Abstract. Somatic and meiotic chromosomal and synaptone- 
mental complex techniques were used to characterize the chromo- 
somal complement and to study the fission heteromorphism of 
chromosome 4 in the FM2 cytotype of Sceloporus grammicus. 
Analysis of silver-stained somatic metaphases revealed that the 
nucleolar organizer region in this cytotype is located at the distal 
end of a pair of medium-sized acrocentric chromosomes, rather 
than on the largest acrocentric chromosomal pair, as previously 
reported. This condition is hypothesized to be the result of at 
least two sequential rearrangements. Analysis of surface-spread 
zygotene and pachytene nuclei indicated that the components of 
the chromosome 4 trivalent initiated synopsis at their distal tel-
omeric regions. Although synopsis of the fission trivalent was 
synchronous with that of the homomorphic autosomal pairs, 
completion of synopsis was delayed in the trivalent. Associa-
tions between the fission trivalent and other autosomal or sex-
chromosomal elements occurred in approximately one third of 
the pachytene nuclei examined. Analysis of secondary sper-
matocytes (metaphase II configurations) revealed low levels of 
nondisjunction in fission heterozygotes. These analyses indicate 
that FM2 individuals heterozygous for the fission rearrange-
ment of chromosome 4 suffer no meiotic deficit.

Traditionally, two fitness-reducing mechanisms have been 
invoked in models of chromosomally mediated speciation (re-
viewed by Sites and Moritz, 1987). These mechanisms include 
disruption of linkage groups by recombination (Shaw et al., 
1990) and production of chromosomally unbalanced gametes 
resulting from heterozygosity for single or multiple rearrange-
ments. Several studies have provided evidence of reduced fit-
ness due to chromosomal heterozygosity (Cattanach and Mosel-
ey, 1973; Gabriel-Robez et al., 1986, 1988; Gustavsson, 1988; 
Searle, 1988). However, chromosomal heterozygosity is of little 
reproductive consequence in organisms where synaptic and 
recombinational phenomena circumvent potential meiotic 
problems (Fletcher and Hewitt, 1978; Moses et al., 1979; Elder 
and Pathak, 1980; Hale, 1986; Wallace and Searle, 1990). Elim-
ation of aneuploid gametotes through meiotic drive also may 
result in no apparent loss of fitness in chromosomal heterozy-
gotes (Stewart-Scott and Bruere, 1987, and references therein).

Heterozygosity for Robertsonian (fission/fusion) rearrange-
ments may disrupt meiosis through incomplete or nonhomolo-
gous pairing during prophase I or through unbalanced chromo-
somal disjunction during anaphase I, resulting in aneuploid (Searle, 1988). Further, the degree of gametic impairment in 
chromosomal heterozygotes may be associated with genetic 
composition, including male-limited hybrid sterility (Coyne 
and Orr, 1989) and/or interactions between specific combina-
tions of chromosomal and genic factors (Gropp and Winking, 
1981; John et al., 1983; Coates and Shaw, 1984; Mahadevaiah et 
al., 1990). Under any of these conditions, Robertsonian hetero-
zygotes should exhibit decreased reproductive fitness.

In the context of chromosomal evolution and speciation, the 
Sceloporus grammicus complex is of particular interest because 
it exhibits both extensive intrapopulational heteromorphism 
and interpopulational fixation for similar types of rearrange-
ments. The FM2 cytotype (2n = 43-45 [males], 44-46 [females]; 
Fig. 1) is considered to be the most chromosomally derived 
cytotype of the S. grammicus complex (Hall, 1973, 1980) and 
differs from the ancestral karyotype ("S" cytotype, 2n = 31 
[males], 32 [females]) in being fixed for centric fissions of chro-
mosomes 1, 2, 3, 5, and 6, and heteromorphic for a fission of 
chromosome 4. Further, FM2 possess an additional pair of 
microchromosomes, hypothesized to be the result of a micro-
chromosomal fission (Hall, 1973).

The FM2 cytotype provides a system for comparing the 
meiotic behavior of a highly derived acrocentric macrochro-
mosomal complement to the primitive and primarily biarmed 
complement of the F5 cytotype (Reed et al., 1992a). The present 
study was designed to assess the meiotic consequences of hetero-
zygosity for a fission rearrangement and determine the potential 
for this rearrangement to contribute to speciation in the S. 
grammicus complex.
Chromosomal fissions in Sceloporus grammicus

FM2 (2n = 43-45/44-46)

Fig. 1. Idiogram of the macrochromosomal complement of the FM2 cytotype. Chromosomes 1, 2, 3, 5, and 6 are fixed for centric fission, and chromosome 4 is heteromorphic for fission. Secondary constrictions (NORs) are terminally positioned on chromosome 2. The diploid number (2n = 43-45 [males], 44-46 [females]) differs between the sexes because of an X\(X_1\)Y/X\(X_1\)X\(X_2\) male/female sex-chromosomal system.

Materials and methods

Specimens of S. grammicus (FM2 cytotype) were collected from a single population (Mexico: Hidalgo; 1.0 mi E Amaque [JWS 2042–2049]; locality 3 in Fig. 1 of Reed et al., 1992b). Mitotic and meiotic chromosomal preparations and surface-spread synaptonemal complexes from five individuals were prepared using the techniques outlined by Reed et al. (1992a). Diakinetic nuclei were examined for the frequency of bivalent and trivalent formation. To estimate the relative frequency of nondisjunction, metaphase II configurations were scored for the numbers of metacentric and acrocentric macrochromosomes and for the presence of either the Y chromosome or the two X chromosomes.

During the course of this study, data regarding chromosome 2 necessitate examination of additional material for comparative purposes. Therefore, somatic preparations from individuals collected from populations of the F5, FM1 (2n = 39-41 [males], 40-42 [females], Mexico: Hidalgo; Huichapan [JWS 2582], and Amealco [JWS 2583-2586]), and FM3 (2n = 37 [males], 38 [females], Mexico: Hidalgo; Huasca [JWS 2463-2465]) cytotypes were also examined.

Voucher specimens are deposited in one of the following collections: the M.L. Bean Life Science Museum, Brigham Young University; the Museo de Zoología-Facultad de Ciencias, Universidad Nacional Autonoma de Mexico; and the Instituto de Biología-Herpetología, Universidad Nacional Autonoma de Mexico.

Results

Diploid numbers were consistent with those previously described for the FM2 cytotype (Hall, 1973). Of the five FM2 males examined, two were homozygous for the alternative morphologies of chromosome 4 (2n = 43 and 2n = 45). The remaining three lizards were fission heterozygotes (2n = 44). Silver-stained chromosomal preparations revealed the presence of nucleolar organizer regions (NORs) on one pair of medium-sized acrocentric chromosomes (Fig. 2A) and not on the largest pair, as might be predicted on the basis of a centric fission of chromosome 2 (see chromosome 2 in Fig. 1).

Examination of mitotic chromosomal preparations from the F3 and FM3 individuals confirmed the expected positions of the NORs on the submetacentric macrochromosome 2 in F5 (Fig. 2B) and on the largest acrocentric pair in FM3 (Fig. 2C). However, analysis of FM1 individuals revealed two NOR-chromosomal morphologies (Fig. 2D). Two of the five FM1 individuals were heterozygous and possessed NORs on the distal end of a large acrocentric chromosome and on the short arms of a large subacrocentric chromosome. The remaining three FM1 lizards were homozygous for this subacrocentric NOR-chromosomal morphology.

Synaptonemal complex (SC) analyses

Surface-spread spermatocytes were prepared from four males of the FM2 cytotype (two fission heterozygotes and two individuals homozygous for the alternative morphologies of chromosome 4). A total of 160 zygote nuclei were analyzed from electron photomicrographs. Axial element and SC formation in the FM2 cytotype was congruent with that previously described for the F5 cytotype (Reed et al., 1992a). Pachytene nuclei from the fission homozygote contained 21 autosomal bivalents and one trivalent corresponding to the sex chromosomes (Fig. 3). Synaptonemal complex analyses provided unequivocal determination of the morphologies of all chromosomes. Although the SCs of all macrochromosomes appeared to be acrocentric, small “short arms” were present on one of the largest and one medium-sized SC element. Consistent with the mitotic data (Fig. 2), a single nucleolus was present at the distal telomere of one acrocentric element. Examination of the SC karyotype showed the number and morphology of the microchromosomes of the FM2 cytotype to be equal to those of the F5 cytotype (see Fig. 4 of Reed et al., 1992a).

Electron-microscopic data from the fission heterozygotes were consistent with the somatic karyotypic data and confirmed the formation of the expected trivalent corresponding to chromosome 4. All acrocentric macrochromosomal elements initiated synapsis at the distal telomeres, with synopsis progressing unidirectionally toward the centromere. Synaptic initiation of the fission trivalent and the remaining homomorphic autosomes was synchronous. Although the fission trivalent represents the largest element in the nucleus, it was usually not distinguishable from other partially paired autosomes until mid-zygotene (Fig. 4A). Pairing of the chromosomal axes proceeded unidirectionally from both sets of telomeres of the metacentric element toward the centromere. This is similar to the pattern of unidirectional synopsis (i.e., proceeding from two terminal initiation sites) observed for the single biarmed element in the chromosome 4 homozygote (Fig. 5A) and the biarmed chromosomal pairs in the F5 cytotype (Reed et al., 1992a). In mid-zygotene nuclei in which the trivalent elements could be followed over their entire lengths, the two acrocentric elements were synapsed over approximately one third to one half of their length. By late zygotene, pairing of the acrocentric elements was one half to two thirds complete (Fig. 4B). Complete pairing of the homomorphic autosomal elements equated with the beginning of pachytene (Fig. 4C). Pachytene nuclei showed progressive pairing of the trivalent, and most chromosome 4 trivalents were completely paired by late pachytene (Fig. 4D).

The extent of SC formation between the acrocentric elements of the chromosome 4 trivalents in S. grammicus was com-
Fig. 2. Silver-stained somatic metaphase nuclei showing the variation in nucleolus organizer region (NOR) position observed within the *S. graminicus* complex. Open arrows denote NORs. (A) FM2 individual (JWS 2047) with NORs on two small acrocentric elements. (B) F5 individual (JWS 2023) representing the metacentric form of chromosome 2. (C) FM3 individual (JWS 2465) homozygous for a centric fission of chromosome 2. (D) FM1 individual (JWS 2586) heterozygous for an inversion of the NOR-bearing chromosome. Bar = 10 μm.

Fig. 3. Synaptonemal complex karyotype prepared from a silver-stained pachytene nucleus of a fission homozygote (JWS 2043). Elements are arranged by size and placed with centromeric regions on the horizontal lines and with presumed fission products in direct opposition. Open arrow denotes nucleolus. Reproduced at 1,275x.
Chromosomal fission in *Sceloporus grammicus* 49

Fig. 4. Electron micrographs of silver-stained primary spermatocytes from two fission heterozygotes (JWS 2042 and 2046). (A) Mid-zygotene nucleus showing several fully paired chromosomal elements. The telomeric regions of several elements are clustered in a bouquet-like configuration. (B–D) Pachytene nuclei showing progressive synapsis of the fission trivalent. (B) Early pachytene nucleus displaying association between the acrocentric elements of the chromosome 4 trivalent (4) and the elements of a forming autosomal bivalent (A). (C) Pachytene nucleus in which the metacentric chromosome 4 element (solid arrowhead) is hooked around two acrocentric elements. Open arrow indicates sex-chromosomal trivalent. (D) Fully synapsed fission trivalent showing association between the acrocentric elements (solid arrowhead). Reproduced at 1,667x.

parable to that reported for other Robertsonian heterozygotes (Moses et al., 1979; Switonski et al., 1987; Ratomponirina et al., 1988; Mittwoch et al., 1990; Wallace and Searle, 1990). In 71.4% of the nuclei with fully paired chromosome 4 trivalents, a segment of a SC was formed between the two acrocentric elements perpendicular to the main SC axis. In the remaining nuclei, the trivalent was either fully paired along its length (19.1%) or displayed a telomeric association between the acrocentric elements and a small asynapsed pericentric region (9.5%). The extent of synapsis of the two acrocentric elements with the metacentric element varied among the nuclei. This difference was the result of synaptic hindrance caused by nonhomologous associations between the chromosome 4 trivalent and other elements. Such nonhomologous associations were observed in 31.6% of the pachytene nuclei examined.

Interactions involving one of the larger autosomes (Fig. 5B) were frequent and accounted for two thirds of the associations between the chromosome 4 trivalent and other SCs. The remaining associations involved the chromosome 4 trivalent and one or more elements of the sex-chromosomal trivalent. Multiple associations involving the chromosome 4 trivalent, another autosome, and the sex-chromosomal trivalent (Fig. 5C) were observed in 3.9% of the pachytene nuclei. The frequency of these various types of associations was virtually identical for the two heterozygotes examined. Associations involving the chromosome 4 trivalent were resolved prior to late pachynema and did not persist in the fully synapsed configurations.

Pairing of the sex chromosomes in the FM2 cytotype was identical to that described for the F5 cytotype (Reed et al., 1992a). Associations between the sex-chromosomal and autosomal elements (during zygonema and pachynema) were observed in 10.7% and 14.4% of the nuclei from chromosome 4 homozygotes and heterozygotes, respectively. The increased frequency in the chromosome 4 heterozygotes was directly attributable to associations between chromosome 4 and the sex-chromosomal trivalent. Because of the telomeric association of the X chromosome with the acrocentric elements of the chromosome 4 trivalent, the sex-chromosomal trivalent, in chromosome heterozygotes, often remained incompletely paired well into pachynema.

**Meiotic chromosomal analyses**

Diakinetic nuclei were examined from three heterozygotes and both homozygotes. Homozygotes contained either 20 bivalents (homozygous for the metacentric form of chromosome 4) or 21 bivalents (homozygous for fission) and one trivalent corresponding to the sex chromosomes. Heterozygotes exhibited 19 bivalents and two trivalents. No attempt was made to quantify the position of chiasmata in the chromosome 4 trivalents. In most cases, the trivalent elements formed a linear configuration,
suggesting terminally positioned chiasmata (Fig. 6A). In only 1 of the 410 nuclei examined from the five individuals did the number of observed elements differ from that expected. This nucleus, from the fission homozygote, possessed two microchromosomal univalents.

Analysis of 292 metaphase II configurations revealed completely normal disjunction in three individuals (JWS 2043, 2045, and 2046; Fig. 6). One heterozygote (JWS 2042) and the individual homozygous for the metacentric form of chromosome 4 (JWS 2047) displayed aneuploidy percentages of 2.0% and 2.9%, respectively. Two nuclei, one from the homozygote and one from a fission heterozygote, showed the loss of an acrocentric element, and a second nucleus in the fission heterozygote possessed two biarmed elements (Fig. 6D). With the exception of the above-mentioned nuclei, balanced secondary spermatocytes (with either alternative haploid configuration) were observed in the heterozygotes (Fig. 6B, C).

Chi-square analyses showed that the frequency of secondary spermatocytes containing either the two acrocentric chromosomes (fission products) or the metacentric chromosome 4 element did not significantly differ from the expected 1:1 ratio (Table I). Because of the potential bias in the scoring of the sex chromosomes (see discussion in Reed et al., 1992a), direct comparisons of sex-chromosome segregation were not made. However, contingency \( \chi^2 \) tests for independence, which are unprejudiced by the potential scoring bias, were performed on euploid MII counts from two chromosome 4 heterozygotes. In both individ-
Table I. Statistical comparison of metaphase II counts from FM2 fission heterozygotes

<table>
<thead>
<tr>
<th>Animal No.</th>
<th>Number of nuclei examined</th>
<th>Number of metacentric macrochromosomes in haploid nuclei</th>
<th>Chi square</th>
<th>Degrees of freedom</th>
<th>P value</th>
</tr>
</thead>
<tbody>
<tr>
<td>JWS 2042</td>
<td>96</td>
<td>46</td>
<td>0.17</td>
<td>1</td>
<td>0.6831</td>
</tr>
<tr>
<td>JWS 2045a</td>
<td>26</td>
<td>11</td>
<td>0.61</td>
<td>1</td>
<td>0.4328</td>
</tr>
<tr>
<td>JWS 2046</td>
<td>100</td>
<td>41</td>
<td>3.24</td>
<td>1</td>
<td>0.0719</td>
</tr>
</tbody>
</table>

* Synaptonemal complex data were not collected from this individual.

Table II. Contingency chi-square tests for segregational independence of fission and sex-chromosomal elements

<table>
<thead>
<tr>
<th>Animal No.</th>
<th>Number of nuclei examined</th>
<th>Sex chromosomes</th>
<th>Number of spermatocytes with 0 or 1 metacentric chromosome</th>
<th>Chi square</th>
<th>Degrees of freedom</th>
<th>P value</th>
</tr>
</thead>
<tbody>
<tr>
<td>JWS 2042</td>
<td>92</td>
<td>Y</td>
<td>21 (26.00)</td>
<td>4.42</td>
<td>1</td>
<td>0.0355</td>
</tr>
<tr>
<td></td>
<td></td>
<td>X1, X2</td>
<td>25 (20.00)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>JWS 2046</td>
<td>79</td>
<td>Y</td>
<td>15 (17.07)</td>
<td>2.14</td>
<td>1</td>
<td>0.1433</td>
</tr>
<tr>
<td></td>
<td></td>
<td>X1, X2</td>
<td>15 (11.92)</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

* Expected number of spermatocytes is shown in parentheses.

Discussion

Two findings based on the somatic and SC karyotypes are inconsistent with the original description of the FM2 cytotype (Hall, 1973). First, the presence of an NOR on a medium-sized acrocentric chromosome is inconsistent with the single fission hypothesized for chromosome 2. Second, the FM2 individuals possessed microchromosomal elements that were similar in size and centromere position to those observed in the F5 cytotype (cf. Fig. 3 of this study with Fig. 4 of Reed et al., 1992a). Based on observations of nondifferentially Giemsa-stained preparations, Hall (1973) reported an extra microchromosomal pair in the FM2 cytotype and hypothesized that it originated through fission of a metacentric microchromosome. Although direct homology cannot be unequivocally determined by comparison of SC elements, both the F5 and FM2 cytotypes exhibit similar microchromosomal complements, including two pairs of metacentric chromosomes. Therefore, it is unlikely that the extra chromosomal pair in the FM2 cytotype is microchromosomal in origin. The presence of the NOR on a medium-sized element may be the result of transposition. However, the corresponding size and number of elements between the F5 and FM2 cytotypes suggest that chromosome 2 has undergone multiple fissions.

Several scenarios involving fissions could account for the various chromosome-2 morphologies of the S. grammicus complex (Fig. 7). While four S. grammicus cytotypes (S, F5, F6, and F5 + F6) retain the ancestral biarmed condition of chromosome 2, the three FM cytotypes possess derived conditions of chromosome 2. The morphology of chromosome 2 in the FM3 cytotype is likely the result of fixation of a centric fission. Chromosome 2 in FM1 is represented by a medium-sized acrocentric chromosome plus either a large acrocentric or subacrocentric NOR-bearing chromosome. The subacrocentric morphology is presumably derived through a pericentric inversion of the acrocentric NOR-bearing chromosome.

Given the above scenario, the derivation of the FM2 morphology of chromosome 2 requires at least one additional rear-
rangement beyond the FM3 condition. Fission of the large acrocentric chromosome of the FM3 complement would directly produce the FM2 morphology of chromosome 2. However, this would require de novo synthesis of a new centromere and telomere. The presence of the inversion heteromorphism in the FM1 cytotype suggests that the evolution of the FM2 morphology may have involved the initial fixation of a pericentric inversion. If a pericentric inversion produced a metacentric NOR-bearing chromosome, the FM2 morphology could then be achieved by a subsequent centric fission. Thus, derivation of the FM2 morphology of chromosome 2 from the ancestral biarmed condition may be the result of three rearrangements (fission → inversion → fission), each followed by subsequent fixation.

The centric fission of chromosome 4 appears to exist within FM2 populations as a balanced heteromorphism. Although determined from a small sample size (eight animals), the frequency of the two chromosomal types (0.5) was identical in the individual animals (five males and three females) collected in Amaque. This observation is consistent with data from other FM2 populations, as well as for other fission heteromorphisms in S. grammicus in which genotypic ratios are present in the frequencies expected in randomly mating populations (Arevalo et al., 1991). Porter and Sites (1985) reported an excess of fission heterozygotes in a highly heteromorphic S. grammicus population and suggested the possibility that hygroscopy for fission rearrangements in S. grammicus has a selective advantage.

The synaptic behavior of the acrocentric (fissioned) chromosomes of the FM2 cytotype was similar to that reported for the acrocentric chromosomes in the F5 cytotype (Reed et al., 1992a). Each element retained the distal synaptic initiation site, with unidirectional synopsis proceeding toward the centromeric region. The presence of additional late-pairing telomeric regions in the nucleus increases the potential for associations to persist into later phases of synopsis. Redi et al. (1990) suggested that telomeric associations increase the potential for centric fusions. However, reduction in chromosomal size through centric fission should diminish the number of synaptic interlockings. The minimum-interaction hypothesis of karyotype evolution (Imai et al., 1986) implicates the misresolution of interlockings as a mechanism in the induction of inversions and reciprocal translocations. The increase in diploid number in the S. grammicus complex and the reduced occurrence of inversions in the highly fissioned FM cytotypes (Arevalo et al., 1991; Reed et al., 1992b) is consistent with this hypothesis.

Retention of the metacentric synaptic pattern (i.e., two distal initiation sites) is instrumental in the proper formation of the fission trivalent. All nuclei in which the chromosome 4 elements could be distinguished displayed some degree of SC formation among the three elements of the trivalent. The telomeric regions of the two acrocentric and the metacentric chromosome 4 elements in S. grammicus apparently remain unaffected by the fission event. Delay in the completion of synopsis of the chromosome 4 trivalent in the FM2 cytotype is similar to that reported for centric fusion heteromorphisms in lemurs (Moses et al., 1979; Ratomponirina et al., 1988), the laboratory mouse (Grao et al., 1989; Mahadevaiah et al., 1990), and the domestic cow (Swiolskį et al., 1987). Moses et al. (1979) suggested that delay in the synopsis of trivalents results from a lack of homology between the centromeric regions of the acrocentric and the metacentric elements, coupled with topological constraints related to the persistent attachment of the acrocentric elements to the nuclear envelope.

Meiotic associations between the sex chromosomes and unpaired autosomal elements occur with varying frequencies and consequences in Robertsonian heterozygotes (Swiolskį et al., 1987; Ratomponirina et al., 1988). Reduced fertility in laboratory mice (Mahadevaiah et al., 1990) and humans (Rosenmann et al., 1985) heterozygous for single rearrangements has been attributed in part to XY/autosome associations. Grao et al. (1989) suggested that increased associations of unpaired autosomal elements with the sex chromosomes may be the result of a non-specific mechanism confined to a limited period of prophase I. Although the heterozygotes in this study showed an increased frequency of sex-chromosome-autosome associations, these associations did not persist at later meiotic stages and, therefore, appear to be of little consequence to individual fecundity.

Robertsonian rearrangements, whether fusion or fission, result in the same number of elements in heterozygotes (one metacentric and two acrocentric chromosomes). However, the processes that produce these rearrangements may result in fundamental differences in the centromeric regions of the elements involved. Centric fusion typically results in the loss of one centromere and a variable portion of associated chromatid (John and Freeman, 1975; Gropp and Winking, 1981; Haaf et al., 1989; see also Redi et al., 1990, for postulated molecular mechanisms). However, fission requires the production of an additional centromere and telomeres.

Centric fissions are considered to be the predominant type of rearrangement in the S. grammicus complex (Hall, 1973, 1980). The observation of two metacentric elements in a single secondary spermatocyte from a fission heterozygote could have been the result of either a spontaneous fusion mutation or a premeiotic nondisjunction. Porter and Sites (1987) found abnormal spermatocytes and apparent spontaneous germ-line fission mutations in 5 of the 30 lizards they examined. The extensive chromosomal repatterning displayed in the S. grammicus complex, including both interpopulational heteromorphisms and intrapopulational fixation, suggests that this species may be more susceptible to mutational events.

Previous studies of nonhuman vertebrates have documented extensive variation in meiotic consequences for single Robertsonian heterozygosity. Based on the examination of offspring or embryos, normal fitness for simple heterozygotes has been estimated in laboratory mice (Britton-Davidian et al., 1990), bulls (Logue and Harvey, 1978), dogs (Larsen et al., 1979), and the arctic fox (Moller et al., 1985). Instances of reduced fitness in single Robertsonian heterozygotes were found in mice (Evans et al., 1967) and boars (Gustavsson, 1988). Likewise, substantial spermatogenic breakdown was observed in mice (Mahadevaiah et al., 1990) and sheep (Long, 1978). The estimated frequency of nondisjunction and aneuploidy in various heterozygotes ranges from 0% to 34% (Ford and Evans, 1972; Cattanach and Mosely, 1973; Gropp and Winking, 1981; Searle, 1986; Porter and Sites, 1987; Stewart-Scott and Bruère, 1987), and in bulls (Logue and Harvey, 1978) and sheep (Long, 1978) heterozygotes
displayed only moderately higher frequencies of nondisjunction than did homozygotes (3.6% and 4.1%, respectively). From these observations it is obvious that no universal statement can be made regarding the fitness effects of single Robertsonian rearrangements.

Although a direct measure of fitness was not within the scope of this study, the low incidence of nondisjunction (as evident from the frequency of aneuploid metaphase II complements) is consistent with previous findings in *S. grammicus* (Porter and Sites, 1987). In 16 of 30 heterozygous and homozygous males, Porter and Sites (1987) found that all of the spermatocytes were completely balanced. In the remaining males, the frequency of aneuploidy ranged from 0.6% to 7.1%, with heterozygotes displaying an average increase in MII aneuploidy of 1.1% over the homozygotes. If the frequency of nondisjunction is assumed to be approximately equal to the frequency of aneuploidy (i.e., each nondisjunction event producing one hypohaploid and one hyperhaploid nucleus [but see Cattanach and Moseley, 1973; Ford and Evans, 1973; Logue and Harvey, 1978; and Guichaoua et al., 1986]), nondisjunction in the individuals examined in the present study ranged from 0% to 2.0% in chromosome 4 fission heterozygotes. However, the highest frequency (2.9%) was observed in the fission homozygote. If this same trend is present in *S. grammicus* females, the fitness of single-fission heterozygotes appears to be no different from that of homozygotes (although see Gropp and Winking, 1981).

White (1973) hypothesized that the presence of at least one chiasma per chromosomal arm facilitates proper orientation and disjunction of trivalents in single Robertsonian heterozygotes. The ubiquitous presence of a trivalent configuration at diakinesis and the balanced segregation observed in metaphase II configurations from the chromosomal heterozygotes examined in this study support this hypothesis. The greater concomitant occurrence of the meioticacentric chromosome 4 element with the Y chromosome and the chromosome 4 acrocentric elements with the two X chromosomes may be a consequence of the frequent association among these elements during prophase I. Association of the acrocentric elements may cause the two trivalents to be oriented such that the metacentric and acrocentric elements of both trivalents are preferentially drawn to opposite poles during anaphase I.

Hall (1973, 1980) hypothesized that fission rearrangements played a primary role in the formation of the *S. grammicus* species complex. To date, seven hybrid zones between various cytotypes of the *S. grammicus* complex have been documented (Hall, 1973; Arevalo et al., 1991). In each case, the hybridizing taxa differed by at least one fission rearrangement (Sites and Davis, 1989). An understanding of the behavior of single rearrangements on a common genetic background is critical in examinations of multiple fission rearrangements with the potential confounding effects of mixed genetic backgrounds found in hybrid zones. The results of the present study and previous meiotic analyses (Porter and Sites, 1985, 1987; Reed et al., 1992b) have determined that rearrangements of the type found in *S. grammicus* (primarily centric fissions) are meiotically neutral. These findings cast serious doubt on the potential for these rearrangements to promote speciation. Nevertheless, it is possible that, within a hybrid zone, the cumulative effect of several slightly deleterious rearrangements may act to reduce heterozygote fitness (Walsh, 1982; Barton, 1983).

Acknowledgements

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References


Britton-Davidian J, Sonjaya H, Catlan J, Cattaneo-Bertelli G: Robertsonian heterozygosity in wild mice: fertility and transmission rates in *Rb(16.17) transrebi* females, the fitness of single-fission heterozygotes appears to be no different from that of homozygotes (although see Gropp and Winking, 1981).

White (1973) hypothesized that the presence of at least one chiasma per chromosomal arm facilitates proper orientation and disjunction of trivalents in single Robertsonian heterozygotes. The ubiquitous presence of a trivalent configuration at diakinesis and the balanced segregation observed in metaphase II configurations from the chromosomal heterozygotes examined in this study support this hypothesis. The greater concomitant occurrence of the meioticacentric chromosome 4 element with the Y chromosome and the chromosome 4 acrocentric elements with the two X chromosomes may be a consequence of the frequent association among these elements during prophase I. Association of the acrocentric elements may cause the two trivalents to be oriented such that the metacentric and acrocentric elements of both trivalents are preferentially drawn to opposite poles during anaphase I.

Hall (1973, 1980) hypothesized that fission rearrangements played a primary role in the formation of the *S. grammicus* species complex. To date, seven hybrid zones between various cytotypes of the *S. grammicus* complex have been documented (Hall, 1973; Arevalo et al., 1991). In each case, the hybridizing taxa differed by at least one fission rearrangement (Sites and Davis, 1989). An understanding of the behavior of single rearrangements on a common genetic background is critical in examinations of multiple fission rearrangements with the potential confounding effects of mixed genetic backgrounds found in hybrid zones. The results of the present study and previous meiotic analyses (Porter and Sites, 1985, 1987; Reed et al., 1992b) have determined that rearrangements of the type found in *S. grammicus* (primarily centric fissions) are meiotically neutral. These findings cast serious doubt on the potential for these rearrangements to promote speciation. Nevertheless, it is possible that, within a hybrid zone, the cumulative effect of several slightly deleterious rearrangements may act to reduce heterozygote fitness (Walsh, 1982; Barton, 1983).

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