

Occurrence of sexual morphs in *Trama troglodytes* von Heyden, 1837 (Hemiptera, Aphididae)

ROGER L. BLACKMAN*¹, EMMA DE BOISE¹ and
ANDRZEJ CZYLOK²

¹*Department of Entomology, The Natural History Museum,
Cromwell Road, South Kensington, London SW7 5BD, UK;
e-mail: r.blackman@nhm.ac.uk*

²*Department of Biogeography and Nature Protection, University of
Silesia, ul. Bédzinska 60, 41-200 Sosnowiec, Poland*

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The root-feeding aphids of the tribe Tramini have been cited as a possible case of ancient apomixis, as there are no substantiated records in the literature of a functional bisexual generation, even in common and well-known European species. The karyotypic variation found in this group, involving considerable structural heterozygosity within species, also pointed to the decay of diploidy that would be an expected consequence of loss of sexuality and absence of meiosis. However, we have now found a small number of oviparae (mating females) and males in populations of the common species *Trama troglodytes*. Fertilized eggs were not obtained, but adult oviparae contained large, yolky eggs. The single adult male was apterous, small and blind, but had fully developed mouthparts and genitalia, and contained mature sperm. Both sexual morphs are described, and the karyotypic variation is reassessed in the light of these findings. Occasional sexual reproduction is in concordance with recent molecular evidence that some recombination occurs in *T. troglodytes* and related species.

KEYWORDS: aphids, Tramini, ancient apomixis, cryptic recombination.

Introduction

Aphids typically have cyclical parthenogenesis, alternating a sequence of thelytokous (all-female, viviparous) generations with a single, usually annual, bisexual generation (of males and mating, oviparous females). The bisexual generation may however be rather easily lost, resulting in continuous, apomictic parthenogenesis, either by some genotypes or populations within a species, or sometimes apparently by the entire species. Even some common and widely distributed aphids seem to be permanent apomicts, but their nearest relatives usually still have a bisexual generation in their life cycle. This suggests that the loss of sexuality in such aphids is an

*To whom correspondence should be addressed.

evolutionarily recent event, as seems to be the case in most other groups with permanently apomictic species (Suomalainen *et al.*, 1976, Hughes, 1989).

It has been proposed, however, that the loss of sexuality may have been a more ancient event in one aphid group in the subfamily Lachninae, the Tramini (Eastop, 1953; Blackman, 1980a; Normark, 1999). Tramini are large, white, invariably ant-attended aphids feeding on roots of Compositae. They are a Palaearctic group of three genera and about 28 species, and it has been suggested that the group as a whole lacks sexual reproduction (Szelegiewicz, 1978; Blackman, 1980a; Czylok, 1990; Heie, 1995). Cytological studies provided supporting evidence for this conclusion, because all species investigated had unusual karyotypes, with large amounts of constitutive heterochromatin (Blackman, 1980a, 1980b, 1990). In the genus *Trama*, karyotypes appear structurally heterozygous, with considerable variation in number and distribution of heterochromatic segments (Blackman, 1980a) and rDNA sites (Blackman *et al.*, 2000). Aneuploidy and structural heterozygosity might be expected in chromosome sets that no longer undergo meiotic pairing and segregation, and Blackman *et al.* (2000) have suggested that the heterochromatic elements might, in whole or in part, be the remains of the ancestral sex chromosomes.

There are, however, a few isolated reports in the literature of sexual morphs in Tramini. Del Guercio (1899) gave an account of the life cycle of a *Neotrama* sp. (as *Trama radialis*) in Italy, including overwintering eggs, fundatrices, oviparae and apterous males. Mordvilko (1935) stated that he might have reared one male of a *Protrama* sp. (as *Trama radialis*), but again gave no description. Verma (1969) found and described a single male of the Indian species *Trama penecaeca* (Stroyan), the karyotype of which is unknown.

In September 1984, a single colony of *Trama troglodytes* von Heyden on *Centaurea oxylepis* in Poland was found to contain females with an oviparous reproductive system (A. Czylok, unpublished observations). No males were found, and colonies on other host plants in the area consisted entirely of viviparous females, so the existence of a functional bisexual generation could not be established.

Further evidence conflicting with the hypothesis of ancient apomixis in Tramini has recently been reported by Normark (2000), who found very low levels of heterozygosity of the EF-1 α gene in *Trama troglodytes* and *Protrama flavescens* (Koch), compared to substantial divergences between these and other species, indicating that some form of recombination must be occurring at this locus. Both these species are common and widely distributed in Europe. Here we report the occurrence of both males and oviparous females in a population of *T. troglodytes* in southern England.

Materials and methods

As part of ongoing studies of karyotype variation in Tramini, mixed colonies of *Trama troglodytes* and *T. maritima* (Eastop) were collected from roots of *Picris echioides* at Church Ope Cove, Portland, Dorset on 8 September 1999. Colonies were sorted into species in the laboratory, both immature and adult *T. maritima* being readily identified by the presence of siphuncular pores, which are absent in all instars of *T. troglodytes*. Second and third instar larvae were dissected in 1% sodium citrate, prior to fixation and preparation of embryonic tissues for cytological examination. One of the two colonies of *T. troglodytes* examined contained five immature oviparae. The reproductive system of oviparous aphids is easily recognized, even in young larvae, because the germaria are much larger than in viviparae and contain

