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X_1X_2O (male) – $X_1X_1X_2X_2$ (female) chromosomal sex determining mechanism in the cricket *Ciclotyloides americanus* (Orthoptera, Grylloidea, Mogoplistidae)

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Abstract

The species of cricket *Ciclotyloides americanus* has males with $2n = 14$ and females with $2n = 16$ chromosomes. The autosomes are metacentrics and the sex determining mechanism is of the X_1X_2O (male) – $X_1X_1X_2X_2$ (female) type, with X_1 submetacentric and X_2 acrocentric. This mechanism is cited for the first time among species belonging to the order Orthoptera.

Key words

Scaly cricket, karyotype, sex chromosome, sex determination, meiosis, segregation

Introduction

Ciclotyloides americanus was described by Saussure in 1874 from specimens collected in Cuba, but the species was later found in North America (T. J. Walker, pers. com.) and Brazil, always associated with human dwellings. Due to its small size (5 to 7 mm) and furtive habits it is rarely seen during the day when it remains in hiding. It only moves to feed at night, at which time the very low intensity male calling song is heard.

The basic chromosomal mechanism of sex determination in crickets, as well as in all other Orthoptera, is XO (male) – XX (female), though departures from this primitive scheme are frequent in Grylloidea. *C. americanus* exhibits two X's and the absence of Y, a mechanism which, though common in other groups of invertebrates, e.g., arachnids, has never been found among orthopteran insects.

Materials and methods

Since 1980, specimens of *C. americanus* have been collected in Rio Claro (São Paulo State, Brazil) and submitted to karyological studies. The meiotic process was analyzed in several males and observations of embryo neuroblasts of both sexes were also carried out in search of mitotic divisions, after 2h pretreatment with 0.05% colchicine in eggs. In both meiotic and mitotic cells, Carnoy I fixative was used, the tissues squashed in lacto-acetic orcein 0.5% and after a few minutes, washed in acetic acid (45%).

Results

C. americanus (Fig. 1a, b) has a diploid number of 14 (male) – 16 (female) (Fig. 2a, b), comprising in males six pairs of metacentric autosomes and two X chromosomes (X_1, X_2) and in females four

X chromosomes (X_1, X_1, X_2, X_2). The autosomes can be grouped in pairs: two large, two medium sized and two small. Within each group it is difficult to identify each pair based on size and morphology. The number of chiasmata from bivalents is two or three and apparently not localized. The X_1 is submetacentric ($r = 5, 7$) and X_2 acrocentric ($r = 3, 1$), near the limit with submetacentric. The X_2 chromosome shows a median light-colored segment in the long arm.

During prophase I, X_1 and X_2 remain together in a single heterochromatic mass until diakinesis (Fig. 3a, b). At metaphase I, X_1 and X_2 remain either connected (Fig. 3f, g, h, i) or independent (Fig. 3c, d, e); but in all cases both chromosomes go to the same pole during anaphase I (Fig. 3j, k). Two kinds of other metaphases are observed, one of them with six autosomes (Fig. 3m), the other with the six autosomes plus the two X's (Fig. 3l).

Discussion

The derived chromosomal mechanisms of sex determination in crickets are apparently more diverse than in grasshoppers, where only species with neo XY and X_1X_2Y males were detected. In addition to these mechanisms, species with $X_1X_2X_3X_4Y$ (Mesa, unpub.) and X_1X_2O (this paper) males have been discovered in crickets.

Since the basic kind of sex determination in orthopteroid insects is that of XO (males) – XX (females), with the X metacentric, the presence of two Xs in *C. americanus* males could be explained by the dissociation of the original X into two sex chromosomes. But as X_2 is submetacentric and X_1 acrocentric with a relatively conspicuous small arm, further pericentric inversion or adding of new chromatin would need to have occurred after the original X splitting.

The presence of two X chromosomes that, in most of the nuclei, behave independently during first meiotic division, presents us with the unsolved question of how X_1 and X_2 always go to the same pole, in disagreement with the second Mendelian law.

Similar paradoxical chromosome behaviors were detected in males with X_1X_2Y chromosomes in the crickets *Eneoptera surinamensis* De Geer and *Euscyrthus* (probably *hemelytrus* De Haan) (Raychaudhuri & Manna 1950, Smith 1953, Ohmachi & Ueshima 1957) as well as in several other X_1X_2Y and $X_1X_2X_3X_4Y$ (male) crickets (Mesa et al. unpub.), species where no prophasic pairing and metaphasic contact took place between the sex chromosomes.

At the chromosomal level, the essence of Mendel's second law consists of the fact that centromeres of maternal and paternal origins of each autosomal bivalent, orientate freely toward opposite

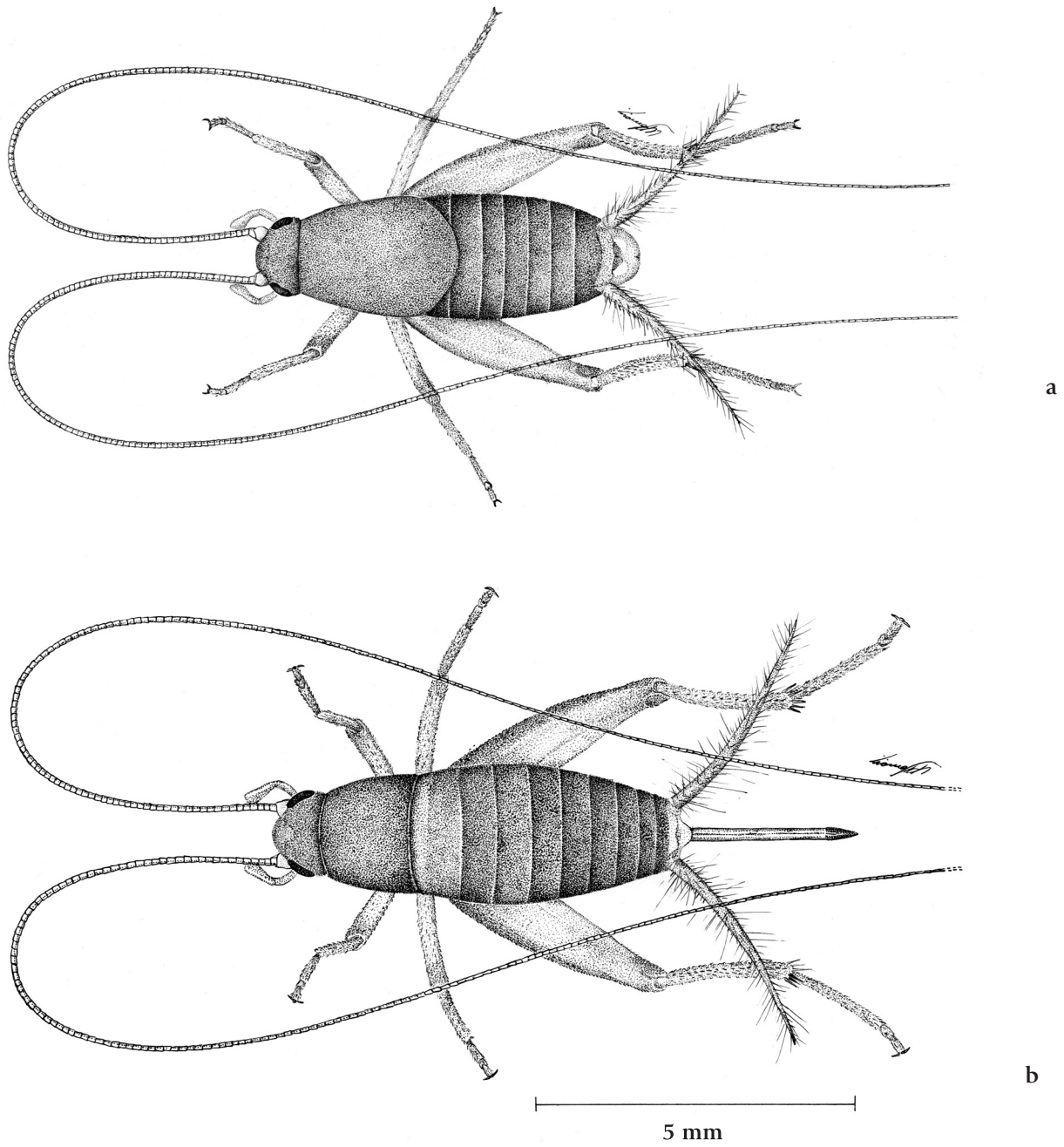


Fig. 1. *Cicloptylodes americanus* a) male, b) female.

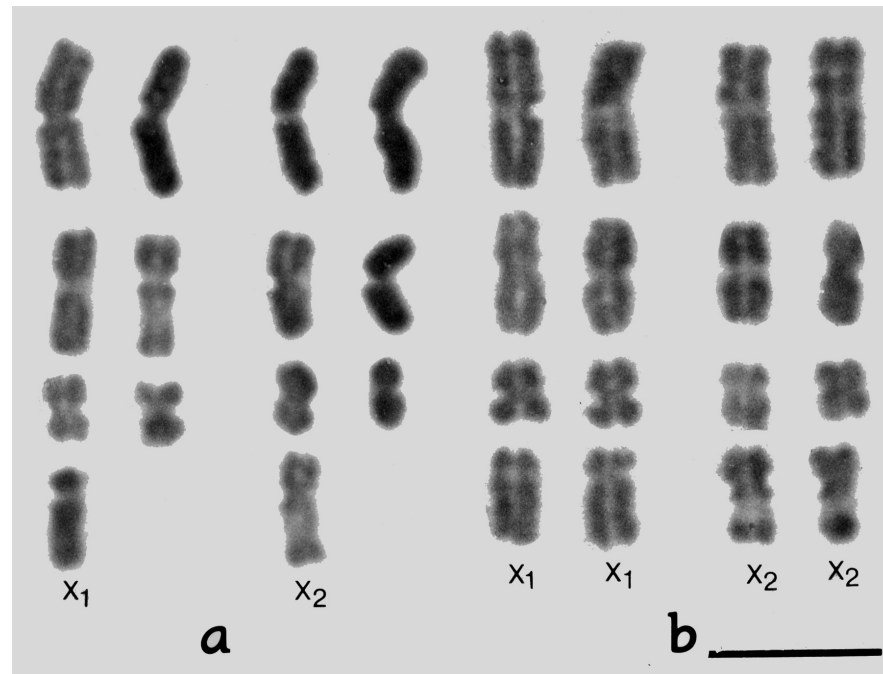


Fig. 2. Metaphase chromosomes from c-treated neuroblasts in embryos of *C. americanus*: a) male with X_1 and X_2 and six pairs of autosomes; b) female with $X_1X_1X_2X_2$ and six pairs of autosomes. Scale = 10mm.

poles during first metaphase, being the neutral poles in this kind of orientation. As a consequence, each bivalent co-orientates its centromeres independently in opposite directions, while the chiasmata momentarily keeps the homologous chromosomes together in the metaphase plate. The same seems to happen in simple or multiple sex chromosomes where a prophase pairing takes place. In those multiple mechanisms with several X and Y chromosomes, these are arranged during metaphase I in a zigzag line, with Xs and Ys alternating positions as in the buprestid *Euchroma gigantea* L. (Mesa & Fontanetti 1984) or in the termite *Neotermes fulvescens* (Silvestri) (Martins & Mesa 1995). When prophase pairing fails in autosomal bivalents, each univalent behaves freely, going in approximately half of the nuclei to the same pole, while in the other half going to the opposite poles.

Slightly different are the XO (male) mechanisms where the X has no chiasmatic link, remaining free and performing several pole to pole movements during first metaphase, until its final transference to one of the poles.

In some species of crickets, in contrast to *C. americanus*, the sex chromosomes do not appear connected by chiasmata or by simple heterochromatin affinities during first metaphase in all or in some nuclei. In other species, neither first prophase pairing takes place. These situations are clearly abnormal, but still the distribution of the sex chromosomes is correct even in the absence of an appropriated metaphase arrangement. For this to happen a temporal structural change in the centrioles, or in the centromeres of the sex chromosomes, or in both of them, is plausible. This must occur in such a way that the direction toward the poles of each sex component is predetermined and in consequence the second Mendelian law is not operative.

Acknowledgements

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Fig. 3. Male meiosis in *C. americanus* a) pachytene; b) diakinesis; c, d, e) first metaphase with X_1 and X_2 unconnected, going to the same pole; f, g, h, i) the same with X_1 , X_2 connected, going to the same pole; j, k) first metaphases with X_1 and X_2 in contact going to the same pole; l) second metaphase, including unconnected X_1 and X_2 ; m) second metaphase without sex chromosomes. Scale = 10mm.