

Achiasmatic male meiosis in *Myrmecobia coleoptrata* (Fn.) (Heteroptera, Microphysidae)

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Abstract — Mitosis and male meiosis were studied in *Myrmecobia coleoptrata* (Fn.), (Heteroptera, Microphysidae). Spermatogonial metaphase revealed 14 chromosomes ($2n=12+XY$). The nucleolar organizing region was found on the X chromosome. No m-chromosomes were present in the complement. Male meiotic prophase was characterized by a prominent condensation stage. At this stage, the sex chromosomes were positively heteropycnotic and appeared as separate univalents, while in autosomal bivalents homologous chromosomes were aligned side by side along their entire length, i.e. meiosis is achiasmatic. Meiosis was pre-reductional for the autosomes and post-reductional for the X and Y chromosomes. Meiosis was further characterized by non-radial arrangement of chromosomes in metaphase I plate and radial arrangement in metaphase II. Cytological characteristics of achiasmatic meioses and their distribution within Heteroptera are discussed.

Key words: achiasmatic meiosis, chromosomes, Heteroptera, Microphysidae.

INTRODUCTION

In general, in meiosis the intimate pairing of homologous chromosomes is followed by the process of recombination resulting in chiasma formation. The chiasma ties the homologous chromosomes together in a bivalent and hence ensures the proper orientation of homologues at prometaphase I and their regular segregation at anaphase I.

In some meioses, however, the bivalent organization is stabilized by achiasmatic means. Achiasmatic meiosis has been reported to occur in the insect orders Mecoptera (ULLERLICH 1961), Orthoptera (WHITE 1965a,b), Trichoptera (SUOMALAINEN 1966), Lepidoptera (SUOMALAINEN *et al.* 1973), Diptera (WHITE 1973), and Coleoptera (SERRANO 1981). In Hemiptera, achiasmatic meiosis has been found both in Homoptera (SCHRADER 1931; NUR 1965; BLACKMAN 1976; HALES 1989) and more recently also in Heteroptera (NOKKALA and NOKKALA 1983, 1984b, 1986a,b). In Heterop-

tera, meiosis without chiasmata has been found in families belonging to either of the two infraorders Leptopodomorpha or Cimicomorpha. However, exact knowledge about the distribution of achiasmatic meiosis within these infraorders is still lacking.

The Microphysidae is a small bug family belonging to the infraorder Cimicomorpha. Members of the family are small in size, predaceous and live among fallen leaves, moss, and lichens. In the present study, the behaviour of meiotic chromosomes in male of *Myrmecobia coleoptrata* (Fn.) was studied paying special attention to the presence or absence of chiasmata.

MATERIALS AND METHODS

Preliminary studies showed that adult males of *Loricula pselaphiformis* Ct., *Myrmecobia exilis* (Fn.), and *M. coleoptrata* (Fn.) displayed only mature sperm, hence nymphal stages of *M. coleoptrata* were used in the present study. Nymphs (30 specimens) and adults (two females and ten males) of *M. coleoptrata* were collected from mosses growing on the trunks of *Quercus* trees in late June in the vicinity of Turku. Specimens were fixed in Carnoy fluid, and stored in fixative.

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Squashes were made in 45% acetic acid. After removing cover slips by dry ice method, the slides were dehydrated in fresh Carnoy fluid for 30 min and air-dried. Slides were stained according to the Feulgen-Giemsa procedure as described by GROZEVА and NOKKALA (1996). Briefly, slides were immersed in IN HCl at room temperature for 20 min, hydrolysed in IN HCl at 60 °C for 7 min, and immersed in Schiff's reagent for 20 min, followed by thorough rinsing with distilled water. Subsequently, slides were rinsed in Sorensen's phosphate buffer, pH 6.8, for 5 min, and stained with 4% Giemsa in the same buffer for 20-30 min at + 4 °C. When appropriately stained, slides were quickly rinsed with distilled water, air-dried, and mounted in Entellan.

RESULTS

Testes dissected from adult males showed mature sperm only, however testes from nymphal stages showed cells undergoing both mitotic and meiotic divisions.

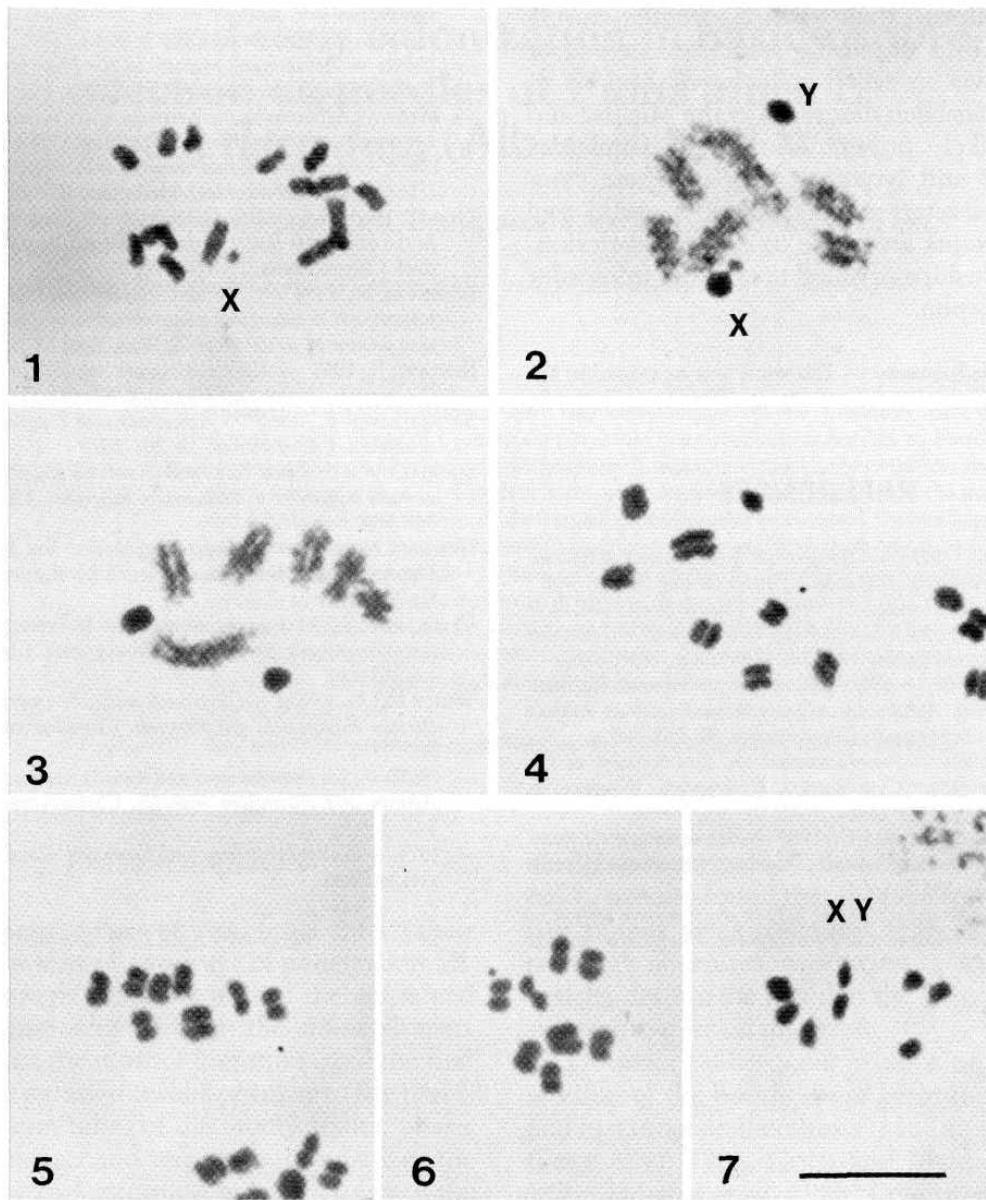
Spermatogonial metaphase cells showed 14 chromosomes, $2n=14$ (Fig. 1). The X chromosome is among the largest chromosomes in the complement and it is easily identified on the basis of a satellite segment located at a distance from the main chromosome. It seems apparent that NOR is located in the X chromosome in this species, resulting in an unstained gap between the satellite-like segment and the main chromosome body. There are no m-chromosomes present in the complement. Condensation stage was most abundant of meiotic stages found in nymphal testes. Nuclei at early condensation stage (Fig. 2) revealed six autosomal bivalents and the positively heteropycnotic X and Y chromosome univalents. Usually, the satellite-like element of the X chromosome was seen at this stage. At mid-condensation stage (Fig. 3) it became apparent that autosomal bivalents consist of parallelaligned homologous chromosomes, i.e. chiasmata are absent in male meiosis or meiosis is achiasmatic. Also size differences between the autosomal bivalents were most clearly observable at this stage. The complement includes one large autosome pair. All other five autosome pairs are smaller and more or less similar in their size. Achiasmatic bivalents were also well seen at late condensation stage (Fig. 4). The staining of autosomal bivalents was similar to the sex chromosomes, indicating that their condensation is similar at this

stage. At metaphase I (Figs. 5 and 6) autosomal bivalents co-orientated with homologous chromosomes facing opposite poles, and the sex chromosomes auto-orientated with sister chromatids facing the poles. Both the six autosomal bivalents and the X and Y chromosome univalents were evenly distributed along the metaphase I plate (Fig. 6). The X and Y chromosomes divided at anaphase I and showed "touch and go" pairing in the center of a ring formed by six autosomal chromosomes at metaphase II (Fig. 7), and segregated at anaphase II. Male meiosis is hence post-reductional for the sex chromosomes.

DISCUSSION

In Heteroptera achiasmatic meiosis has been so far described in five families in the infraorder Cimicomorpha: Microphysidae, Miridae, Cimicidae (NOKKALA and NOKKALA 1986a), Anthocoridae (NOKKALA and NOKKALA 1986b), Nabidae (NOKKALA and NOKKALA 1984b), and in the Saldidae in the infraorder Leptopodo-morpha (NOKKALA and NOKKALA 1983). However, male meiosis is chiasmatic in species belonging to two families in the infraorder Dipso-choromorpha (GROZEVА and NOKKALA 1996) considered to be more primitive than the infraorders Leptopodomorpha and Cimicimorpha. These observations evidence that achiasmatic meiosis has evolved relatively late in the evolution of Heteroptera, presumably delineating a monophyletic lineage within the order. The families with achiasmatic meiosis in the Cimicomorpha belong to the superfamilies Cimicoidea and Miroidea. Achiasmatic meiosis might be restricted to these superfamilies, since data available on male meiosis in the family Tingidae (JANDE 1960; NOKKALA and NOKKALA 1984a) in the superfamily Tingoidea and in the Reduviidae (for references see UESHIMA 1979) in the Reduviidoidea suggest the presence of chiasmata. This favours the view of polyphyletic origin of families in the infraorder Cimicomorpha.

In evolutionary sense the achiasmatic meiosis in Heteroptera must be of old origin, since some divergence has occurred in its cytological characteristics during the course of evolution. Most common is the meiosis like that found in



Figs. 1-7 — Mitotic and meiotic chromosomes in *M. coleoptrata*. 1. spermatogonial metaphase, $2n = 14$. The X chromosome has a satellite-like segment located at a distance from the main chromosome. 2. Early condensation stage showing six autosomal bivalents and positively heteropycnotic X and Y chromosomes. The satellite-like segment of the X chromosome still seen separately. 3. Mid condensation stage. The homologous chromosomes within autosomal bivalents are aligned side by side. The X and Y chromosomes lie separately. 4. Late condensation stage. The condensation of autosomal bivalents and the sex chromosomes is similar. 5. Metaphase I in side view showing orientation of homologous chromosomes in autosomal bivalents and sister chromatids of the sex chromosomes to opposite poles. 6. Metaphase I in polar view. The metaphase plate is non-radial. 7. Metaphase II. The X and Y chromosomes show "touch and go" pairing in the center of radial metaphase plate. Bar = 10 μm .

the Microphysidae, characterized by side by side alignment of homologous chromosomes during meiotic prophase, non-radial arrangement of bivalents in the first metaphase plate and "touch and go" pairing of X and Y chromosomes in the center of a radial metaphase II plate. This type of meiosis has been found in the Anthocoridae (NOKKALA and NOKKALA 1986b)

and Saldidae (NOKKALA and NOKKALA 1983). Meiosis in the Nabidae differs slightly but distinctly, showing "distance" pairing instead of "touch and go" pairing of the X and Y chromosomes at metaphase II (NOKKALA and NOKKALA 1984b). The third type of meiosis differs most from the others. The homologous chromosomes in this type of meiosis are not physically

aligned along their entire length during prophase, but physically associated in one or two sites via so called collochores. Meiosis of this type has been described in the Miridae and is most likely present also in the Cimicidae (NOKKALA and NOKKALA 1986a). These cyto-logical characters might provide a useful tool when attempts are made to explore evolutionary relationships of allied taxa in the infraorder Cimicomorpha.

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