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Spermatogenesis in the aphid *Amphorophora tuberculata* (Homoptera, Aphididae)

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Abstract. Spermatogenesis was studied in *Amphorophora tuberculata* Brown & Blackman, a species of aphid with $n=2$. Spermatogonia have $2n=3$ (AA+XO). In early prophase I the autosomal homologues are united terminally to form a tandem bivalent. No evidence could be found of synapsis or of the formation and terminalisation of chiasmata. The terminal connection of the autosomes is retained until late in prophase II. Sister chromatids separate, and autosomal half-bivalents move apart at anaphase I, but the division is incomplete, the X chromosome forming a thin chromatin bridge between the two autosomal half-bivalents. In prophase II the autosomal half-bivalents double back on themselves, so that non-sister chromatids become aligned in parallel. The X chromosome then becomes associated with one of the autosomal half-bivalents. Anaphase II separates the non-sister chromatids, and meiosis is thus "post-reductional."

Introduction

The holocentric chromosomes of Hemiptera generally behave in a characteristic way during the first division of meiosis. Pairing of homologues and crossing over are followed by an opening out of the bivalent, so that at metaphase I the homologues are joined end-to-end, in tandem fashion, by a single terminal chiasma. The orientation of these tandem bivalents on the first division spindle is then either axial, with the long axis of each bivalent lying along the spindle, or equatorial, with the long axis at right angles to the spindle. Equatorial orientation will lead to an "inverse" meiosis, in which the first meiotic division is equational for regions of the chromosome that have not crossed over, and the second division is the reductional one (see reviews by Battaglia and Boyes 1955; Sybenga 1981). "Post-reductional" meiosis was at one time thought to be the general rule in aphids and scale insects, and was referred to by Hughes-Schrader (1948) as the "aphid-coccid" type of meiosis, although in the case of aphids the generalisation was based on observations of a single species.

Meiosis in the Hemiptera in general thus seems to require obligate formation and terminalisation of chiasmata (White 1973). However, Blackman (1976) found no evidence of chiasmata or end-to-end alignment of homologues in spermatogenesis of the aphid *Euceraphis betulae*. In this species, homologues remain closely aligned in parallel as they condense into metaphase I, and anaphase I separates the products of pairing in a strictly reductional manner. A similar type of achiasmate male meiosis has recently been reported in two families of Heteroptera, Saldidae and Nabidae (Nokkala and Nokkala 1983, 1984).

The discovery of a new species of aphid with $n=2$), *Amphorophora tuberculata*, from which males could easily be reared in the laboratory (Brown and Blackman 1985), prompted a detailed study of the behaviour of its chromosomes in spermatogenesis. The main aims were to find out whether or not chiasmata were formed and to establish whether meiosis was normal (pre-reductional) or inverted (post-reductional).

Materials and methods

Viviparous, parthenogenetic females of *A. tuberculata* were reared on excised leaves of their host plant, *Geranium macrorrhizum* L., in controlled environment rooms at 18° C with a 16-h photoperiod, and at 15° C with a 12-h photoperiod. Males were produced in both regimes, in the middle of the larviposition sequence of each mother, after an initial batch of entirely female offspring. Males produced at 18° C and 16 h were alate or brachypterous, whereas those produced at 15° C and 12 h were all apterous.

Testes were dissected from first, second, and third instar larvae in slightly hypotonic (0.75%) potassium chloride solution and fixed in cold methanol/acetic acid (3/1). They were then either hydrolysed for 5 min in 1 N hydrochloric acid at 65° C and stained with Feulgen before squashing, or squashed directly in a drop of 45% propionic acid for examination by phase contrast prior to freezing off the coverslip and staining with Giemsa. Some preparations were C-banded (Blackman 1976).

To study zonation in the testis and obtain information about the chronological sequence of events in meiosis, some of the Feulgen-stained testes were examined in distilled water under a coverslip without squashing. These preparations were then studied (using a Zeiss Planapo 63 oil-immersion objective) as the water was displaced by running 45% propionic acid under the coverslip to swell the cells and render their cytoplasm transparent. This technique was