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Specialist and generalist cecidomyiid predators on aphids, mites, scale insects and other invertebrates

ABSTRACT

Published information on predaceous Cecidomyiidae is briefly reviewed and check-lists of the known species of specialist predators on aphids, mites and scale insects are provided. Two species are now used as commercially marketed biocontrol agents, namely *Aphidoletes aphidimyza* (Rondani) against aphids and *Feltiella acarisuga* (Vallot) against tetranychid mites. Larvae of most known species of specialist predators (currently assigned to *Coccodiplosis* De Meijere, *Dentifibula* Felt, *Diadiplosis* Felt, *Dicrodiplosis* Kieffer, *Megommata* Barnes and *Triommata* Barnes) feed on Coccoidea (mealybugs and scale insects). Many species in the large and cosmopolitan genus *Lestodiplosis* Kieffer have been recorded as specialist predators on various invertebrate hosts, including mites, cecidomyiid larvae and lepidopterous caterpillars, but recent observations in the UK indicate that at least some of these 'species' may represent opportunistic general predators feeding on a range of different hosts. Past and present studies of the Cecidomyiidae have been hampered by inadequate taxonomic treatment and there is an obvious need for new biosystematic studies to provide a better information base for further research and application.

Key words: Cecidomyiidae, predators, aphids, mites, scale insects, mealybugs.

1. INTRODUCTION

About 5300 species of Cecidomyiidae have been formally named and described but the cecidomyiid fauna of most parts of the world is still poorly known. There must therefore be many undescribed and unstudied species awaiting discovery and much to be learned about their biology.

The larvae of most known species are either mycetophagous or phytophagous and the latter group includes many major pests of cultivated plants and also species that induce plant galls. Many zoophagous species are also known and in these cases the larvae feed as predators on other invertebrates or, in a few instances, as endoparasitoids.

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The main predaceous species and genera are briefly reviewed here to provide a summary of the present state of knowledge. Good summaries of information on the morphology and biology of Cecidomyiidae and key references to the extensive literature are given in GAGNÈ (1989 and 1994) and a literature review by NIJVELDT (1969) is a useful bibliographic source for information on zoophagous species published before that date. More recent literature is accessible through the CABPESTCD database (CAB INTERNATIONAL, 1992-1997).

2. PREDATORS ON APHIDS

Aphidoletes aphidimyza (Rondani) was first recorded in 1847 when the eminent Italian dipterist, Camillo Rondani, published a detailed description of a gall midge species that he named *Cecidomyia aphidimyza*. He described how he had observed larvae in Italy feeding among aphids on peach, cherry, sowthistle and roses and he stated that he had suspected for a long time that these larvae fed on the aphids and not on the plants. He saw that the cecidomyiid larvae perforated the integument of the aphids with their mouth-parts and sucked out the body fluids, leaving the aphids dead and shrivelled. He also stated quite clearly that this species attacked different aphid species on different plant hosts.

Over the next century, European and North American taxonomists ignored Rondani's observations and described many allegedly new species and genera on the assumption that these predaceous 'species' were narrowly restricted to different aphid hosts. BARNES (1929) recorded 37 specific and 10 generic names that had been applied to aphidophagous cecidomyiids but we now know that most of these are synonyms (HARRIS, 1973). The extent of the taxonomic confusion that masked the true biological situation is indicated by the fact that E. P. Felt, who was for many years the American world expert on Cecidomyiidae, described Rondani's species under seven different names on the same page of one of his publications, which must be some sort of record! Clarification of the situation began, quite appropriately, with a detailed, well-illustrated study of the morphology and biology of larvae, pupae and adults of *A. aphidimyza* by ROBERTI (1946), working in Italy a hundred years after Rondani. This was followed by work in the Netherlands (NIJVELDT, 1954), in the USSR (MAMAEVA, 1964; MAMAEV and KRIVOSHENINA, 1965), in the USA (GAGNÈ, 1971) and in the UK (HARRIS, 1973) and by further detailed morphological and anatomical studies in Italy by SOLINAS (1968).

We now know that *A. aphidimyza* is a specialised predator on aphids, attacking many different species. It was probably European in origin but, with a few exceptions, now occurs world-wide in the cooler temperate and sub-tropical areas where aphids are most abundant. Adults emerge from the soil or other substrates, usually in the early

morning, but are inactive during the day. Mating and oviposition proceed as light intensity falls at dusk and females then search for aphid-infested plants and lay up to 100 eggs each on leaves and stems near aphid colonies. It has been shown by experiment that this host location is so exact that females are able to find a single aphid-infested plant hidden amongst 75 uninfested plants in a greenhouse (EL TITI, 1974). Eggs hatch after 3-4 days and first instar larvae crawl over plant surfaces to search for aphid prey. Once an aphid is found, larvae pierce a leg joint or other body part with their serrated mandibles and inject a toxin that quickly immobilizes the prey. They then digest and imbibe the aphid's body fluids over a few days and feed successively on a number of aphids. After 3-4 days at 21-27°C or up to three weeks at 18°C they are fully fed and about 2.5-3.0 mm long. Development can be completed on as few as 5 large aphids but *Aphidoletes* larvae often kill more aphids than they consume, with a record observed overkill rate of 20 *Phorodon humuli* in 30 minutes (BARNES, 1929). Fully-fed larvae usually go to the soil to pupate in small silken cocoons and pupal development is normally completed in 15-32 days at an average temperature of 18°C. But at lower temperatures larvae diapause in cocoons for six months or more before pupating. This is the normal way of overwintering for natural populations in temperate areas, such as northern Europe, where adults first emerge in May and larvae of successive generations are present on plants until the end of September. *Aphidoletes aphidimyza* has been widely and successfully used as a biological control agent against aphids, especially in glasshouses, but also on outdoor crops. The main target species have been *Aphis gossypii* Glover, *Aphis pomi* De Geer, *Myzus persicae* (Sulzer), *Aulacorthum solani* (Kaltenbach) and *Macrosiphum euphorbiae* (Thomas). Mass production techniques have been developed and the species is available from commercial suppliers in Europe, where it was first used, and in North America. Additional information on this species is available in the Crop Protection Compendium Global Module (CAB INTERNATIONAL, 2001).

A few species related to *A. aphidimyza* are known to be specialist predators on aphids and adelgids (HARRIS, 1973) and one of them has been used in classical biological control of an introduced adelgid pest in North America. All are morphologically similar, but easily distinguished by characters of the third larval instar and of adult males. A number of other species were described from Italy by Del Guercio but have not been recognised again since their original description.

Aphidoletes thompsoni Möhn is a common predator on *Adelges piceae* (Ratzeburg) and *A. nordmannianae* (Eckstein) in Europe and during the 1950s was introduced to the Pacific Northwest (Oregon and Washington States) as part of a biocontrol programme against the balsam woolly aphid, *A. piceae*, which is a major pest of *Abies* spp. A similar, possibly identical, species, *Aph. abietis* (Kieffer), has been recorded preying on *A. abietis* on *Picea* in France and the UK.

Aphidoletes urticariae (Kieffer) is morphologically and biologically similar to *A. aphidimyza* and their aphid host ranges overlap, to the extent that larvae of both species may feed on the same colony of aphids. It probably occurs throughout the northern hemisphere, possibly with a more northerly geographic range than *A. aphidimyza*. It has not been used in biological control but might merit investigation, especially if it can develop at lower temperatures than *A. aphidimyza*.

Monobremia subterranea (Kieffer) is also similar to *A. aphidimyza* but has been placed in a separate, monotypic, genus. It is known only from various countries in Europe and the former USSR and is generally uncommon.

3. PREDATORS ON MITES

Feltiella acarisuga (Vallot) is another species that has a long and confused taxonomic history. It was first described by Vallot in 1827 and by the time of the first thorough revision of this group by GAGNÈ (1995), had been renamed by various taxonomists in four different genera under nine species names. In Europe it was long known as *Feltiella tetranychi* Rübsaamen or *Therodiplosis persicae* Kieffer and, as in the case of *A. aphidimyza*, taxonomic confusion hindered the acquisition of information on its biology.

It is now known to be a specialist predator on tetranychid mites, with a cosmopolitan distribution throughout Europe, the Middle East, Asia and North America. It is also present in New Zealand, where it was probably accidentally introduced. ROBERTI (1954) also pioneered the modern study of this species in Italy and there have subsequently been many additional studies in various parts of the world. Its host range includes a number of pest species, especially the glasshouse red spider mites, *Tetranychus urticae* Koch and *T. cinnabarinus* (Boisduval). Females lay about 30 eggs near mite colonies and the larvae hatch after about a week. They feed for about a week on all stages, but preferably on mite eggs, before pupating in cocoons that they spin on the leaves. The life cycle is completed within about three weeks when temperatures are favourable and in greenhouses, where temperatures are regulated, *F. acarisuga* can be an effective predator throughout the year, especially when used in conjunction with the predatory phytoseiid mite, *Phytoseiulus persimilis* Athias-Henriot, and is particularly effective on tomato plants.

Of the other species dealt with by GAGNÈ (1995), *Feltiella occidentalis* (Felt) is an important natural enemy of tetranychid mite pests of strawberries in California.

4. PREDATORS ON SCALE INSECTS AND MEALYBUGS

This is a large and widespread group of species, some well known but others hardly

known at all. A taxonomic revision on a worldwide basis by HARRIS (1968) provided a basis for morphological studies but has now been much modified, especially at the generic level, by GAGNÈ (1973 and 1994) and a new biosystematic revision is now needed. The following account of the most important genera is therefore a provisional summary. The genera and species recorded as predators on armoured scale insects (Diaspididae) were reviewed by HARRIS (1990) and of the soft scales (Coccidae) by HARRIS (1997).

Coccodiplosis De Meijere

This genus currently contains about seven morphologically distinct species (Table 1), most of which are predators on mealybugs (Pseudococcidae) in Africa and the Pacific. Little is known about their biology and population dynamics but *C. coffeae* is a common predator on mealybug pests of cacao in West and East Africa and *C. smithi* has been recorded as an important predator on mealybugs in the Philippines and Papua New Guinea (HARRIS, 1968).

*Dentifibula F*elt

At least three species of *Dentifibula* have been recorded as predators on *Hemichionaspis* and/or *Aspidiotus* in the USA and Sri Lanka and there are additional unpublished records of this genus from Japan. Records are relatively infrequent and little is known about the biology of the species involved.

*Diadiplosis F*elt

[= *Kalodiplosis* Felt, *Cleodiplosis* Felt, *Olesicoccus* Borgmeier, *Phagodiplosis* Blanchard, *Ghesquierinia* Barnes, *Nipponodiplosis* Harris, *Vincentodiplosis* Harris and probably other genera, such as *Megommata* Barnes (see below)].

This cosmopolitan genus contains at least 25 species (Table 1) all of which are, (with one exception on whiteflies), specialised predators on Coccoidea (scale insects and mealybugs). These predators are essentially tropical and sub-tropical in distribution, as are their hosts. Information on their biology is incomplete and often minimal. The biology of one species, *D. coccidivora* Felt, which occurs in the Caribbean and South America, has been described in some detail by BORGMEIER (1931) and PARNELL (1966). Females lay eggs on ovisacs of *Pulvinaria* and *Saissetia* and larvae feed on the eggs and possibly on immature males. They pupate in the ovisacs and the pupal skins are left protruding from the ovisacs after adults emerge. Adults fly over coccid colonies on hot mornings and evenings and breeding continues while conditions are favourable. Borgmeier observed a colony of *Pulvinaria ficus* for three months and

thought that the coccid was controlled by the midge.

Table 1 - Check-list of *Diadiplosis* predators on Homoptera: Coccoidea.

	Geographic range	Host genera
cocci Felt	St. Vincent	*Saissetia* *Parasaissetia*
coccidarum (Cockerell)	Caribbean	*Pseudococcus* *Planococcus* *Dysmicoccus* *Phenacoccus* *Saccharicoccus* *Dactylopius* *Aspidiotus* *Orthezia* *Parlatoria*
coccidivora (Felt)	Bermuda USA (Florida) Jamaica Panama Argentina	*Saissetia* *Pulvinaria* *Coccus* *Eriococcus* *Alichtensia*
donaldi Harris	Nigeria	*Planococcus*
duni Harris	PNG (New Britain) Indonesia (Java)	*Planococcus*
floridana (Felt)	USA (Florida) Cuba Paraguay	*Hypogeococcus*
hirticornis Felt	Japan USA (introduced)	*Pseudococcus* *Planococcus*
japonicus (Grover and Prasad)	Japan	*Pseudococcus*
koebelei Koebele	Australia New Zealand Hawaii USA (introduced)	*Pseudococcus* *Megaspidiotus* *Nipaecoccus*
megalamellae (Barnes)	E Africa Zaire W Africa	*Planococcus* *Pseudococcus*
multifila (Felt) = *coccidarum* (Felt) [Dicrodiplosis] = *buscki* Felt	Caribbean Guyana Brazil Fiji	*Icerya* *Planococcus*
pseudococci (Felt) = *pseudococci* (Felt)	Mexico Jamaica	*Dysmicoccus*

[*Lobodiplosis*]	Honduras Guatemala Guyana Brazil Hawaii (introduced)	
pulvinariae (Felt) = *moznetttei* (Felt)	USA (Florida) Caribbean Guyana Venezuela	*Philephreda* *Protopulvinaria*
tortuosa Harris	Nigeria	*Pseudococcus*
trinetris Grover and Bahkshi	India	no host data
unca Harris	Nigeria	*Pseudococcus* *Planococcus*
vaupedis (Harris)	Colombia	unidentified coccid

Dicrodiplosis Kieffer

This is another widespread genus with eight species recorded from various parts of the world (Table 2). The best known species is *D. pseudococci*, which was studied in detail by BODENHEIMER and GUTTFELD (1929) and BODENHEIMER (1951). In 1925 it was troublesome in laboratory cultures of *Planococcus citri* in Palestine and was also common in citrus orchards. Development was completed in 40 days at 15.9°C and 10 days at 27.3°C, giving a potential 16-17 generations a year – twice the number of mealybug generations. There seem to have been no further detailed studies of this species but it is known to occur in many countries around the Mediterranean and south as far as northern Nigeria.

Another species, *D. manihoti*, is a predator on the cassava mealybug, *Phenacoccus manihoti* Matile-Ferrero, in sub-Saharan Africa. It is also present in Israel, Iraq, Iran and Yemen where it is a predator on *Planococcus citri, Phenacoccus madeirensis* Green and *Nipaecoccus viridis* (Newstead).

Megommata Barnes

Six species are currently placed in this genus, which is classified in the supertribe Oligotrophidi. It is possible that this is a misplacement as all of the other known predators are included in the supertribe Cecidomyiidi. *Megommata* differs from *Diadiplosis* mainly in having gynecoid antennae and may be closely related to that genus (Gagné, pers. com., 2001). So far as is known, almost all species of *Megommata* are predators on *Pulvinaria* and its geographic range extends from West Africa, through

south-east Asia, to the Philippines.

Triommata Barnes

Two species have been recorded as predators, mainly on mealybugs. These are *T. coccidivora* (Felt) in India and Sri Lanka and *T. coccotroctes* Barnes in Africa. Little is known about their biology.

Species in various other genera (*Arthrocnodax* Rübsaaman, *Epidiplosis* Felt, *Silvestrina* Kieffer) have been recorded as predators on Coccoidea but more and better information is needed before their status can be clearly established.

At least four species of *Lestodiplosis* have been recorded as predators on Coccoidea but this genus is in a state of considerable taxonomic confusion and it is impossible to be certain that these are specialist, not generalist predators (see below).

Table 2 - Check-list of *Dicrodiplosis* predators on Homoptera: Coccoidea.

	Geographic range	Host genera
antennata Felt	USA	*Phenacoccus*
californica Felt	USA	*Pseudococcus*
fulva (Felt)	Sri Lanka India Tanzania	*Saissetia* *Parasaissetia*
guatemalensis Felt	Guatemala Tenerife *	*Dysmicoccus* *
kimberleyensis Harris	South Africa	*Pseudococcus*
manihoti Harris	Congo Senegal Iran Iraq Israel* Oman* Yemen*	*Phenacoccus* *Nipaecoccus* *Planococcus*
pseudococci (Felt)	Italy Spain Morocco Turkey Israel* Saudi Arabia Yemen	*Planococcus* *Nipaecoccus*
quercina (Felt)	USA	??

* New records based on recent identifications supported by voucher specimens in The Natural History Museum, London, and on reassessments of some of the older records that were included in HARRIS (1968).

5. GENERALIST PREDATORS

Lestodiplosis Kieffer

This is a large and cosmopolitan genus containing at least 160 nominal species. Most of these species have been recognised by host associations rather than morphological differences and, although difficult to prove, it seems likely that this approach has masked the existence of a number of opportunistic species that have wide host ranges. Recent studies of the *Lestodiplosis* species present in buds and young growths of oak trees (*Quercus robur* L.) in Wytham Wood, Oxford, UK, have highlighted this problem. Direct observation and circumstantial evidence showed that two morphologically distinct species are opportunistic predators on various invertebrates, including mites, other cecidomyiid larvae and lepidopterous caterpillars, especially *Operophtera brumata* (L.) and *Tortrix viridana* (L.), but attempts to identify the species failed because of the confused taxonomy of the 80 nominal species of *Lestodiplosis* recorded in the Palaearctic Region, 37 of which have been recorded in the UK (COLE and HARRIS, 2002). The species of *Lestodiplosis* that have been recorded as specialist predators on Coccoidea may therefore be much more generalist in their feeding habits but whether or not this is the case can only be proved by further research in which DNA sequencing, used in conjunction with comparative morphology of adults, larvae and pupae, may help to clarify the situation.

BAYLAC (1986), working in France, published the results of a detailed study of the biology and ecology of an unidentified species of *Lestodiplosis* whose larvae prey on the felted beech scale, *Cryptoccus fagisuga* Lindinger, in western Europe. In natural conditions, two peaks of adult emergence occur during the season, the first in May – July and the second in August - September. Females lived for up to six days and laid eggs near colonies of the scale insect. First and second instar larvae fed on hosts by puncturing the integument with their fine mandibles and injecting a clear salivary fluid which caused general paralysis within 5 to 10 minutes. The tissues of the prey were then liquidized and ingested within 3 to 6 hours. Fully fed larvae pupate within the thicker layers of wax produced by the host and development from egg to adult took a minimum of two months during the summer. Larvae of the second generation overwintered in colonies of the scale insect and pupated in the following spring. This may be a common pattern of development of *Lestodiplosis* in temperate areas.

An unusual feature of the species studied by Baylac was the occurrence of a pre-mating nuptial parade by the males which, during the first three hours after emergence, approach females, vibrate their wings and make contact with their antennae before copulating. This was the first occasion on which such behaviour has been recorded in *Lestodiplosis* and merits further study.

Silvestrina Kieffer

This is a monotypic genus containing a single widespread species, *S. silvestrii* Kieffer [= *S. cincta* (Felt)]. This is a generalist predator that has been recorded from mites, scale insects, caterpillars, bees and beetles. It is present in the Americas, Africa, Asia and Europe.

6. EVOLUTION OF ZOOPHAGY

Zoophagy in the Cecidomyiidae seems to have evolved mainly, and possibly solely, in the supertribe Cecidomyiidi of the subfamily Cecidomyiinae. This is the supertribe that also contains most of the phytophagous and mycetophagous species but their phylogenies are still far from being fully understood. The genera reviewed here are currently classified in at least four lineages: Lestodiplosini (*Lestodiplosis*, *Feltiella*, *Arthrocnodax*); Aphidoletini (*Aphidoletes, Monobremia*); and two unplaced sets (*Diadiplosis* / *Megommata* and *Silvestrina*). But these associations are provisional and must be clarified by further biosystematic research. They suggest that zoophagy has evolved on a number of different occasions, which is feasible but as yet unproven. ROSKAM (1985) noted that the zoophagous groups may have evolved polyphyletically from either mycetophagous or phytophagous ancestors but that no conclusion about their origin was possible. That is still the case.

7. CONCLUSIONS

Most of the known predaceous species feed on scale insects and mealybugs and this possibly indicates adaptation to feeding on relatively small and immobile eggs and other stages. But the ability to attack larger and more active hosts is apparent in *Aphidoletes, Monobremia* and *Lestodiplosis.* In *Aphidoletes* the presence of harpoon-like mandibles and a powerful salivary toxin must be adaptations to feeding on more mobile and relatively larger prey. There is also some evidence that *Lestodiplosis* larvae are able to immobilize larger prey by the injection of a toxin.

There are clearly three groups of specialist predators associated respectively with aphids, mites and Coccoidea, which suggests long evolutionary association. That long association is also suggested by the wide geographic ranges of these groups but these may have been substantially influenced by recent inter-continental movements of infested cultivated plants by humans. That certainly seems to be the case with some widespread mealybug species, such as *Planococcus citri*. The generalist predators are less clearly understood but may have interesting effects on the population dynamics of pest and other species.

There is obvious need for further biosystematic studies of both specialist and generalist predators in field and laboratory to obtain better information than is

presently available. The funding of such research may be at least partly justified by the beneficial effects that these predators may have both as natural control agents and as biocontrol agents of pest species. The effective use of *Aphidoletes aphidimyza* and of *Feltiella acarisuga* in commercial biocontrol indicates what can be achieved and there is potential for further developments along these lines.

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9. RIASSUNTO

CECIDOMIIDI PREDATORI SPECIALISTI E GENERALISTI DI AFIDI, ACARI, DIASPINI E ALTRI INVERTEBRATI

Viene presentata una breve rassegna di notizie pubblicate sui cecidomiidi predatori e una check-list di specie note predatrici specializzate di afidi e di cocciniglie. Due specie sono oggi distribuite commercialmente come agenti di controllo biologico: *Aphidoletes aphidimyza* (Rondani) contro afidi, e *Feltiella acarisuga* (Vallot) contro acari tetranichidi. Le larve della maggior parte dei cecidomiidi predatori specializzati (correntemente assegnate ai generi *Coccodiplosis* De Meijere, *Dentifibula* Felt, *Diadiplosis* Felt, *Dicrodiplosis* Kieffer, *Megommata* Barnes and *Triommata* Barnes) si sviluppano a spese di Coccoidei. Molte specie del vasto genere cosmopolita *Lestodiplosis* Kieffer sono state segnalate come predatrici specializzate di svariati invertebrati tra cui acari, larve di altri cecidomiidi e perfino di lepidotteri, ma recenti osservazioni condotte in Inghilterra evidenziano che almeno alcune di queste specie rappresentano generici predatori opportunisti che si alimentano di una serie di vittime differenti. Studi antichi e recenti sui cecidomiidi sono stati penalizzati dalla carenza di accurate determinazioni tassonomiche, ed esiste la necessità di nuovi studi biosistematici atti a fornire conoscenze di base per ulteriori ricerche conoscitive e applicate.

Parole chiave: Cecidomyiidae, predatori, afidi, acari, diaspini, pseudococcidi.

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