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Structural homologies between germ line limited and soma chromosomes in *Acricotopus lucidus* (Diptera, Chironomidae)

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Abstract

Parts of the germ line limited chromosomes (Ks) of *Acricotopus lucidus* (Diptera, Chironomidae) were translocated into soma chromosomes (Ss) by X-irradiation of sperms. The structure of these chromosome parts was analyzed in the polytene salivary gland chromosomes. Besides heterochromatic segments, the polytenized K parts consisted of sections with S-homologous banding patterns. As a result of the irradiation experiments of the last years, it was established that the nine K types of *A. lucidus* contain at least 32% of the bands of the S set and that 41% of the bands in two of the three Ss were registered in the Ks.

Introduction

Additional chromosomes, limited to the germ line and eliminated from the prospective soma cells during early cleavage divisions, were found in the dipteran families of the Cecidomyiidae, the Chironomidae, and the Sciaridae (Bauer and Beermann 1952; Metz 1938; Stuart and Hatchett 1988).

The focus of most of the investigations was the complex chromosome cycles through which the germ line limited chromosomes (called E = eliminated, K = "Keimbahn," or L = limited chromosomes) and the somatic chromosomes (Ss) pass (for review, see Gerbi 1986; White 1973).

The presence of the Ks in the germ cells is a prerequisite to a normal gametogenesis (Bantock 1970; Geyer-Duszynska 1966). Explanations of their origins have claimed the Ks to be derived from the Ss by endopolyploidy (Nicklas 1960; Painter 1966) and/or by rearrangements (Staiber and Thudium 1986).

The structure of the Ks was investigated in the chironomids *Smittia parthenogenetica* and in *Acricotopus lucidus* on X-ray induced K-S-rearrangements in the giant salivary gland chromosomes (Bauer 1970; Staiber and Thudium 1986). In *A. lucidus* the translocated polytenized K sections consisted of heterochromatic segments and/or of euchromatic sections with banding patterns homologous to sections of the salivary gland Ss.

In the last years further X-irradiation experiments were made to collect K-derived S-homologous sections and to determine to what extent sections of the S set are present in the K complement of *A. lucidus.* The present paper is a final report of these experiments.

Materials and Methods

Male imagines of *Acricotopus lucidus* kept from laboratory stocks were X-rayed in different experiments with various doses from 1,500 R to 5,000 R using either a Seifert X-ray machine "Eresco 200" or a Philips X-ray machine "Macrotank G 300" (200 kV, 5 mA, equal to about 94 R/min in 20 cm focus distance). After X-raying, I placed males with nonirradiated females.

Salivary glands explanted from F_1 larvae were fixed in 3:1 ethanol-acetic acid and stained in carmine-acetic acid and then in orcein acetic-lactic acid, as described in Staiber and Behnke (1985).

Results and Discussion

I found chromosome mutations resulting from X-irradiations of male imagines in the salivary gland chromosomes of 403 F_1 larvae from a total of 1982 larvae examined. The category of K-S-rearrangements was represented with 16 mutations (about 4%, Table 1): ten cases of insertions of euchromatic sections with banding patterns - nine with S-homologous (no. 1 and nos. 3-10, Figure 1A,B), and one with unidentified bands (no. 11); five cases of insertions of heterochromatic segments (nos. 12-16, Figure 1A,C); and one case of a S-linked K part composed of heterochromatic segments and S-homologous sections (no. 2).

In *A. lucidus* male meiosis is completed in all germ cells in the prepupal stage, and the X-irradiated imagines contain exclusively differentiated sperms. Beside the Ks, a sperm contains each of the three Ss only once. Duplications of S sections and insertions of heterochromatic segments found in the salivary gland chromosomes of the F, larvae must therefore derive only from the Ks, since the polytene Ss showed no deletions, complete band sequences, or intact heterochromatic centromere blocks.

The numbers of bands of the K-derived euchromatic insertions range from 8-159 (Table 1). In most cells the K insertions are somatically paired with the homologous S section (Figure 1B). The band patterns of the K sections of animals nos. 1-10 were homologized with sections of the polytene salivary gland S set. In Figure 1A the extents of the S-homologous K sections are indicated with bars, and the insertion points of the K-derived heterochromatic segments are

marked with arrowheads. The borders of the S-homologous K insertions of animal nos. 1 and 4 could not be determined exactly as one band. Also, in Figure 1A the extent of the S-homologous

Table 1. Composition of K sections in X-ray induced K-S-rearrangements in the polytene salivary gland chromosomes of *A. lucidus*

Animal no.	Composition and designation of bands[a] of the translocated K sections	No. of bands
1[b]	1C95—1E9, 11	58–59
2[b]	3C85—3D11/HS[c] 3D25—3F55/HS	130
3	3E65—3F31	34
4	4B97—4E19, 21, 23	112–114
5	4H13—4I91	90
6	5D51—5G25	138
7	5D57—5F99	122
8	5F49—5G57	55
9	6E93—6I9	159
10[b]	6F39—6G3	33
11	?	8
12[b]	HS	
13	HS	
14[b]	HS	
15[b]	HS	
16[b]	HS	

[a] Nomenclature of bands according to the chromosome maps in Staiber and Behnke (1985).

[b] From Staiber and Thudium (1986).

[c] HS = heterochromatic segment.

section of a small K, which probably escaped from the soma elimination and occurred spontaneously and polytenized in the salivary gland cells (Staiber 1987), is indicated by a broken bar in the short arm of soma chromosome SI. The eight-band sequence of the K insertion in animal no. 11 is too short to identify. In Table 1 this is indicated with a question mark. No pairing of this short section with any part of the S set was observed. An insertion exhibiting a K-specific banding pattern was not found in the mutated F_1 larvae.

A total of 703 to 706 bands of the 2216 bands drawn in the salivary gland chromosome maps of *A. lucidus* (n = 3, Staiber and Behnke 1985) were found in the K-derived sections of animal nos. 1-10 (Table 2). This means that at least 32% of the bands of the three Ss are parts of the nine different K types that form, in various combinations, the sperm K complements of *A.lucidus* (Staiber 1988). Besides the three Ss, up to 16-18 Ks (Staiber 1988; Staiber and Thudium 1986) may be present in a sperm. Looking at the soma chromosomes SII and SIII only, the percentage of S-bands detected in the K insertions even reach 41%.

As may be seen in Figure 1A, some K-derived S-homologous sections overlap. That is, some K insertions contained the same sequences of S-bands, some sections of the short arm of SII (e.g., nos. 2,3), some sections of the short arm (nos. 6,7,8), and some sections of the long arm of SIII (nos. 9,10). Possibly these sections are present more frequently in the sperm K complements than in others. This may come from the fact that these sections exist repeatedly in the nine K types.

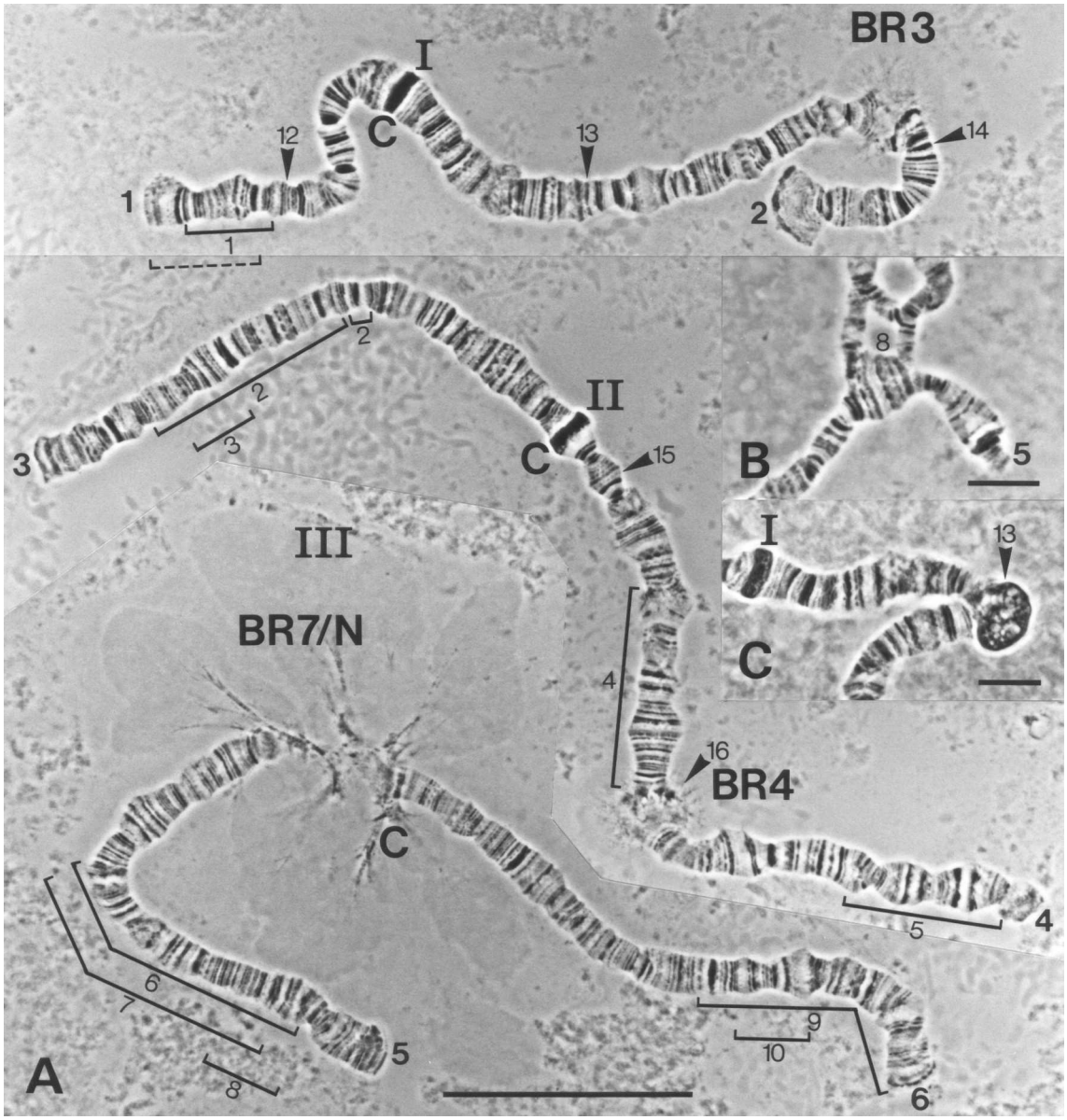

Figure 1. (**A**) Polytene somatic (S) chromosome set from the anterior lobe of a larval salivary gland of *Acricotopus lucidus* indicating the S-homologous sections (bars, animals nos. 1-10) found to exist in the germ line limited chromosomes (Ks) and the insertion points of the K-derived heterochromatic segments (arrowheads, animals nos. 12-16). The broken bar in the short arm of I shows the extend of the S-homologous section of a sponaneously polytenized small K (see text). (**B**) Insertion of a K-derived S-homologous section somatically paired with the homologous region in the short arm of III, animal no. 8. (**C**) Insertion of a K-derived heterochromatic segment, animal no. 13. Chromosome I, II, III; BR = Balbiani ring; C = centromeric region; N = nucleolus; boldface numbers: 1, 3, 5 short and 2, 4, 6 long chromosome arms. Bars represent 50 µm (**A**) and 10µm (**B**, **C**).

Table 2. S-homologous sections demonstrated to exist in the Ks of *A. lucidus*

S-homologous sections	No. of bands	Animal no.
1C95—1E9, 11	58–59	1
3C85—3D11	14	2
3D25—3F55	116	2, 3
4B97—4E19, 21, 23	112–114	4
4H13—4I91	90	5
5D51—5G57	154	6, 7, 8
6E93—6I9	159	9, 10
Total	703–706	

Multivalents formed by nonhomologous K types recently reported for the male meiosis of *A.lucidus* (Staiber 1989), probably initiated by crossing over between homologous sections in otherwise nonhomologous Ks, would support this point of view. Another interpretation might be that some K types are present more frequently, with more homologues per K complement, than others. This fact was established for the germ line limited chromosome K4, which was found to be present mostly with 2-5 exemplars per K complement (Staiber 1988). The results presented here raise remarkably the number of S-homologous bands demonstrated to exist in the nine K types of *A. lucidus* from 10% in an earlier study (Staiber and Thudium 1986) to 32% in the present study. The high percentage of bands of the S set found to exist in the K complement strongly corroborates the idea that the Ks derived from the Ss by way of endopolyploidy (Nicklas 1960; Painter 1966) and/or by way of rearrangements (Staiber and Thudium 1986).

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References

Bantock CR, 1970. Experiments on chromosome elimination in the gall midge, *Mayetiola destructor.* J Embryol Exp Morph 24:257-286.

Bauer H, 1970. Rearrangements between germ-line limited and somatic chromosomes in *Smittia parthenogenelica* (Chironomidae, Diptera). Chromosoma 32:1-10.

Bauer H and Beermann W, 1952. Der Chromosomencyklus der Orthocladiinen (Nematocera, Diptera). Z Naturforsch 7b:557-563.

Gerbi SA, 1986. Unusual chromosome movements in sciarid flies. In: Results and problems in cell differentiation:Vol. 13. Germ line-soma differentiation CHennig W, ed). Berlin, Heidelberg: Springer-Verlag; 71-104.

Geyer-Duszynska I, 1966. Genetic factors in oogenesis and spermatogenesis in Cecidomyiidae. Chromosomes Today 1:174-178.

Metz CW, 1938. Chromosome behavior, inheritance and sex determination in Sciara. Am Nat 72:485-520.

Nicklas RB, 1960. The chromosome cycle of a primitive cecidomyiid - *Mycophila speyeri.* Chromosoma 11:402- 418.

Painter TS, 1966. The role of the E-chromosomes in Cecidomyiidae. Proc Natl Acad Sci USA 56:853-855.

Staiber W, 1987. Unusual germ line limited chromosomes in *Acricotopus lucidus* (Diptera, Chironomidae). Genome 29:702-705.

Staiber W, 1988. G-banding of germ line limited chromosomes in *Acricotopus lucidus* (Diptera, Chironomidae). Chromosoma 97:231-234.

Staiber W, 1989. Multivalent formation and pairing benavior of germ line limited chromosomes in male meiosis of *Acricotopus lucidus* (Diptera, Chironomidae). Genome 32:941-945.

Staiber W and Behnke E, 1985. Developmental puffing activity in the salivary gland and Malpighian tubule chromosomes of *Acricotopus lucidus* (Diptera, Chironomidae). Chromosoma 93:1-16.

Staiber W and Thudium D, 1986. X-ray induced rearrangements between germ-line limited and soma chromosomes of *Acricotopus lucidus* (Diptera, Chironomidae). Genetica 69:149-156.

Stuart JJ and Hatchett JH, 1988. Cytogenetics of the Hessian fly: II. Inheritance and behavior of somatic and germ-line-limited chromosomes. J Hered 79:190- 199.

White MJD, 1973. Animal cytology and evolution, 3rd ed. London: Cambridge University Press.