Karyotypes of the Five Monotypic Species Groups of Lizards in the Genus *Sceloporus*

By Charles J. Cole

**INTRODUCTION**

Smith (1939) recognized 15 species groups in the large iguanid genus *Sceloporus*, which includes approximately 60 species. From one to 11 species are assigned to each group on the basis of relationships inferred from traits of external morphology. Five species of *Sceloporus* (some of them polytypic) are each sufficiently distinctive in external morphology to warrant assignment to monotypic species groups, implying that these five species appear to have no particularly close relatives extant. The present cytological investigation was undertaken to determine whether the karyotypes of these monotypic species groups are consistent with the data on external morphology, and whether the karyotypes suggest evolutionary relationships of these groups.

The five species of *Sceloporus* that each comprise a monotypic group are: *Sceloporus chrysothrichus* Cope, *S. gracilis* Baird and Girard, *S. maculosus* Smith, *S. merriami* Stejneger, and *S. utiformis* Cope. Each group is named for the species comprising it. My analysis of karyotypes from individuals of both sexes of each of these species forms the basis of the present report.

**METHODS**

Chromosome preparations were made by means of the colchicine, hypo-
tonic citrate technique used by Patton (1967), slightly modified for lizards (Lowe, Wright, and Cole, 1966). I used bone marrow and testicular tissues, and examined chromosomes in approximately 340 dividing cells from 28 lizards (19 males, 9 females; see Specimens Examined). Chromosome terminology is that used earlier for Sceloporus (Cole, 1970).

RESULTS AND CONCLUSIONS

The *chrysostictus* Group

I examined chromosomes in approximately 70 cells from four individuals (three males, one female) of *Sceloporus chrysostictus*. The diploid number is 34 chromosomes (2n = 34), of which 12 are macrochromosomes and 22 are microchromosomes. The chromosomes are arranged in pairs and numbered in order of decreasing length (fig. 1). Among the macrochromosomes, number 1 is metacentric to submetacentric, numbers 3, 4, and 5 are metacentric, and numbers 2 and 6 are submetacentric. The shape of most of the microchromosomes remains unresolved; at least two pairs are bi-armed, whereas the majority seem to be uni-armed. Nevertheless, among the larger microchromosomes there is a distinctive pair of subtelocentric chromosomes bearing a secondary constriction that appears as a gap near the centromere. This is the only consistent location of secondary constrictions in this species. No conspicuous satellites occur terminally on chromosome number 2, which is their characteristic location in numerous other species of *Sceloporus*, including representatives of most other species groups.

![Karyotype](image)
In most cells the macrochromosomes are individually recognizable, whereas the microchromosomes are not, excepting the large distinctive pair bearing the secondary constrictions. The Y is also distinctive among the microchromosomes in males. It is minute, conspicuously smaller than any of the others, and synapses with a larger microchromosome (the X) in meiosis, thus forming a bivalent representing a heteromorphic pair of chromosomes (figs. 1, 2). The female did not exhibit the minute chromosome designated as the Y in males, but instead possessed another of the somewhat larger microchromosomes. Therefore, these lizards have an inconspicuous XY(♂):XX(♀) sex chromosome system similar to that discovered in lizards of the genus *Uta* by Pennock, Tinkle, and Shaw.
(1969), and similar to that found in other species of Sceloporus (see below; Cole, In press).

Smith (1939, pp. 294–295) noted strong similarities between S. chrysostictus and members of both the variabilis and siniferus species groups. But Sceloporus chrysostictus lacks the traits considered as key characteristics for both groups (for example, chrysostictus lacks a postfemoral dermal pocket and keeled preanal scales in females, respectively). The absence of these characteristics and the possession of certain others (for example, clearly enlarged postanal scales in males) suggest that S. chrysostictus is not particularly morphologically specialized, although it does exhibit some unusual features: for example, the anterior section of the frontal scale is regularly divided longitudinally, and males lack distinctive ventral coloration. Smith concluded that although S. chrysostictus is closely related to both the variabilis and siniferus groups, it is more primitive than both and is more closely related to the siniferus group (Smith, 1939, p. 28, pp. 294–295, and p. 300).

I conclude, however, that S. chrysostictus is clearly most closely related to members of the variabilis species group. This is evident to me because all members of the variabilis group whose chromosomes I have examined to date have karyotypes extremely similar, if not identical, to those of S. chrysostictus, and these are distinct from the karyotypes of the members of the siniferus group whose chromosomes I have examined. The significant karyotypic detail in this regard is that the members of the variabilis group analyzed to date also lack satellites on chromosome number 2 and instead have secondary constrictions situated near the centromere on one of the largest pairs of microchromosomes, as in S. chrysostictus. Thus, it also seems suggestive of close relationship that the unusual characteristic of the anterior section of the frontal scale being regularly longitudinally divided occurs likewise in S. chrysostictus and in most species of the variabilis group (Sceloporus parvus of the variabilis group is an exception in this regard). In view of all this, Smith’s (1939, p. 295) following statement appears as further evidence of this relationship: “It is noteworthy that three species (cozumelae, teapensis, and chrysostictus) of two groups (variabilis and chrysostictus) of two groups (variabilis and chrysostictus) of two groups (variabilis and chrysostictus) occupying a compact area (Yucatan Peninsula and adjacent territory) lack or tend to lose the subnasal.”

The graciosus Group

Description of the karyotype of Sceloporus graciosus is based on the examination of chromosomes in approximately 90 dividing cells from 14 individuals (10 males, four females). This species has 2n = 30 chromosomes, of which 12 (six pairs) are macrochromosomes and 18 (nine pairs)
COLE: LIZARD KARYOTYPES

are smaller (fig. 3). The macrochromosomes are nearly the same as those described above for *S. chrysostictus*; the apparent differences are that in *graciosus* there is a terminal satellite on the long arm of chromosome number 2, and secondary constrictions are not present on any of the smaller chromosomes. Among the nine pairs of smaller chromosomes are several pairs composed of clearly bi-armed elements. The two largest pairs of the smaller chromosomes are approximately twice as large as many of the others, and include one pair of *ca.* metacentric chromosomes and one pair of subtelocentric chromosomes. Perhaps these relatively larger chromosomes evolved through whole-arm translocations between microchromosomes in the ancestral stock. In most cells the macrochromosomes are individually recognizable, whereas the smaller chromosomes are not.

The karyotype described here for *S. graciosus* provides detail additional to that of the initial report of Lowe, Wright, and Cole (1966) and is similar to that reported by Jackson and Hunsaker (1968, 1969a, 1969b, 1970). The latter authors reported essentially the same thing in several papers, which was partly the consequence of confusing the identities of the lizards whose chromosomes they described in their first report. In that report they described the karyotype of *S. graciosus* (2n = 30) as being that of *S. occidentalis* (2n = 22), which is quite different (see also Lowe, Wright, and Cole, 1966; Cole, Lowe, and Wright, 1967). In later papers comparing the karyotypes of *S. graciosus* and *S. occidentalis*, Jackson and Hunsaker (1969b, 1970) commented that the chromosomes of *S. occidentalis* are more reasonably referred to as 12 macrochromosomes plus 10 microchromosomes, rather than as 10 + 12, as first reported by Lowe,

**Fig. 3.** Karyotype from male *Sceloporus graciosus* (2n = 30; U.A.Z. No. 21865). Line represents 10 μ.
Wright, and Cole (1966) and by Cole, Lowe, and Wright (1967). I agree that the 12 + 10 reference for *S. occidentalis* is more reasonable, and thus I have used it more recently for similar karyotypes of species in the same group (e.g., *S. virgatus*; see Cole and Lowe, 1968) and for species in the related *spinosus* group (Cole, 1970), in which cases it makes most sense particularly in view of the hypotheses concerning karyotype evolution in *Sceloporus*. Nevertheless, for species with reduced numbers of the smaller chromosomes it is not fitting to refer to all of them as "microchromosomes"; some (as in *S. graciosus*) or all (as in *S. occidentalis*) probably evolved from centric fusions of two original microchromosomes each, and thus the derived ones are approximately twice the size of the ancestral ones, which are the true microchromosomes (see above; Lowe, Cole, and Patton, 1967; Cole, 1970).

The karyotype of *Sceloporus graciosus*, with 2n = 30 chromosomes, is quite distinctive. Indeed, I have not yet found this same karyotype in any other species of *Sceloporus*, and yet the same one occurs in the 14 specimens of *S. graciosus* that I have examined from various localities in Arizona, California, Colorado, and Utah. This is compatible with the recognition of *S. graciosus* as representative of a monotypic species group within the genus *Sceloporus*.

Specimens examined represent the subspecies *S. graciosus graciosus* and *S. g. vandenburgianus*.

The *maculosus* Group

Description of the karyotypes of *Sceloporus maculosus* is based on the examination of chromosomes in nearly 100 dividing cells from three lizards (two males; one female). In the female, 2n = 34 chromosomes, whereas in the males 2n = 33. In both sexes there are 12 macrochromosomes (six pairs); in addition, females have 22 microchromosomes (11 homomorphous pairs), whereas males have only 20 microchromosomes plus an apparently unpaired telocentric to subtelocentric chromosome that is distinctly larger than the microchromosomes (figs. 4, 5).

The six pairs of macrochromosomes are similar to those described above for *S. graciosus*; pair number 1 is metacentric to submetacentric, numbers 3, 4, and 5 are metacentric, and numbers 2 and 6 are submetacentric. In *S. maculosus*, however, the secondary constrictions occupy a particularly distinctive position near the end of the slightly shorter arm of chromosome number 1. Thus, chromosome number 1 bears a terminal satellite. This satellite, which is extremely small, is difficult to see in many cells. Among the microchromosomes, at least one pair is composed of bi-armed elements, but most of the microchromosomes are too small to
Fig. 4. Karyotypes from two individuals of *Sceloporus maculosus*. A. Male, \((2n = 33; \text{U.A.Z. No. 24221})\), with 12 macrochromosomes, 1 intermediate-sized telocentric to subtelocentric chromosome, and 20 microchromosomes. The macrochromosomes include six homomorphic pairs, whereas the microchromosomes include nine homomorphic pairs plus one \(X_1\) and one \(X_2\), the last two of which synapse with the \(Y\) (the intermediate-sized chromosome) in meiosis I to form a trivalent (figure 5). Designation of the \(X\) chromosomes is for purposes of illustration; whether those individuals are really the \(X\) chromosomes is presently unknown. The satellites on chromosome number 1 are not evident in this photograph. Line represents 10 \(\mu\). B. Female \((2n = 34; \text{U.A.Z. No. 24228})\), with 12 macrochromosomes, no intermediate-sized chromosome, and 22 microchromosomes. The macrochromosomes are as in the male, and the microchromosomes include 11 homomorphic pairs, with a pair each of the \(X_1\) and the \(X_2\). Precisely which elements are the \(X\) chromosomes is presently unknown. The satellites on chromosome number 1 are not evident in this photograph.

be well resolved. In most cells the macrochromosomes are individually recognizable, whereas the microchromosomes are not. In males, the “unpaired” telocentric to subtelocentric chromosome that is larger than the microchromosomes is clearly recognized in nearly every cell.
Analysis of spermatogonia and spermatocytes from both males reveals that testicular tissues have the same karyotype as that in bone marrow cells. In meiosis I (analyzed at diplotene, diakinesis, and metaphase I; N = 12 cells), the larger, “odd” telocentric regularly forms a trivalent together with two of the microchromosomes, and the remaining chromosomes all synapse to form bivalents. Thus, the 12 macrochromosomes form six bivalents, 18 of the microchromosomes form nine bivalents, and the remaining three small chromosomes form a trivalent (fig. 5).

Examination of large series of secondary spermatocytes from one male revealed that preferential segregation from the trivalent occurred during anaphase I. Of 42 cells analyzed, 20 cells possessed six macrochromosomes plus the large “odd” telocentric plus nine microchromosomes (n = 16, composed of 6 + 1 + 9; fig. 5), and 22 cells possessed six macrochromosomes plus 11 microchromosomes (n = 17, composed of 6 + 0 + 11; fig. 5). This suggests that during anaphase I, in a primary spermatocyte, segregation from the bivalents is normal and segregation from the trivalent is such that the larger subtelocentric to telocentric chromosome moves to one pole while the two microchromosomes with which it was synapsed move together to the opposite pole (χ² = 0.0952; 0.80 > P > 0.70). Thus this is an X₁X₂Y (♂):X₁X₁X₂X₂(♀) sex chromosome system. The larger “odd” telocentric to subtelocentric chromosome of males is the Y chromosome, and the X chromosomes are among the microchromosomes. A similar sex chromosome system occurs in members of the torquatus species group (Cole, Lowe, and Wright, 1967), but in them the Y chromosome is metacentric rather than telocentric to subtelocentric.

I suggest that the female condition (2n = 34, composed of 12 + 22 chromosomes) is the primitive one. The Y chromosome probably evolved from a translocation involving an X₁ and X₂, which resulted in the larger, “odd” telocentric to subtelocentric.

Smith (1939, pp. 290–291) commented on the distinctiveness of Sceloporus maculosus and also suggested that it may be related to the variabilis group. Relationship with the variabilis group is not implied by the karyotypic data, however. The very distinctive karyotype of S. maculosus is compatible with recognizing the species as comprising a monotypic species group, as I have not found the same karyotype in any other species in the genus. Distinctive cytological features are: (1) the terminal satellites on the shorter arm of chromosome number 1, (2) the X₁X₂Y (♂):X₁X₁X₂X₂(♀) sex chromosome system with a telocentric to subtelocentric Y, and (3) the occurrence of 20 microchromosomes in males and 22 in females of a species possessing this particular sex chromosome system.
Fig. 5. Spermatocytes from an individual of *Sceloporus maculosus* (same specimen illustrated in fig. 4A). A. Primary spermatocyte (diakinesis) with 6 bivalents of macrochromosomes + 9 bivalents of microchromosomes + 1 sex chromosome trivalent (arrow; \( n = 16 \)). B. Secondary spermatocyte (metaphase II) with 6 macrochromosomes + 1 intermediate-sized chromosome (arrow; the Y chromosome) + 9 microchromosomes (\( n = 16 \)). C. Secondary spermatocyte (metaphase II) with 6 macrochromosomes + 11 microchromosomes (\( n = 17 \)).
THE \textit{merriami} Group

Description of the chromosomes of \textit{Sceloporus merriami} is based on the examination of approximately 50 mitotic cells from five individuals (three males, two females). This species has $2n = 46$ chromosomes, which is the highest number known in the genus. All the chromosomes are similar in shape (subtelocentric or telocentric), and when arranged in order of gradually decreasing length (fig. 6) they do not show the great distinction between macrochromosomes and microchromosomes that characterizes most species of \textit{Sceloporus}. Nevertheless, one can recognize 24 macrochromosomes and 22 microchromosomes, as one would expect considering that many other species in the genus have 12 \textit{ca.} metacentric macrochromosomes and 22 microchromosomes. Thus, the number of major chromosome arms within the genus is rather conservative relative to the number of chromosomes.

All of the 24 larger chromosomes are subtelocentric. Satellites occur terminally on the long arm of either chromosome pair number 1 or 2 (they are about equal in size). A few pairs of microchromosomes appear subtelocentric in some cells, but otherwise they are too small to resolve in detail. In males, one individual microchromosome is significantly smaller than the others (figs. 6, 7), which is not the case in females, and

\begin{figure}[h]
\centering
\includegraphics[width=\textwidth]{karyotype.png}
\caption{Karyotype from male \textit{Sceloporus merriami} ($2n = 46$; U.A.Z. No. 24191). Note satellites on pair number 1. Among the microchromosomes, the Y is designated; for purposes of illustration it is paired with another of the smallest chromosomes apparent in the cell, but whether that one is really the X is presently unknown. Line represents 10 \textmu.}
\end{figure}
thus *S. merriami* has an inconspicuous XY(♂):XX(♀) sex chromosome system similar to that found in *S. chrysostictus* (see above) and *S. utiformis* (see below).

The karyotype of *Sceloporus merriami* is extremely distinctive within the genus and certainly is compatible with Smith's (1939) recognition of the species as comprising a monotypic group. Although the chromosome number of *S. merriami* (2n = 46) is more than twice that of the species possessing the lowest number in the genus (2n = 22, as in *S. spinosus*; see Cole, 1970), polyploidy is not involved. The very large macrochromosomes that are generally ca. matacentric in these other species, the significantly smaller macrochromosomes that are subtelocentric (with very small short arms) in *S. merriami*, and the relative sizes of the macrochromosomes to the microchromosomes in these dissimilar chromosome complements all reveal that the karyotypic evolution occurred by means of whole-arm translocations.

From the viewpoint that the evolution of amphibian and reptilian karyotypes may have often involved centric fusions (see Matthey, 1951, and White, 1954, for reviews), the karyotype of *S. merriami* appears extremely primitive. This is compatible with other morphological traits and with the distribution of this species. Considering that the species is recognized as comprising a monotypic species group, it may also be inferred to be relatively ancient if viewed as a sole survivor. Also, the occurrence of this species in isolated populations (e.g., in the Chisos Mountains, Brewster County, Texas, and in the vicinity of Cuatro Cienegas, Coahuila) is indicative of a relictual distributional pattern.

Only two other species of *Sceloporus* whose karyotypes have been examined to date have chromosome complements nearly similar to those of *S. merriami*; these species are *S. melanorhinus* and *S. clarkii* of the *spinosus* species group, whose karyotypes are extremely similar to one another (Cole, 1970). A common karyotype in these two species (they both exhibit polymorphism) includes 2n = 40 chromosomes, with 20 macrochromosomes (two pairs are submetacentric, the rest telocentric or essentially so) plus 20 microchromosomes. If the two submetacentrics were unfused in these species, they would have 24+20 chromosomes, which, in most respects, would be extremely similar to those of *S. merriami* (less two microchromosomes). It is reasonable to conclude that *S. clarkii*, *S. melanorhinus*, and *S. merriami*, all of which appear primitive in several regards, have primitive karyotypes, and that the strong differences in external morphology between the species of the *spinosus* group and that of the *merriami* group reflect the long time interval in which there has been divergence. Apparently, an opposite hypothesis would be proposed
Fig. 7. Primary spermatocyte at metaphase I from an individual of Sceloporus merriami ($n = 23$; same individual illustrated in fig. 6). The bivalent of microchromosomes indicated with an arrow represents heteromorphic X-Y pair, in which the Y is minute.
by several other investigators. Gorman, Atkins, and Holzinger (1967) and Gorman, Baptista, and Bury (1969) concluded that the primitive karyotype of sceloporines, and indeed of all iguanid lizards, contained 12 ca. metacentric macrochromosomes; they considered karyotypes with more numerous subtelocentric and telocentric macrochromosomes as having been derived through centric fission (a mechanism for which they have not clarified). An extension of this view would require that the generally similar karyotypes of such distinctive sceloporines as Sceloporus melanorhinus and Sceloporus merriami resulted from convergence.

The specimens examined represent all three subspecies: S. merriami merriami, S. m. annulatus, and S. m. australis.

The *utiformis* Group

Description of the chromosomes of *Sceloporus utiformis* is based on the analysis of approximately 30 cells from two individuals (one of each sex). There are 2n = 34 chromosomes (fig. 8), including 12 macrochromosomes (six pairs) and 22 microchromosomes (11 pairs). Among the macrochromosomes, number 1 is metacentric to submetacentric, numbers 3, 4, and 5 are metacentric, and numbers 2 and 6 are submetacentric. There is a terminal satellite on the long arm of chromosome number 2. At least two pairs of microchromosomes are bi-armed, but the details of the majority of them cannot be resolved. One of the male microchromosomes is significantly smaller than the others (fig. 9), which is not the case in the female; thus, *S. utiformis* has an XY(♂):XX(♀) sex chromosome system similar to that found in *S. chrysostictus* and *S. merriami* (see above).

Smith (1939, pp. 324–325) concluded that although *S. utiformis* is

![Fig. 8. Karyotype from female Sceloporus utiformis (2n = 34; U.A.Z. No. 21122). The satellites on chromosome number 2 are not evident in this photograph. Line represents 10 μ.](image-url)
Fig. 9. Primary spermatocyte at diakinesis from an individual of *Sceloporus utiformis* (*n* = 17; U.A.Z. No. 29951). The bivalent of microchromosomes indicated with an arrow represents the heteromorphic X-Y pair, in which the Y is minute.

quite distinct, it is closely related to the *siniferus* species group, and that the similarities in external morphology between *S. utiformis* and *S. merriami* were a result of a "parallel development" (1939, p. 285) rather than of intimate common ancestry. Karyotypic data largely support these conclusions. The chromosomes of *Sceloporus utiformis* are virtually identical to those of the species in the *siniferus* species group whose karyotypes I have determined to date. They are likewise rather similar to those of species in the *pyrocephalus* species group (particularly *Sceloporus gadoviae* and *S. nelsoni*; Cole, In press). Furthermore, the chromosomes of *S. utiformis* (*2n* = 34) are vastly different from those of *S. merriami* (*2n* = 46; see above). Thus it seems reasonable that *S. utiformis* is more closely related to species in the *siniferus* group than it is to *S. merriami*.

**SUMMARY**

The karyotypes of the five species of *Sceloporus* that comprise monotypic species groups are described on the basis of examination of chromosomes in approximately 340 cells from 28 lizards (19 males, 9 females),
and the following broad conclusions are reached: (1) *Sceloporus chrysostictus* \((2n = 34)\) has karyotypes (including an X–Y sex chromosome system) virtually identical to those of species in the *variabilis* group and unlike those of other species in the genus, which indicates that its affinities lie with that group. (2) *Sceloporus graciosus* \((2n = 30)\) has a karyotype distinctly different from that of all other species analyzed in the genus, which is compatible with its comprising a monotypic group. (3) *Sceloporus maculosus* \((2n = 33\) in males; \(2n = 34\) in females) has distinctive karyotypes [including an \(X_1X_2Y(\delta):X_1X_1X_2X_2(\varphi)\) sex chromosome system] that are different from those of all other species analyzed in the genus, which is consistent with its comprising a monotypic group. (4) *Sceloporus merriami* \((2n = 46)\) has the highest chromosome number known in the genus and also has distinctive karyotypes (including an X–Y sex chromosome system) that are different from those of all other species analyzed in the genus. (5) *Sceloporus utiformis* \((2n = 34)\) has karyotypes (also including an X–Y sex chromosome system) virtually identical to those of species in the *siniferus* group, which, together with features of external morphology, indicates that its affinities lie with that group.

**SPECIMENS EXAMINED**

All specimens \((N = 28)\) from which chromosomes were examined are catalogued individually in the herpetological collection of the Department of Biological Sciences at the University of Arizona (U.A.Z.; catalogue numbers in parentheses).

*Sceloporus chrysostictus* \((N = 4;\) three males, one female): Mexico: Yucatan: near Aguada Kamal, 16.2 km. (by road) south of Yaxcopoil (18132); 12.5 miles east of Sisal (18136, 19077); Pisté (29538).


*Sceloporus maculosus* \((N = 3;\) two males, one female): Mexico: Coahuila: 125 miles west of Saltillo, 1 mile west of junction of Mex. 40 (Matamoros) and Mex. 40 (San Pedro) (24190, 24221, and 24228).

*Sceloporus merriami* \((N = 5;\) three males, two females): Mexico: Coahuila: 13 miles east of Cuatro Cienegas (39 miles west of Monclova) (24217, 24219). United States: Texas: Brewster County: along Window Trail, Chisos Basin,
5400 ft., Chisos Mountains, Big Bend National Park (18528); Juniper Canyon, east side of Chisos Mountains (24905). Val Verde County: 1 mile north of old Devil's River Bridge, near Devil's River (24191).

Sceloporus utiformis (N = 2; one male, one female): Mexico: Jalisco: just north-west of Puerto Los Mazos (12 miles west of Ayutlan on route 80), 4600 ft. (21122). Sinaloa: 5 miles (by Mex. 15) southeast of Rosario (29951).

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