geoflora and the newer Madro-Tertiary Geoflora in the Miocene. These lizards had a karyotype essentially identical to the typical $2n = 40$ karyotype (20 macrochromosomes + 20 microchromosomes) occurring in S. melanorhinus and S. clarki today.

The prototype became isolated (probably geographically rather than ecologically) into two populations; these constituted the ancestral stocks for the western and eastern phylads. Although the initial isolation was not accompanied by very different ecological adaptations, the karyotype of the western group experienced relatively little or no alteration, while that of the eastern group evolved predominantly by means of centric fusion (whole-arm translocation) into the highly derived $2n = 22$ condition that generally characterizes its Recent representatives today. This karyotypic evolution probably included nine centric fusions (four among the macrochromosomes and five among the microchromosomes), as illustrated (Fig. 14A).

Not long hereafter, still in the Miocene, the first divergence near the base of each phylad occurred in response to increased aridity such that the western phylad included populations represented by S. melanorhinus (or a direct ancestor thereto) and S. clarki (or a direct ancestor thereto), and the eastern phylad split into S. lundelli (or its directly ancestral form) and S. edwardtaylori (or its direct ancestor). The more ancestral forms (S. melanorhinus and S. lundelli) were associated with the more humid to semi-humid tropical forests, while the newly derived forms (S. clarki-like and S. edwardtaylori-like) were associated with the newer semi-humid to semi-arid subtropical forests. This was not accompanied by extensive karyotypic alterations within either phylad, but those that had earlier occurred between the phylads could have been at least partly responsible for the successful sympatry of species belonging to the two subgroups (e.g., S. melanorhinus and S. edwardtaylori).

Fig. 14. Composite Mock-up "Karyotypes" of Sceloporus lundelli, Sceloporus orcutti, and Sceloporus magister

A. Haploid complements of S. melanorhinus [n = 20; left chromosome(s) of each "pair"] and S. lundelli [n = 11; right chromosome of each "pair"] illustrating how nine centric fusions of particular chromosomes of S. melanorhinus could produce the karyotype typical of S. lundelli and all of the species in the lundelli subgroup. Compare with Fig. 6B. The haploid complement of S. melanorhinus is from the same cell illustrated in Fig. 4B, while that of S. lundelli is from the same cell illustrated in Fig. 6B.

B. Haploid complements of S. clarki [n = 20; left chromosome(s) of each "pair"] and S. orcutti [n = 17; right chromosome of each "pair"] illustrating how four centric fusions of particular macrochromosomes of S. clarki could produce the karyotype typical of S. orcutti. Compare with Fig. 5A. Note that centromere positions in the derived form (S. orcutti) indicate that three of the four fusions are different from those proposed for the lundelli subgroup (Fig. 14A). The origin of chromosome No. 17 in S. orcutti is not obvious. Perhaps it represents one of the remaining centromeres (not lost) resulting from one of the four centric fusions (whole-arm translocations). The haploid complement of S. clarki is from the same cell illustrated in Fig. 1C, while that of S. orcutti is from the cell illustrated in Fig. 5A.

C. Haploid complements of S. orcutti [n = 17; left chromosome(s) of each "pair"] and S. magister [n = 13; right chromosome of each "pair"] illustrating how three centric fusions of microchromosomes of S. orcutti could produce a karyotype generally similar to that of S. magister. Differences in centromere positions in nos. 1 and 3 suggest that pericentric inversions occurred in S. magister. The fate of the S. orcutti chromosome no. 17 is unknown. Compare with Fig. 5B. The haploid complement of S. orcutti is from the same cell illustrated in Fig. 5A, while that of S. magister is from the cell illustrated in Fig. 5B.

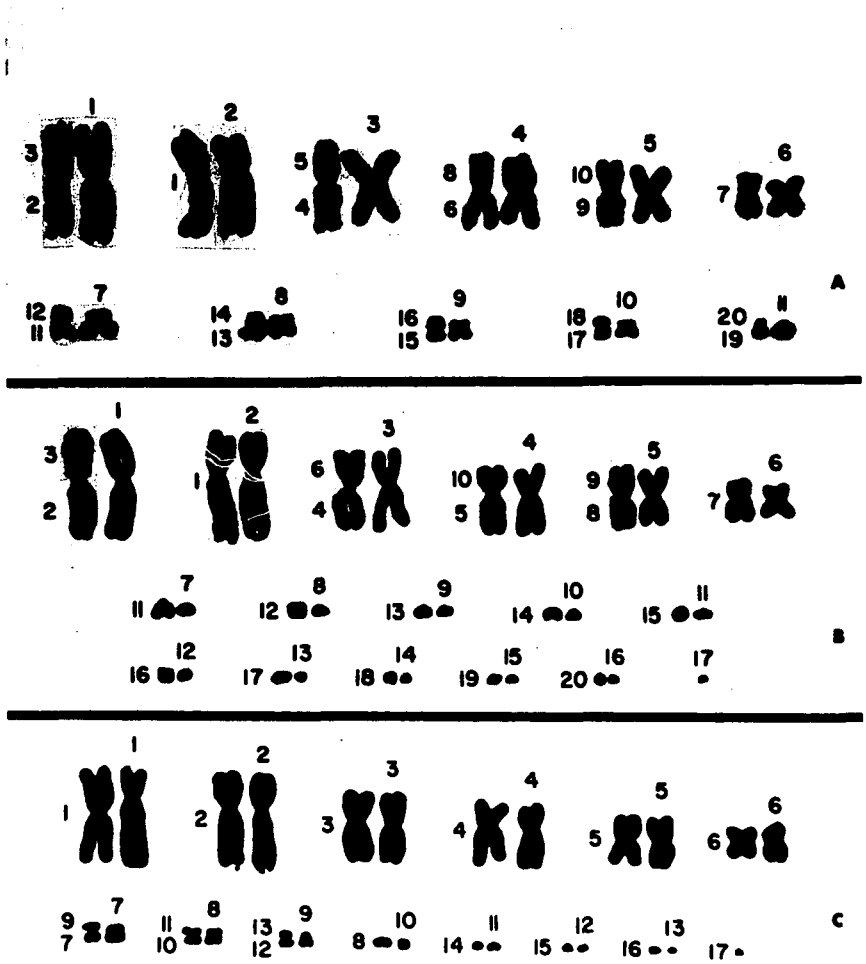

Fig. 14. Composite Mock-up "Karyotypes" of Sceloporus lundelli, Sceloporus orcutti, and Sceloporus magister

Further diversification occurred later in the Miocene; in the western populations the clarki-like stock diverged into S. clarki and an orcutti-like stock, while the eastern populations split into S. edwardtaylori and an olivaceus-like stock. In both cases the more newly derived forms associated with the more semi-arid habitats, with both the orcutti-like and olivaceus-like stocks occurring in subtropical woodlands, chaparral, savanna, thorn forest, and thornscrub. While divergence in the eastern phylad did not involve extensive karyotypic modifications, speciation in the western phylad was accompanied by four centric fusions among the macrochromosomes in the orcutti-like stock, which thus evolved a karyotype similar to that of S. orcutti today (Fig. 14B). Disparities between S. orcutti and the members of the lundelli subgroup in particular centromere positions suggests that in some cases centric fusion of different elements is involved, which further supports the hypothesis that centric fusion occurred independently in the two phylads (compare Figs. 14A and 14B).

The remainder of the diversification at the species level occurred in the Mio-Pliocene and later in the Pliocene, still resulting from the trend toward increased aridity. General southward restriction of the more mesic, ancestral tropical forests was accompanied by southward restriction of the associated ancestral lizards (e.g., S. melanorhinus and S. lundelli). Meanwhile, in the eastern phylad, the olivaceus-like stock diverged into Sceloporus olivaceus and a spinosus-like stock. The former remained with the semi-arid subtropical woodland, thorn forest, and riparian communities to the north and east

as they were displaced from the Mexican Plateau by the developing semi-arid to arid desertscrub in which the newly derived spinosus-like stock developed; shortly thereafter it diverged into S. spinosus (to the east) and S. horridus (to the west), without involving extensive karyotypic alterations. By now, the more ancestral and arboreal Sceloporus edwardtaylori and S. olivaceus were geographically separated, due to the interstitial development of more arid-adapted vegetative communities and their associated lizards.

Meanwhile, the orcutti-like stock of the western phylad diverged into S. orcutti and S. magister, also in response to increasing aridity. Sceloporus magister, which probably evolved in the Sonoran Desert while S. orcutti was restricted to California and Baja California, has become most highly adapted to the desert environment. This divergence was accompanied by karyotypic evolution including two pericentric inversions among the macrochromosomes and three centric fusions among the microchromosomes in the populations directly ancestral to Sceloporus magister (Fig. 14C). The two inversions are suggested by the different centromere positions in chromosome nos. 1 and 3. The former is metacentric in S. orcutti and submetacentric in S. magister, while the latter is submetacentric in S. orcutti and metacentric in S. magister (Fig. 14C). Revelation of S. orcutti as representative of an evolutionary intermediate between S. clarki and S. magister has resulted in modification of some of the hypotheses concerning detailed macrochromosome arm homologies of S. clarki and S. magister as presented by Lowe, Cole, and Patton (1967; compare their Fig. 2 with the present Fig. 14B, C). It is noteworthy

also that those authors correctly hypothesized the occurrence of a pericentric inversion in chromosome no. 1 following centric fusion of the ancestral chromosomes from which it was derived.

The remainder of the Pliocene and the Pleistocene to Recent were of importance primarily in subspeciation and in establishing present geographic ranges of the species in the spinosus group. In this regard, it is particularly noteworthy that the more arid-adapted, generally more northern, most recently derived forms in each subgroup are those having the greatest number of subspecies for their respective phylads, revealing their most recent intraspecific evolutionary experimentation and diversification.

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