

Československá Akademie Věd
Entomologický Ústav
Praha (ČSSR)

PETE STARÝ

A study on the relationship of the Anuraphidina and their aphidiid parasites in Europe

(Homoptera: Aphidoidea/Hymenoptera: Aphidiidae)

Introduction

This is another part of the author's studies on the relationship of various aphid groups and their aphidiid parasites in Europe. It is the purpose of this work to discover the factors that influence the host-specificity in the Aphidiidae and the aphid and parasite relationship in general. Such a kind of study is thought to be necessary for the theoretical appreciation of the possibility of using certain aphidiid species as biological control agents.

This paper deals with the relationship of the anuraphidine aphids and their aphidiid parasites in Europe. The said aphid group includes some serious pests of orchards and gardens, whose parasites are of certain interest for the above-mentioned reasons.

The aphid group Anuraphidina

The Anuraphidina represent the most primitive and specialized group of the subfamily Aphidinae. As regards its phylogeny, this group is connected with plants of the family Rosaceae, especially with the subfamilies Maloideae and Prunoideae. Many species pass on to herbs.

The phylogenetically original group of aphids is mesophilic and connected with the phylogenetically older, original and mesophilic plant subfamily Maloideae. On Prunoideae, which are a phylogenetically younger and more xerophilic group, there occurs a phylogenetically younger aphid group. Therefore the phylogeny of the Anuraphidina corresponds to the main phylogenetic tendency of aphids, i.e. the transition from conifers to deciduous trees, from trees to shrubs and then to herbs; this means practically the adaptation to conditions of a drier climate.

The anuraphidine group is not homogeneous. On the one hand it includes species whose life-cycle is passed on trees, on the other hand it includes species that migrate facultatively or obligatorily from trees and plants to herbs. They occur in mesophilic conditions of forests and in the open landscape of steppes and on mountains.

The biological specialization of the Anuraphidina is apparent in their specific leaf-curling of primary host plants as well as in their adaptation to the life as root aphids on secondary host plants.

In this paper the classification of SHAPOSHNIKOV (1956) that is based on a highly detailed study of phylogeny, morphology and ecology of the Anuraphi-

dina has been followed. For this reason into BÖRNER's classification (1952), dividing the anuraphidine group into various tribes and subtribes, was not accepted.

On the base of the classification of the parasites we must support SHAPOSHNIKOV's classification (1956), so that the genus *Cryptosiphon* BUCKTON, the parasites of which are quite different from those of the Anuraphidina, has not been included in the said aphid group.

Host parasite catalogue

This is an original list of the Anuraphidina and their aphidiid parasites in Europe. Literary data have been omitted as they include many doubtful and incorrect records.

Anuraphis DEL GUERCIO

Anuraphis farfarae KOCH

Ephedrus plagiator (NEES) — *Pirus communis*.

Anuraphis subterranea WALKER

Paralipsis enervis (NEES).

Dysaphis BÖRNER

Dysaphis crataegi KALTENBACH

Ephedrus persicae FROGGATT — *Crataegus oxyacantha*, *Ephedrus plagiator* (NEES) — *Crataegus oxyacantha*, *Monoctonus cerasi* (MARSHALL) — *Crataegus oxyacantha*, *Paralipsis enervis* (NEES) — *Daucus carota*.

Dysaphis devecta (WALKER)

Ephedrus persicae FROGGATT — *Malus silvestris*. *Ephedrus plagiator* (NEES) — *Malus silvestris*. *Lysiphlebus ambiguus* (HALIDAY) — *Heracleum sibiricum*. *Trioxys angelicae* (HALIDAY) — *Malus silvestris*.

Dysaphis lappae KOCH

Lysiphlebus fabarum (MARSHALL) — *Arctium lappa*. *Paralipsis enervis* (NEES) — *Arctium lappa*.

Dysaphis mali FERRIÈRE

Ephedrus persicae FROGGATT — *Malus pumillus*. *Monoctonus cerasi* (MARSHALL) — *Malus* sp.

Dysaphis sorbi (KALTENBACH)

Ephedrus persicae FROGGATT — *Sorbus aucuparia*. *Ephedrus plagiator* (NEES) — *Sorbus aucuparia*.

Dysaphis ssp.

Ephedrus persicae FROGGATT — *Crataegus* sp., *Sorbus torminalis*, *Malus silvestris*, *Pirus communis*. *Ephedrus plagiator* (NEES) — *Crataegus* sp., *Pirus communis*. *Monoctonus* sp. — *Malus silvestris*. *Praon volucre* (HALIDAY) — *Malus silvestris*. *Trioxys angelicae* (HALIDAY) — *Crataegus oxyacantha*.

Allocotaphis BÖRNER**Allocotaphis quaestionis** BÖRNER*Ephedrus persicae* FROGGATT — *Malus silvestris*.**Brachycaudus** DEL GUERCIO**Brachycaudus ballotae** (PASS.)*Paralipsis enervis* (NEES) — *Ballota nigra*.**Brachycaudus cardui** (LINNAEUS)*Aphidius picipes* (NEES) — *Prunus spinosa*, *Prunus cerasifera*. *Ephedrus plagiator* (NEES) — *Prunus spinosa*, *Prunus cerasifera*. *Lipolexis gracilis* FÖRSTER — *Carduus* sp., *Prunus domestica*. *Lysiphlebus fabarum* (MARSHALL) — *Arctium lappa*, *Arctium* sp., *Matricaria maritima*, *Carduus nutans*, *Carduus* sp., *Cirsium* sp., *Carduus pycnocephalus*, *Prunus spinosa*. *Paralipsis enervis* (NEES) — *Carduus crispus*, *Arctium lappa*.**Brachycaudus helichrysi** (KALTENBACH)*Diaeretiella rapae* (MCINTOSH) — *Senecio vulgaris*. *Ephedrus persicae* FROGGATT — *Anthemis* sp., *Matricaria maritima*, *Matricaria discoidea*, *Hieracium laevigatum*. *Ephedrus plagiator* (NEES) — *Prunus domestica*. *Praon volucre* (HALIDAY) — *Melandrium album*, *Silene cucubalus*.**Brachycaudus mordwilkoii** HILLE RIS LAMBERS*Lipolexis gracilis* FÖRSTER — *Echium vulgare*, *Paralipsis enervis* (NEES) — *Echium vulgare*.**Brachycaudus rumexicolens** PATCH*Diaeretiella rapae* (MCINTOSH) — *Rumex acetosella*. *Lysiphlebus fabarum* (MARSHALL) — *Rumex acetosella*.**Brachycaudus tragopogonis** (KALTENBACH)*Lysiphlebus fabarum* (MARSHALL) — *Tragopogon pratensis*.**Brachycaudus** ssp.*Aphidius picipes* (NEES) — *Matricaria* sp., *Diaeretiella rapae* (MCINTOSH) — *Rumex acetosella*, *Matricaria* sp. *Ephedrus persicae* FROGGATT — *Prunus persica*, *Prunus spinosa*, *Prunus domestica*. *Ephedrus plagiator* (NEES) — *Prunus domestica*. *Lipolexis gracilis* FÖRSTER — *Prunus domestica*, *Tanacetum vulgare*, *Arctium lappa*, *Arctium* sp., *Carduus* sp., *Cirsium vulgare*, *Prunus persica*. *Lysiphlebus fabarum* (MARSHALL) — *Carduus crispus*, *Senecio jacobaea*, *Carduus acanthoides*, *Prunus domestica*, *Prunus persica*. *Trioxys angelicae* (HALIDAY) — *Rumex acetosella*, *Prunus persica*. *Paralipsis enervis* (NEES) — *Arctium lappa*.**Roepkea** HILLE RIS LAMBERS**Roepkea marchali** (BÖRNER)*Ephedrus persicae* FROGGATT — *Prunus mahaleb*.**Acaudinum** BÖRNER**Ceruraphis** BÖRNER**Ceruraphis eriophori** (WALKER)*Ephedrus plagiator* (NEES) — *Viburnum opulus*. *Trioxys angelicae* (HALIDAY) — *Viburnum lantana*.

Discussion

As shown by the ecological data, the Anuraphidina group of aphids occurs both in forest and steppe types of habitats. The change of the type of habitats is connected with the migration from primary to secondary host plants.

The author's studies on the host specificity of the Aphidiidae establish that it is conditioned by two main factors: 1. By the habitat, 2. By the occurrence of a suitable host within this habitat. The host suitability is determined on the one hand by the phylogenetic adaptation of the parasite and on the other hand by the ecological plasticity, i. e. the ability of the parasite to infest and develop in a host that has a similar mode of life but different phylogenetic relations. Thus the aphids which change the type of habitat (forest and steppe) usually by migration from primary to secondary host plants, are infested in this case by several different species of parasites (or complexes of parasites) that correspond to different types of habitats (Note: If the secondary host plant occurs in the same type of habitat as the primary host plant, the parasites may be identical on both host plants).

The following appreciation of the Anuraphidina from this viewpoint may be given:

Bionomics and ecology

The Anuraphidina include both forms that do not change the type of habitat as they occur on trees exclusively and forms that change the type of habitat by migration from trees and bushes (primary host plants) to herbs (secondary host plants). They occur therefore in forest and steppe types of habitats.

The Anuraphidina have typical bionomical features: In forest habitats, on primary host plants, they occur as leaf-curling species; in steppe habitats, on secondary host plants, they occur on herbs — on roots, root collars, lower or upper parts of plants.

Phylogeny

There are two groups of Anuraphidina: The first group is older, mesophilic, occurring on Maloideae; the second group is younger, more xerophilic, occurring on Prunoideae.

Judging from the author's studies, the Anuraphidina have to be infested in forest habitats by parasites that occur in the given type of habitat and are adapted for parasitism on leaf-curling aphids. Their hosts can be phylogenetically related or not. Such a complex is represented by *Ephedrus plagiator* (NEES), *Ephedrus persicae* FROGGATT, etc.

Ephedrus persicae FROGGATT is a typical parasite of leaf-curling aphids, occurring in forest habitats exclusively. It seems that it is the anuraphidine group (i. e. its ancestors) of aphids that includes the phylogenetic hosts of this parasite as it infests the greatest part of the anuraphidine genera. It is also known as a common parasite of myzine and aphidine groups that have a similar mode of life as the Anuraphidina.

Ephedrus plagiator (NEES) is a largely specialized species that infests quite a number of aphid groups in forest habitats. It seems that this parasite prefers leaf-curling aphids or such living in dense colonies. It occurs more rarely in intermediate and steppe habitats. Its host range is so wide that it can be hardly determined today to which group of aphids its phylogenetic hosts belong.

Monoctonus cerasi (MARSHALL) is a parasite of various leaf-curling aphids.

Trioxys angelicae (HALIDAY) is a typical parasite of aphids living in dense colonies, preferring members of the Aphidine group. It is a typical inhabitant of forest habitats, occurring more rarely in intermediate habitats.

The Anuraphidina, occurring in steppe habitats on root collars, lower or upper parts of herbs, are infested mostly by largely specialized aphidiid species of steppe habitats — by *Lysiphlebus fabarum* (MARSHALL) and by *Lipolexis gracilis* FÖRSTER.

Lysiphlebus fabarum (MARSHALL) is a largely specialized species, parasitizing especially members of the Aphidiina. It is a typical member of the community in steppe habitats.

Lipolexis gracilis FÖRSTER, on the contrary, occurs also in habitats of intermediate type (edges of woods, orchards) where it infests *Brachycaudus cardui* (LINNAEUS), *Myzus cerasi* FABRICIUS, *Anoecia* spp., on primary host plants; but it prefers a distinctly steppe type of habitats, where it is known as a common parasite of *Aphis* spp. Both species mentioned are typical as parasites of smaller aphids living in dense colonies.

The following parasite of the Anuraphidina seems to represent a specialized species: *Lysiphlebus melandriicola* STARÝ, probably a monophagous parasite of *Brachycaudus lychnidis* LINNAEUS on *Melandrium*.

Diaeretiella rapae (MCINTOSH) infests mostly the Myzine aphids in steppe type habitats.

Aphidius picipes (NEES), too, is a parasite mostly of Myzine aphids in steppe type habitats.

Praon volucre (HALIDAY) is a largely specialized parasite, occurring mostly in forest and intermediate habitats.

The Anuraphidina living on root collars or on roots of herbs in steppe habitats are parasitized by a typical parasite of root aphids: *Paralipsis enervis* (NEES). This parasite attacks the Anuraphidina, the Eriosomatidae and some other groups of root aphids that have a similar mode of life. This parasite is a rather specialized species, and it is hardly possible today to determine its phylogenetic group.

If both complexes of parasites — the forest and the steppe type habitat complexes — are compared, it is remarkable that although the Anuraphidina represent an old and specialized group of aphids, no monophagous species are known as their parasites, except possibly *Lysiphlebus melandriicola* STARÝ. They are parasitized almost exclusively by largely specialized parasite species in both types of habitats in which they occur. Moreover, both complexes of parasites include noticeably few species.

If the fact that the Anuraphidina are primarily a mesophilic group of aphids is taken in consideration, the parasite-complex of forests would be more original, too.

Judging from the host range of different species of this complex, *Ephedrus persicae* FROGGATT seems to be the original parasite of the Anuraphidina in forest habitats, as it infests the greatest part of genera of this group of aphids. It is most probably a parasite that has gradually included in its host range also other aphid groups that have a similar mode of life on primary host plants as the Anuraphidina. A similar conclusion could be made with respect to *Ephedrus plagiator* (NEES), which may be considered as phylogenetically connected with the Anuraphidina, but has gradually transferred its preference to other aphid groups.

As to the Anuraphidina occurring in the steppe habitats, living freely or on roots, it is hardly possible to classify any of their parasites as specialized species. Both *Lysiphlebus fabarum* (MARSHALL) and *Lipolexis gracilis* FÖRSTER are largely specialized species, which distinctly prefer other aphid groups, and the Anuraphidina may be classified only as their subsidiary or facultative hosts. The parasites of root aphids of the Anuraphidina can also hardly be classified as specialized parasites, as *Paralipsis enervis* (NEES) is generally adapted to parasitism on root aphids.

Summary

Aphids of the group Anuraphidina represent a natural group occurring in mesophilic and xerophilic kinds of habitat. Quite a number of anuraphidine species change the type of habitat by migration from primary to secondary host plants. The aphidiid parasites of the Anuraphidina are distinctly differentiated with regard to habitat, so that dioecious aphid species, which change the type of habitat (forest and steppe) by migration, are attacked by complexes of parasites that are typical of a given type of habitat. The given host species, therefore, is attacked by different parasite species depending on the habitat in which it occurs.

Zusammenfassung

Die Aphiden der Gruppe Anuraphidina stellen eine natürliche Gruppe dar, die in mesophilen und xerophilen Lebensräumen auftritt. Eine ganze Anzahl von anuraphidinen Arten ändert den Lebensraum durch Wanderung von primären zu sekundären Wirtspflanzen. Die aphidiiden Parasiten der Anuraphidina sind in bezug auf den Lebensraum deutlich differenziert, so daß diöke Arten von Aphiden, die ihren Lebensraum (Wald oder Steppe) durch Wanderung ändern, von Parasitenkomplexen befallen werden, die für den jeweiligen Lebensraum typisch sind. Die jeweilige Wirtsart wird daher von verschiedenen Parasitenarten befallen, je nach dem Lebensraum, in dem sie auftritt.

Резюме

Тли из группы Anuraphidina образуют естественную группу, которая живёт в мезофильных и ксерофильных биотопах. Многие виды этой группы меняют свой биотоп миграцией с первичных на вторичные растения-хозяины. Паразиты этой группы относительно биотопа чётко дифференцированы, поэтому на виды, которые меняют свой биотоп (лес или степь) путём миграции, напа-

дают комплексы паразитов, которые типически для этого биотопа. Хозяин имеет поэтому разные виды паразитов, в зависимости от биотопа, в котором он живёт.

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