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Perianal structures in myrmecophilous subterranean aphids (Insecta: Hemiptera: Aphididae) – Comparative morphology of trophobiotic organ with its first description in Lachninae

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ABSTRACT

Scanning electron microscopy (SEM) and light stereoscopic microscopy (LSM) were used for the first time to elucidate the external morphology of the so called "trophobiotic organ" on the end of abdomen of apterous viviparous females of six aphid species (Insecta: Hemiptera: Aphididae), representatives of the myrmecophilous, subterranean aphids from the subfamilies Anoeciinae (*Anoecia furcata*), Eriosomatinae (*Forda formicaria*, *Geoica utricularia*, *Tetraneura ulmi*), and Lachninae (*Protrama flavescens*, *Trama troglodytes*). We examined and compared the external morphology in the parthenogenetic generation living on roots of deciduous plants. FE-SEM images based on HMDS preparation techniques revealed great similarity of perianal structures even between not closely related groups. Rectangular, vertically positioned anal plate, extremely shortened cauda and setae around the anus seem to be common features of these aphids. However, some differences in the number and length of setae, their arrangement and inclination of anal plate may be observed. The discussion focuses on the adaptive importance of such modifications, with respect to underground life mode and myrmecophily, but with reservations concerning living in galls by representatives of Eriosomatinae, which is hypothesized to be a factor driving the development of such modifications of perianal structures in this group of aphids.

1. Introduction

Since the beginning of studies on the mutualistic relations of aphids and ants, some special attention was given to the modes of transferring the excreted honeydew droplet from aphid to ant. For most of aphid species involved in such a relationship the main morphological adaptations are regarded the shortening of the cauda and longer setae in the anal region. They are believed to form a sort of a basket that holds the honeydew droplet until it is collected by an ant worker (Kunkel, 1973; Hölldobler and Wilson, 1990). The special organ developed for this purpose is called the "trophobiotic organ" and it was noticed as early as in 1907 by Mordvilko (Zwölfer, 1958a). The term was later applied and repeated by many authors, with special attention given to it in the vast study of subterranean aphids by Zwölfer (1958a, b, c, d). According to Zwölfer, all subterranean aphids (of the subfamilies: Anoeciinae and Eriosomatinae *s. lat.*), studied by him and involved in symbiosis with ants have developed the trophobiotic organ. This is most spectacularly developed in the aphid tribe Fordini (Eriosomatinae), with species of the genus *Geoica* Hart, 1894 as a leading example of such morphological adaptations (Heie, 1987).

The organ of *Geoica* spp. consists primarily of a well developed, sclerotized anal plate bearing numerous short or rows of long setae (Zwölfer, 1958c) and an abdominal tergite VIII which also bears a few longer setae. The anal plate is the most distinguishable morphological feature of apterous viviparous females of *Geoica* spp. living on its secondary host – roots of Poaceae. The anal plate is in its dorsal part inclined towards the proximal part of body and the droplet of honeydew may be propped by setae until the ant worker collects the droplet. If it is not collected, the droplet may be retracted back, possibly to the distal part of intestine which has an anal vesicle (Mróz et al., 2016). Similar mechanisms and morphological structures are also present in the related genera *Baizongia* Rondani, 1848, *Forda* von Heyden, 1837 (Fordini) and *Tetraneura*

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Hartig, 1841 (Tetraneurini) (Galli and Bonvicini-Pagliai, 1998) and retracting the honeydew back towards the abdomen is known feature of other myrmecophilous aphids (Kunkel, 1973). On the other hand, all these genera are gall producing on their primary host, and such life mode resembles living in an underground chamber. Thus, we cannot be sure, if the existence of a trophobiotic organ results from honeydew excreting problems in limited space or from myrmecophily.

So far, no such organ was described in detail in other aphid genera and families, although many studies on their mutualistic relationships with ants were conducted. There is only the general concept of the existence of the perianal ring of setae in many myrmecophilous aphids as an adaptation to myrmecophily (Shaposhnikov, 1985). This especially concerns the aphid subfamily Lachninae, where a significant number of species is believed to be obligatorily myrmecophilous. Between the species of Lachninae, the genus *Trama* von Heyden, 1837 shares many ecological and morphological features with other subterranean and myrmecophilous aphids studied by Zwölfer. And there is no information about the possible existence of modified perianal structures playing the role of a trophobiotic organ in this genus (Czylok, 1990).

Because the subject of influence of ants on aphid evolution seems to be intriguing, when we take into account recent discoveries concerning both Lachninae (Endo and Itino, 2013; Depa et al., 2016) as well as Fordinae (Salazar et al., 2015), it seems important to take again a detailed look at the subject of "trophobiotic organ". Some systematic groups of aphids as whole have a shortened cauda (e.g. Lachninae), and yet there are few species among them which are considered as non myrmecophilous (e.g. *Eulachnus* spp., *Cinara* (*Schizolachnus*) spp., *Pseudessigella brachychaeta* in Lachninae). Other Aphididae have a well-developed cauda but their members are equally non myrmecophilous, facultatively myrmecophilous or obligatorily myrmecophilous (e. g. within Aphidinae or Chaitophorinae). In respect of these discrepancies, and possible independent development of mutualistic relations within some genera (e. g. *Chaitophorus* Koch, 1854 – Shingleton and Stern, 2003) it is important to re-investigate morphological structures of aphids, with focus on "trophobiotic organ", in wide specter of systematic and ecological groups of aphids.

In this paper, we revise and present in detail the perianal structures in underground living aphids, which are considered to be obligatorily myrmecophilous. Also, we present for the first time the modifications of perianal structures in the aphid genera *Trama* and *Protrama* Baker, 1820 (Lachninae: Tramini) which may be connected to their obligatory myrmecophily and underground life mode.

This paper is the first of a series concerning morphology and modifications of perianal structures in relation to the degree of myrmecophily and the life mode of aphids. In this paper, we revise the basics of the concept of the trophobiotic organ in myrmecophilous subterranean species, which in case of Eriosomatinae was the leading example of such modifications.

2. Material and methods

2.1. Taxon sampling

For studying the structure of the trophobiotic organ of subterranean myrmecophilous aphids we used following species:

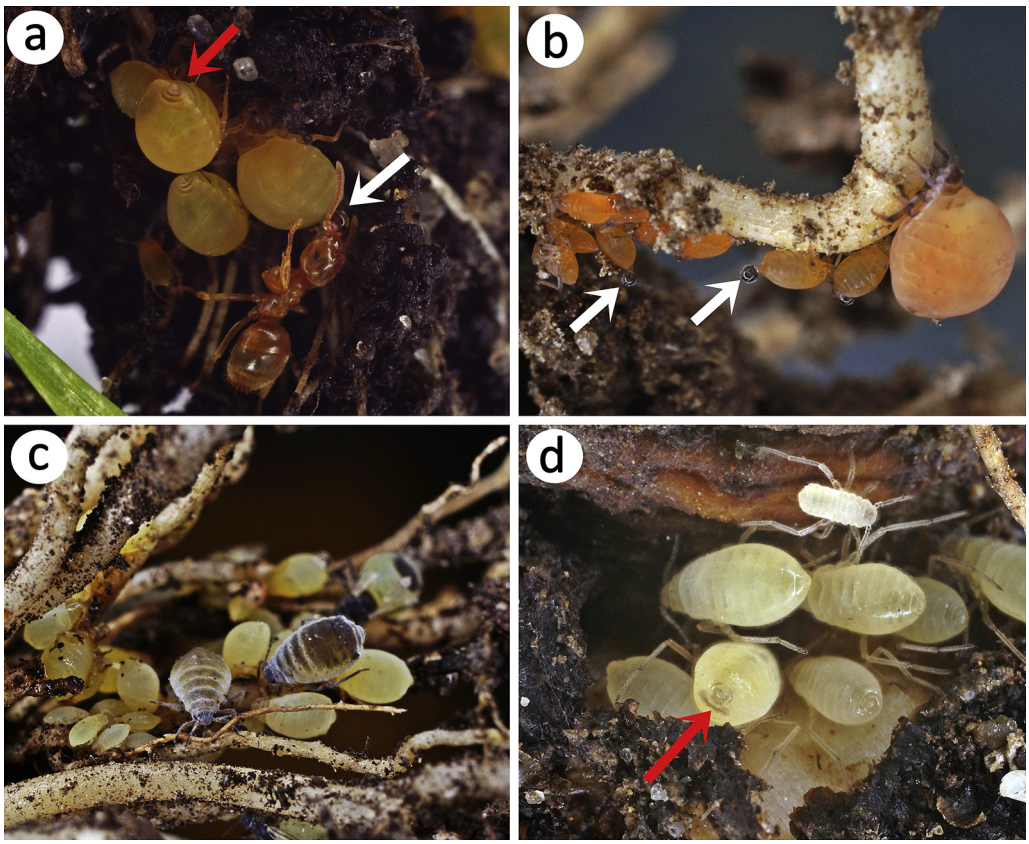

Fig. 1. Subterranean aphids in life: **a** – apterous viviparous females of *Forda formicaria* with visible sclerotized perianal structures (red arrow), visited by *Lasius flavus* worker which takes the honeydew droplet (white arrow); **b** – apt. viv. female and larvae of *Tetraneura ulmi* with visible honeydew droplets (white arrows); **c** – apt. viv. females and larvae of *Anoecia furcata*; **d** – apt. viv. females and larva of *Trama troglodytes* with visible sclerotized perianal structures (red arrow).

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