Sex Chromosomes in Lizards

Abstract. *Karyotypes of many species of the genus* Sceloporus *support the generalization that there are no morphologically recognizable sex chromosomes in lizards; however, there is a marked sexual dimorphism in the karyotypes of* Sceloporus jarrovi *and* Sceloporus poinsetti. *During meiosis in males, whose diploid number of chromosomes is 31, preferential segregation of chromosomes from a trivalent results in heterogamety.*

The question of sex chromosomes in lizards has been controversial. Some investigators have reported sex chromosomes for several species in which the males have an even diploid number of chromosomes ($2n$), whereas the females have $2n - 1$ and are thus heterogametic (*1*). However, other workers (*2, 3*) have found no sex chromosomes in the lizards they have studied [including *Lacerta vivipara*, for which Oguma (*1*) reported female heterogamety], and, therefore, more recently it has been generally accepted (*3, 4*) that the karyotypes of both sexes of a given species of lizard are the same. This is typical of various species in the genus *Sceloporus* (for example, *S. occidentalis* Baird and Girard, $2n = 22$, Fig. 1), which is composed of 15 species-groups (*5*), species of which occur widely throughout the United States, Mexico, and Central America.

Nevertheless, *Sceloporus jarrovi* Cope and *Sceloporus poinsetti* Baird and Girard have marked sexual dimorphism in their karyotypes. Our examination of the chromosomes from a total of 297 mitotic cells from 17 individuals (eight males, nine females) of these species reveals that their karyotypes are very similar, if not identical, and that if they are different the difference is only in detailed morphology (*6*).

In the karyotypes of both *S. jarrovi* and *S. poinsetti* (Fig. 2), males ($2n = 31$) and females ($2n = 32$) have six pairs of macrochromosomes (metacentric and submetacentric). In addition, males have 18 microchromosomes (submetacentric, subtelocentric, and telocentric) plus one metacentric chromosome (unpaired) intermediate in size between the macro- and microchromosomes. The females of both species, however, have 20 microchromosomes (submetacentric, subtelocentric, and telocentric) and lack the intermediate, unpaired metacentric found in males. Hence, males have one chromosome (the intermediate metacentric) that is not present in females, and females have two chromosomes (microchromosomes) that are not present in males; these are regarded here as sex chromosomes (Fig. 2).

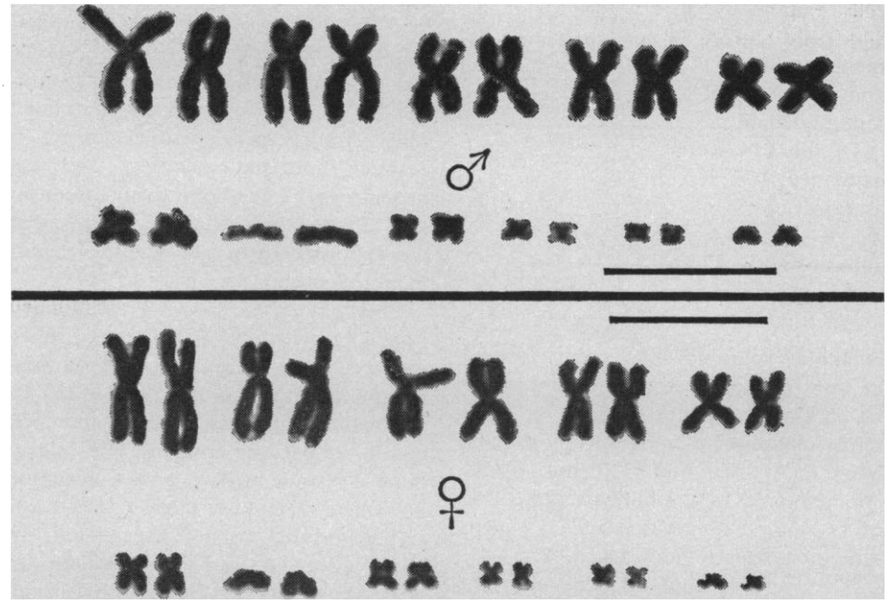

Fig. 1. Photomicrographs of karyotypes of *S. occidentalis* ($2n = 22$; UAZ numbers 15979 and 15981) having no apparent sex chromosomes. Lines represent 10 μ.

Spermatogonia of both species ($N =$ 66 cells examined) have the same karyotypes as bone marrow cells ($N =$ 231 cells examined). In meiosis I, the unpaired metacentric chromosome forms a trivalent with two of the microchromosomes, whereas the remaining

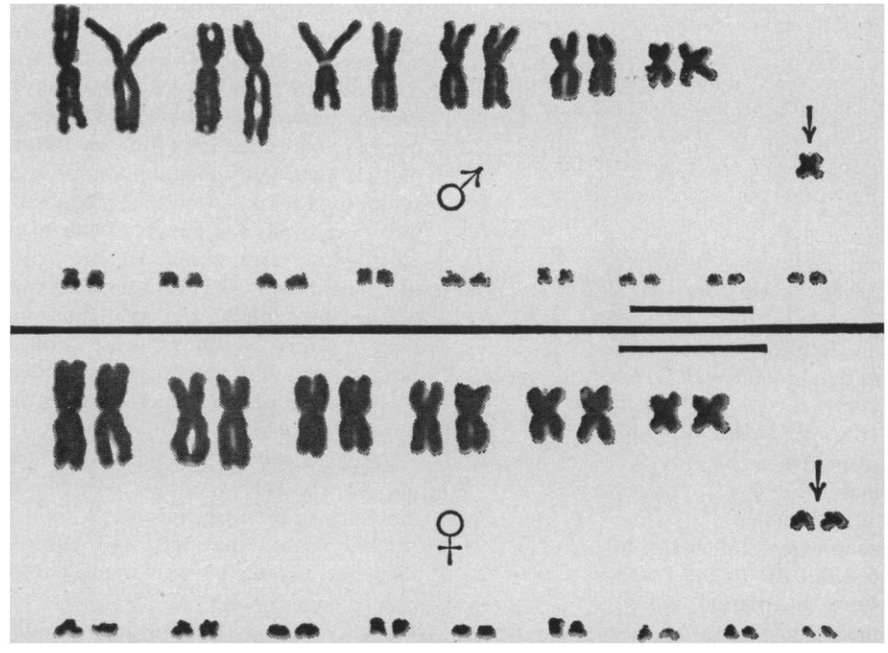

Fig. 2. Photomicrographs of karyotypes of *S. poinsetti* (UAZ numbers 15972 and 15976) having apparent sex chromosomes. Male, $2n = 31$; female, $2n = 32$. Arrangement of the chromosomes is designed to most clearly demonstrate sexual dimorphism in the karyotypes (arrows). The microchromosomes in males are considered to comprise eight pairs of homologues plus the two nonhomologues that synapse with the intermediate metacentric in meiosis. The microchromosomes in females are considered to comprise ten pairs of homologues (see text). Lines represent 10 μ.

chromosomes form bivalents ($N = 60$ cells examined). In meiosis II ($N = 144$ cells studied at prophase II and metaphase II), cells with n equal to 15 and with n equal to 16 appear with essentially equal frequency (Table 1).

Of the 144 secondary spermatocytes examined, 100 were from the best preparations of *S. jarrovi* for analysis of the detailed morphology of the microchromosomes. Of those 100 cells, 48 had n equal to 15, and 45 had n equal to 16. In all except one of the cells having n equal to 15, the chromosomal complement was clearly 6 macrochromosomes, the intermediate metacentric, and 8 microchromosomes (Fig. 3). In all of the cells having n equal to 16, the chromosomal complement was clearly 6 macro- plus 10 microchromosomes (Fig. 3). These data indicate that, in a given primary spermatocyte, preferential segregation from a trivalent occurs such that the two microchromosomes go to one pole while the intermediate metacentric goes to the other. Therefore, males normally produce two types of spermatozoa and are heterogametic; 50 percent contain 6 macrochromosomes, 1 intermediate metacentric, and 8 microchromosomes ($n = 15$); 50 percent contain 6 macrochromosomes, no intermediate metacentric, and 10 microchromosomes ($n = 16$).

We have not studied meiosis in females because we have not yet determined the best time to fix oogonia and oocytes for chromosome analysis. We assume that gametogonia of females have the same karyotype as bone marrow cells, since this is the case in males. Considering that females have a diploid number of 32, composed of 12 macrochromosomes, no intermediate metacentric, and 20 microchromosomes, we assume that meiosis results in 100 percent of the ova having n equal to 16 (6 macrochromosomes, no intermediate metacentric, and 10 microchromosomes). Thus, in fertilization, a $6 + 0 + 10$ spermatozoan ($n = 16$) syngametic with the $6 + 0 + 10$ ovum ($n = 16$) would restore the normal $12 + 0 + 20$ complement ($2n = 32$) of females. A $6 + 1 + 8$ spermatozoan ($n = 15$) syngametic with the $6 + 0 + 10$ ovum ($n = 16$) would restore the normal $12 + 1 + 18$ complement ($2n = 31$) of males, and the intermediate metacentric chromosome unique to males would be retained only in males.

As neither sexual dimorphism nor heteromorphic "pairs" of chromosomes occur in the karyotypes of most lizards studied to date, it is likely that the sexual dimorphism in the karyotypes of these species evolved from saurian ancestors having neither sexually dimorphic karyotypes nor heteromorphic "pairs" of chromosomes. It is likely that such evolution occurred by means of centric fusion of two nonhomologous microchromosomes in an ancestral karyotype similar to, if not identical with, that of the females of *S. jarrovi* and *S. poinsetti* today.

Table 1. Frequency of observation of the haploid (n) numbers of chromosomes of secondary spermatocytes (prophase II, metaphase II) from six individuals of *S. jarrovi* and *S. poinsetti* ($N = 144$ cells studied).

n	Cells with n (No.)	Cells with n (%)
13	3	2.1
14	6	4.2
15	64	44.4
16	68	47.2
17	3	2.1

Genetic factors determining sex in lizards are unknown, and, therefore, it is obviously difficult to relate the sex chromosome mechanism of *S. jarrovi* and *S. poinsetti* to a named mechanism (for example, XY) known to occur in other organisms. Considering that the mechanism in these lizards apparently evolved as a result of centric fusion between two nonhomologous but morphologically similar chromosomes in a diploid complement similar to that of females today, we regard the female constitution as $X_1X_1X_2X_2$, the designation X being based on similar morphology of the chromosomes, and the subscripts indicating homologues. Hence, the males could be considered as X_1X_2Y, the Y being the unpaired metacentric (Figs. 2 and 3) resulting from centric fusion of an X_1 and X_2. Thus, this mechanism might be referred to as an X_1X_2Y (♂) : X_1X_1-X_2X_2 (♀) mechanism on the basis of chromosome morphology. This same notation has been used to denote a sex chromosome mechanism in invertebrates (see *4* for a review).

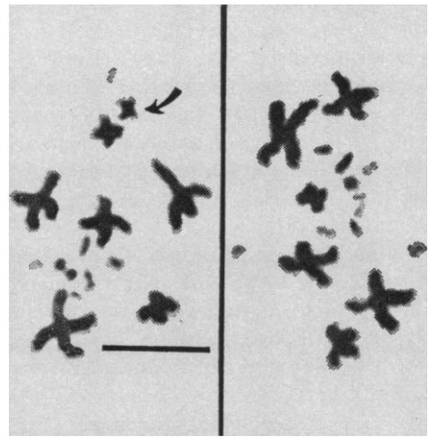

Fig. 3. Photomicrographs of chromosomes from secondary spermatocytes (metaphase II) of *S. jarrovi* (UAZ number 15966). Left ($n = 15$), composed of 6 macrochromosomes, 1 intermediate metacentric (arrow), and 8 microchromosomes. Right ($n = 16$), composed of 6 macrochromosomes, no intermediate metacentric, and 10 microchromosomes. Line represents 10 μ.

Since birds and mammals are relatively conservative in sex chromosome mechanisms, it is of particular interest that at least two different mechanisms occur within one close phyletic lineage in reptiles (genus *Sceloporus*).

Note added in proof. We have just read that sex chromosomes have also been recognized in lizards of the genus *Auolis* (*7*).

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References and Notes

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6. Chromosomes of cells from bone marrow, spermatogonia, and spermatocytes were examined on slides prepared by means of Patton's (J. L. Patton, *J. Mamm.*, in press) modification of the colchicine–hypotonic citrate method of Ford and Hamerton [C. E. Ford and J. L. Hamerton, *Stain Tech.* **31**, 247 (1956); C. H. Lowe, J. W. Wright, C. J. Cole, *Mamm. Chrom. Newsletter No. 22*, (1966), p. 201]. Specimens examined are catalogued in the herpetological collection, Department of Zoology, University of Arizona, as follows: *S. occidentalis*, Nos. 15977–981 (three males, two females); *S. jarrovi*, Nos. 15964–971 and 15983–985 (six males, five females); *S. poinsetti*, Nos. 15972–976 and 15982 (two males, four females). Sex verified by dissection.
7. G. C. Gorman and L Atkins, *Amer. Nat.* **100**, 579 (1966).
8. We thank K. K. Asplund, R. L. Bezy, E. J. Braun, S. R. Goldberg, E. A. Halpern, J. T. Harralson, D. S. Hinds, R. D. Krizman, J. R. Lannom, J. L. Patton, and O. H. Soule for assistance in the field work; we thank Dr. W. B. Heed and J. L. Patton for reading the manuscript. This work was carried on incidental to investigation of the cytogenetics of lizards (genus *Cnemidophorus*); supported in part by NSF grant GB 5647.

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