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Stability of a multiple X chromosome system and associated B chromosomes in birch aphids (*Euceraphis* spp.; Homoptera: Aphididae)

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Abstract. Autosomal dissociations are a common feature of aphid karyotype evolution, but multiple X chromosome systems are rare. Birch-feeding aphids of the genus *Euceraphis*, however, have X_1X_2O males as a general rule, X_1 being always much larger than X_2. Only one species has XO males, and this condition appears to be secondary. Most *Euceraphis* karyotypes also have one or more, usually heterochromatic, elements that occur in the same numbers in both males and females, yet behave like X chromosomes at male and female meiosis I. They appear to be supernumerary, "non-functional" X chromosomes, although showing greater within-species stability in size and number than typical B chromosomes. *Euceraphis gillettei* forms a separate group within the genus and feeds on alders (*Alnus* species), yet has a similar system, and the two most closely related genera, *Symydobius* and *Clethrobius*, also have additional chromosomal elements possibly representing non-functional X chromosomes. Thus the multiple X chromosome system in these aphids seems to be a primitive condition.

Introduction

In aphids, males are XO, and are usually produced in autumn. Autosomal dissociations are a common feature of aphid karyotype evolution (Blackman 1980), but multiple X chromosome systems are rare. *Euceraphis betulae* (Koch), a common aphid on the European silver birch, *Betula pendula* Roth, was originally reported to have $X_1X_2X_3X_4O$ sex determination (Shinji 1931), but Blackman (1976) showed that males of this species have only two chromosomes fewer than females and are therefore X_1X_2O (Fig. 1). The other two elements, believed by Shinji to be X chromosomes, are heterochromatic and behave in most respects like B chromosomes. In female somatic cells of *E. betulae* these resemble the larger pair of X chromosomes in size and general appearance. Although they do not undergo reduction during the maturation of the male egg, they are both stretched on the anaphase I spindle at spermatogenesis in an identical manner to the X chromosomes, before passing with the Xs into one daughter spermatocyte. This strongly suggests that they are B chromosomes of X chromosomal origin, as is thought to be the case with the larger type of B chromosome found in certain grasshoppers (Hewitt 1973). However, unlike most B chromosomes they are consistently present, at least in British populations of *E. betulae*.

A second European species, *E. punctipennis* (Zetterstedt), feeds on downy birch, *B. pubescens* Ehrh., and has a different number of autosomes to *E. betulae*, but a similar X chromosome/B chromosome system (Fig. 1). In *E. punctipennis*, however, there is some variation in the size and number of B chromosomes, although at least one is always present (Blackman 1976).

Most other *Euceraphis* species occur in North America. This paper reports the karyotypes of the North American species and gives a preliminary account of their cytogenetics, paying particular attention to the system of sex determination.

Material and methods

Karyotypes were analysed by examination of dividing cells of female embryos from parthenogenetic viviparous females in spring and summer populations and comparing these with (i) dividing somatic cells of male embryos from parthenogenetic viviparous females in autumn, and (ii) meiotic stages in immature males and sexual females (oviparae) in autumn. Aphids of all developmental stages were collected from the field and fixed directly in freshly mixed 3/1 methanol/acetic acid. For somatic cell preparations embryos were dissected from viviparous females in 75% methanol, transferred to 1 N hydrochloric acid (5 min), thence to distilled water, and then squashed under a coverslip in a drop of 45% propionic acid. Only the youngest embryos, from the upper parts of the ovarioles close to the germaria, were used. For germ cell preparations, testes and ovarioles were dissected from sexual morphs in their first or second instar.

Preparations were observed and photographed either by phase contrast without staining, or after staining with Giemsa (Gurr's R66).

Results

Karyotypes

Populations of *Euceraphis* on five native North American *Betula* species all have distinct karyotypes (Table 1, Fig. 1). Two are previously described species, *E. lineata* Baker on *B. populifolia* Marsh and *E. mucida* (Fitch) on *B. lenta* L. The other three are all very similar morphologically to the European species *E. betulae*, and share with it the same