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High diversity of structurally heterozygous karyotypes and rDNA arrays in parthenogenetic aphids of the genus *Trama* (Aphididae: Lachninae)

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Karyotypes of permanently parthenogenetic aphids of three species of the genus *Trama* show great diversity, particularly in the number and distribution of chromosomal elements containing highly repetitive sequences. Sampling at only a few sites in southern England, chromosome number varied from 14 to 23 in *T. troglodytes*, 9–12 in *T. caudata* and 10–14 in *T. maritima*, with some colonies having individuals of more than one karyotype. This variation was paralleled by differences in the number and distribution of rDNA arrays revealed by *in situ* hybridization. This high intraspecific karyotype diversity contrasts with very low genetic diversity in the same populations, suggesting rapid karyotype evolution. Although *T. troglodytes* feeds on many species of composite plants there was no evidence of any karyotype-associated host race formation.

Keywords: aneuploidy, clonal reproduction, heterochromatin, repetitive DNA.

Introduction

Aphids primitively and typically exhibit cyclical parthenogenesis, alternating a single annual (sometimes biennial) bisexual generation with several unisexual (all-female) generations. The bisexual generation may be lost secondarily, so that reproduction is then exclusively by apomictic parthenogenesis. This often happens within species, particularly in those which have been widely distributed by man. Presumably in such cases the loss of bisexual reproduction is a very recent event, but it is nevertheless often accompanied (or followed) by chromosomal rearrangements, giving rise to aneuploid karyotypes and structural heterozygosity (Blackman, 1980a), suggesting that such changes can occur quite rapidly.

One group of aphids, the tribe Tramini, may have a longer history of parthenogenesis, as functional sexual reproduction has not been observed in any members of this tribe (Mordvilko, 1935; Eastop, 1953). Tramini colonize the roots of composite plants and are obligatorily associated with ants. *Trama troglodytes*, the best-known species in the principal genus *Trama*, shows a remarkable degree of karyotypic diversity, notable especially in the variable distribution of constitutive (C-) heterochromatin (Blackman, 1980a,b, 1990). Large blocks of C-heterochromatin, indicating the presence of tandem arrays of highly repetitive DNA sequences (Lohe & Hilliker, 1995), are a characteristic feature of this group of aphids, comprising about 40% of the genome (Blackman, 1980b).

Another feature of permanently parthenogenetic aphid populations, providing further evidence of rapid karyotype evolution, is the frequent occurrence of a single rDNA array, as opposed to the pair of rDNA arrays usually found on the X chromosomes in species that have regular sexual reproduction. Blackman & Spence (1996) reported such a single rDNA array in the one population of *T. troglodytes* that they examined.

In contrast to the high karyotypic diversity of *T. troglodytes*, a low level of genetic diversity was found for both a nuclear and a mitochondrial gene within this and several other species of Tramini (Normark, 1999). The very low heterozygosity of the elongation factor 1α gene in two species of this group, *T. troglodytes* and *Protrama flavescens*, indicated that some form of recombination must be occurring at this locus. The absence of any records of sexual morphs in these two common species and the structural heterozygosity of the karyotype shown by *T. troglodytes* seem

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