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Multiple sex-linked reciprocal translocations in a termite from Jamaica[1]

P. Luykx and R.M. Syren

Laboratory for Quantitative Biology, Department of Biology, University of Miami, Coral Gables (Florida 33124, USA),
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Summary. Males of the termite *Incisitermes schwarzi* from Jamaica have a diploid chromosome number of 32. In male meiosis there are 7 bivalents, and a ring of 18 chromosomes equivalent to sex chromosomes, 9 X's and 9 Y's. This is the largest reciprocal translocation complex so far described for any plant or animal species.

The males of several species in the primitive termite family Kalotermitidae are multiple translocation heterozygotes, having rings or chains of chromosomes in meiosis; females are structural homozygotes, showing only bivalents in meiosis[2,3]. Disjunction of chromosomes from the rings or chains in the first meiotic division in males takes place in regular alternate fashion, with the translocated set of chromosomes segregating to male-determining sperm, the standard set with which it is associated segregating to female-determining sperm. The geographic variation seen in the chromosome rearrangements in some species[3] suggests that these multiple sex chromosome systems have recently been built up by successive reciprocal translocations or Robertsonian fusions between autosomes and the original sex chromosomes. Among these species is *Incisitermes schwarzi* Banks, which occurs in southern Florida, throughout the West Indies, in Mexico, and probably also in Central America and northern South America. The male meiotic chromosome arrangements found in *I. schwarzi* prior to this report are shown in the first 3 lines of the table[2,3].

Several colonies were collected in northwestern Jamaica. Good chromosome preparations were obtained from the males of one colony about 2 miles east of Discovery Bay. Reproductives were injected with Colcemid; the gonads were dissected out several hours later in a 0.45% sodium citrate solution, fixed and spread by the method of Imai, Crozier and Taylor[4], and stained with Giemsa.

The diploid number from spermatogonial mitoses is 32 (fig. 1). There are 2 acrocentric pairs; most of the other chromosomes are metacentric or submetacentric. Among the several chromosomes that do not occur as precise homologous pairs are 3 distinctive and easily recognizable ones (arrows, fig. 1): a large submetacentric (the largest chromosome of the diploid set), and 2 very small chromosomes (the 2 smallest of the diploid set, one slightly larger than the other). In male meiosis these 32 chromosomes are arranged as 7 bivalents and a multivalent ring of 18 (fig. 2). The bivalents comprise 4 pairs of metacentrics, 2 pairs of acrocentrics, and one small submetacentric pair. The elements of the ring are joined by terminal and subterminal chiasmata; in about 30% of the meiotic cells, the multivalent takes the form of a chain (fig. 3) rather than a ring, probably because of the failure of one chiasma. The multivalent has proved difficult to analyze in detail, but fairly consistently the large submetacentric, the second smallest, and the smallest chromosomes can be recognized at positions numbered 1, 7 and 15, respectively (arbitrarily starting with the large submetacentric as No. 1, and counting in the direction of its long arm) (see fig. 3). With alternate segregation, all even-numbered chromosomes (in

Geographic variation in male meiotic chromosome arrangements in *Incisitermes schwarzi*

Meiotic chromosomes	Location	References
$10^{II} + C^{XI}$	Tulum (Yucatan, Mexico)	Luykx and Syren[3]
$9^{II} + O^{XIV}$	Dania, South Miami, Florida Keys, Everglades City (Florida)	Syren and Luykx[2]; Luykx and Syren[3]
$8^{II} + O^{XVI}$	Miami (Florida) and New Providence Island (Bahamas)	Syren and Luykx[2]; Luykx and Syren[3]
$7^{II} + O^{XVIII}$	Discovery Bay (Jamaica)	This report

II = bivalents; C = chain; O = ring.

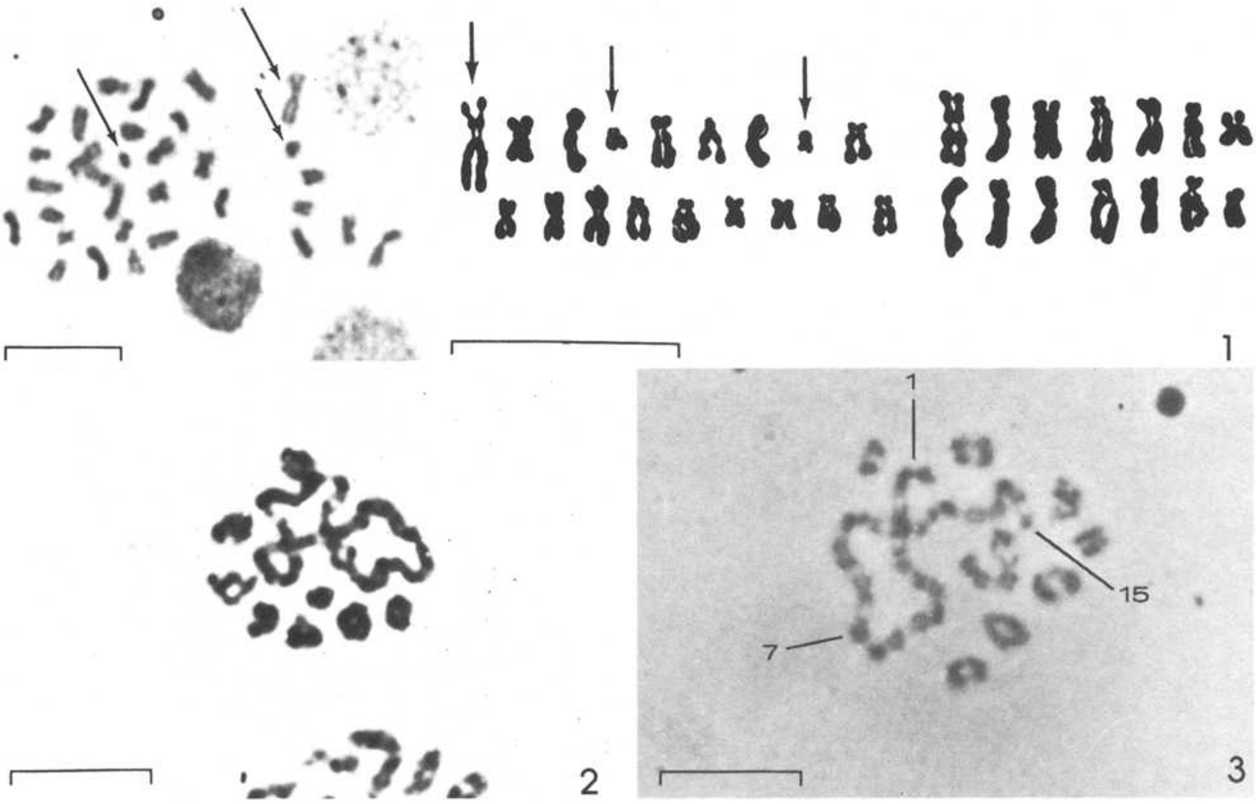

Fig. 1. Mitotic chromosomes of male *Incisitermes schwarzi* from Jamaica, shown as a group of 18 (left) and 7 pairs (right), corresponding to the pairing association seen in meiosis. The chromosomes on the left, corresponding to the meiotic ring of 18, have been put in alternating (zig-zag) arrangement to indicate alternate meiotic disjunction; chromosomes on the top row would segregate to one daughter cell in meiosis, those on the bottom row to the other. The distinctive large submetacentric and the 2 smallest chromosomes (arrows) are in correct segregational relation to one another; other chromosomes have not been unequivocally identified with their counterparts in meiotic cells, and have been arranged arbitrarily. The bar represents 10 µm in all figures. Fig. 2. Male meiosis, with seven bivalents and a ring. 2 or 3 nonterminal chiasmata are visible in the ring. Fig. 3. Male meiosis; seven bivalents and a chain of 18 chromosomes. With the position of the largest chromosome arbitrarily designated as No. 1, the second-smallest chromosome occurs at position No. 7, and the smallest at position No. 15.

this numbering scheme) would segregate together to one daughter cell, while odd-numbered chromosomes - including the marker chromosomes at positions 1, 7 and 15 - would segregate to the other daughter cell. (This expectation is incorporated in the arrangement of the chromosomes for the karyotype of figure 1.) Whether the largest and the 2 smallest chromosomes (and the other odd-numbered chromosomes with which they are associated in the ring) should be regarded as X's or as Y's cannot be determined without information on the karyotype of females.

This ring of 18 chromosomes represents the largest translocation complex so far discovered in any plant or animal species. Other large translocation complexes have been found in a centipede (chain of 9)[5], a copepod (ring of 14)[6], and another termite (*Kalotermes approximatus*, with a ring of 16)[3] among animals, and in the plants *Clarkia*[7], *Isotoma*[8], *Viscum*[9] (all with rings of up to 10 chromosomes), *Rhoeo*[10] (ring of 12), and *Oenothera*[11] (ring of 14).

The chromosome arrangements so far discovered in *Incisitermes schwarzi* (see table) evidently form part of an evolutionary series in which successive translocations between autosomes and sex chromosomes have occurred. If the ancestral condition consisted of an XY metacentric pair with homology in both arms, then a minimum of 8 successive gonosomal-autosomal translocations must have occurred to give a ring of 18. If the ancestral condition were X0, as in cockroaches, then 2 or 3 prior translocations must have occurred to give an XY ring-bivalent as a starting point[12,13].

The selective advantage of this remarkable sex-linked translocation heterozygosity in males is not known, but may be related to its effect in reducing recombination in the species, or the differential fitness of certain gene combinations in the 2 sexes[14].

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