BIOLOGICAL CONTROL OF INSECT PESTS: SOUTHEAST ASIAN PROSPECTS

D.F. WATERHOUSE

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Australian Centre for International Agricultural Research
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Foreword

Since its inception in 1982, ACIAR has been a very strong supporter of classical biological control as a key element in the management of exotic arthropod and weed pests. When practiced with appropriate safeguards, it often provides a sustainable and environmentally friendly alternative to the growing use of pesticides, particularly when integrated, if necessary, with the use of resistant plant varieties and cultural controls.

Classical biological control has been very successful in regions of the world (e.g. Australia, California, New Zealand, Oceania) where a large number of the major insect pests and weeds are exotic. This situation applies to a far lesser extent to Southeast Asia but, in a recent survey commissioned by ACIAR, Waterhouse (1993b) identified 40 major arthropod pests that merited evaluation as possible targets for biological control. Not all of these (e.g. the indigenous fruit flies) are attractive targets, but some at least are.

The present volume is a companion to *Biological Control of Weeds: Southeast Asian Prospects* (Waterhouse 1994). It summarises what is known about the natural enemies (principally the parasitoids) of the major exotic insect pests and indicates prospects for their biological control. The aim has been to facilitate, for countries of the region, the selection of promising individual, or collaborative, priority insect pest targets. This should also provide donor agencies with a readily accessible overview of the region's major exotic insect pest problems and with an evaluation, where possible, of prospects for their amelioration by introduction of natural enemies. This should assist in the selection, for support, of projects that are best suited to their individual terms of reference.

R. Clements
Director
Australian Centre for International
Agricultural Research

1 Abstract

Biological control programs have been mounted in some region(s) of the world against 13 of the 16 dossier pests and substantial or partial success has been achieved in one or more countries for 8. On the basis of available information there are good to excellent prospects for reducing, in at least some parts of the region, the damage caused by the following: *Leucinodes orbonalis*, *Nezara viridula*, *Ophiomyia phaseoli* and *Planococcus citri*. There are also good reasons for believing that there will prove to be valuable natural enemies for the following: *Agrius convolvuli, Anomis flava*, *Aphis craccivora*, *Aphis gossypii*, *Diaphorina citri*, *Dysmicoccus brevipes*, *Hypothenemus hampei*, *Phyllocnistis citrella* and *Trichoplusia ni*. There seems to be little prospect for classical biological control of *Dysdercus cingulatus,* too little is known about *Deanolis sublimbalis* and the prospects for control of *Cosmopolites sordidus* are unclear, although its lack of pest status in Myanmar is puzzling.

2 Estimation of biological control prospects

Insect	**Rating**	**Family**	**Any biological control successes**	**Attractiveness as a target in SE Asia**
Agrius convolvuli	7	Sphingidae	yes	medium
Anomis flava	10	Noctuidae	yes	low to medium
Aphis craccivora	15	Aphididae	?	medium
Aphis gossypii	19	Aphididae	yes	medium
Cosmopolites sordidus	13	Curculionidae	?	uncertain
Deanolis sublimbalis	3	Pyralidae	no	uncertain
Diaphorina citri	8	Psyllidae	yes	medium
Dysdercus cingulatus	11	Pyrrhocoridae	no	v. low
Dysmicoccus brevipes	10	Pseudococcidae	yes	medium
Hypothenemus hampeii	12	Scolytidae	yes	medium
Leucinodes orbonalis	15	Pyralidae	no	medium to high
Nezara viridula	10	Pentatomidae	yes	high
Ophiomyia phaseoli	14	Agromyzidae	yes	high
Phyllocnistis citrella	16	Phyllocnistidae	yes	medium
Planococcus citri	7	Pseudococcidae	yes	high
Trichoplusia ni	7	Noctuidae	yes	medium

3 Introduction

Waterhouse (1993b) published information, collected from agricultural and weed experts in the 10 countries of Southeast Asia, on the distribution and importance of their major arthropod pests in agriculture. Ratings were supplied on the basis of a very simple system

+++	very widespread and very important
++	widespread and important
+	important only locally
P	present, but not an important pest

The advantages and limitations of this system were discussed by Waterhouse (1993b). Of 160 insect and mite pests nominated as important in Southeast Asia, a subset of 47 was rated as particularly so.

The aim of the present work has been to summarise information relevant to the prospects for classical biological control of the most important of those of this subset of 47 that are thought to have evolved outside Southeast Asia. The assumption is that many of these have been introduced without some (sometimes without any) of the natural enemies that help to control them where they evolved. The chances are very much lower for arthropod pests that evolved in Southeast Asia of introducing effective, sufficiently host-specific, organisms from outside the region. On the other hand, there is reason to believe that some parasitoids of pests that are thought to have arisen in, or adjacent to, the Indian subcontinent may not yet occur throughout the eastern region of Southeast Asia and several such pests are dealt with.

In regional considerations of this sort, it is to be expected that not all of the top 20, or even the top 10, of any one country's arthropod pests will necessarily be included. Indeed, at least some of those omitted might well merit the production of additional dossiers if they are of such importance locally that a biological control program might be justified. ACIAR would be interested to learn of pests that might be considered in this category.

The summary accounts presented are designed to enable a rapid review to be made of (i) the main characteristics of the principal insect pests of agriculture that are believed to be exotic to part or all of Southeast Asia, (ii) what is known of their enemies, particularly those that have high or moderate levels of host specificity and (iii) what the prospects appear to be for reducing their pest status by classical biological control.

In most instances four databases (and particularly CABI) were searched for relevant information:

AGRICOLA (Bibliography of Agriculture) 1970+
BIOSIS (Biological Abstracts) 1989+
CABI (CAB International) 1972+
DIALOG (Biological Abstracts) 1969+

In addition, in many instances abstracting journals and other published sources prior to the above commencement dates were also searched. Furthermore, useful information was also obtained from other references and from unpublished records. Nevertheless, in many cases the search cannot be described as exhaustive. Even more relevant than attempting an exhaustive search would be a fresh, detailed, field survey targeted on the pest in the region where it is causing problems. This is in order to determine what natural enemies are already present and, in particular, whether any of the organisms that might be considered for introduction are already present.

The species dealt with are drawn from tables 4 and 5 of 'The Major Arthropod Pests and Weeds of Agriculture in Southeast Asia: Distribution, Importance and Origin' (Waterhouse 1993b). It is quite possible that additional arthropod pests rating highly in these tables will prove to be exotic to Southeast Asia (or significant parts of it) and, alternatively, that some considered to be exotic will, on further evidence, be shown to have evolved in the region. The ratings of the pests in the Pacific and Southern China included at the beginning of each dossier are based on information in Waterhouse (1997) and Li et al. (1997).

The natural enemies most commonly selected against insect pests in modern classical biological practice are specific or relatively specific parasitoids. Although predators also clearly play an important role in reducing pest numbers (and have achieved considerable successes against scale insects and mealybugs) the majority of predators attack a wide spectrum of hosts. National authorities responsible for approving the introduction of biological control agents are becoming increasingly reluctant to do so for natural enemies that may possibly have adverse effects on non-target species of environmental significance. For this reason far more emphasis has been placed in the dossiers on parasitoids than on predators.

There appears to be a widespread view that, when biological control alone results in a spectacular reduction in pest populations (as it often does) it is very worthwhile, but a lesser reduction is of little or no value. Nothing can be further from the truth, since far lower levels can have a major impact when integrated with other means of pest control. This applies particularly to integration with the use of plant varieties that are partially resistant to the pest (Waterhouse 1993a).

Plant resistance serves to decrease numbers, in particular by lowering reproductive rate and slowing growth rate. Resistance can be brought about inter alia by alteration of the physical characteristics (e.g. hairiness, cuticle thickness) of the plant and/or its chemical composition. If, as usually occurs, parasitoids and predators are not affected to an equal extent, an improved ratio of natural enemy to the pest will result and the impact of biological control will be increased. This was pointed out many years ago (van Emden 1966; van Emden and Wearing 1965) and is well illustrated by glasshouse tests with the aphis *Schizaphis graminum* on susceptible and resistant barley and sorghum varieties and the parasitoid *Lysiphlebus testaceipes* (Starks et al. 1972). If it is assumed, as in the illustrative example in Figure 1, that the economic injury level is 100 aphids per plant, then neither the resistant variety alone, nor the parasitoid alone will prevent the injury level being exceeded, whereas the combination of resistance and parasitoids achieves this by a wide margin. As another example, biological control of *Myzus persicae* with *Aphidius matricariae* was only effective on chrysanthemums if the variety involved was partly aphid resistant (Wyatt 1970).

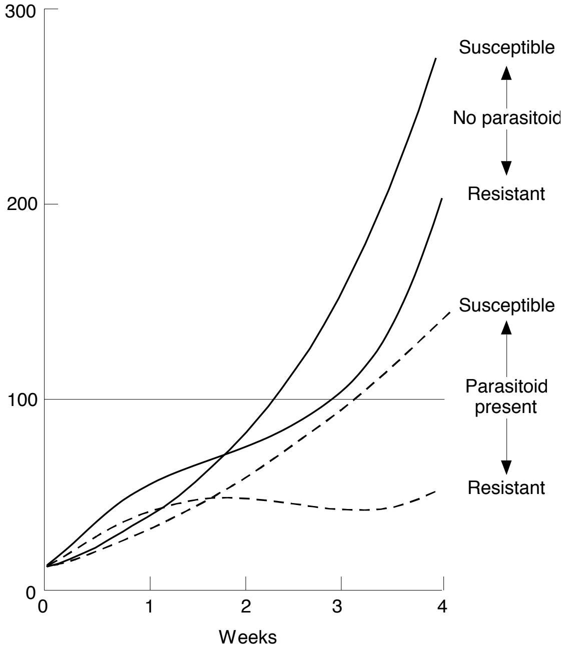

Figure 1. Population growth of *Schizaphis graminum* on susceptible and partly resistant barley in the presence and absence of the parasitoid *Lysiphlebus testiceipes*.

Efforts to achieve pest control by high levels of plant resistance alone may prove counterproductive if significant energy or other resources are diverted by the plant, since they cannot then be used for growth or reproduction. Thus, van Emden (1991) quotes data on 31 pigeon pea varieties screened at the International Crops Research Institute for the Semi Arid Tropics for insect pod damage. These data predicted a 31% yield loss for 90% resistance to insects. To accept a loss of this order is surely an unacceptable 'solution' to the problem, particularly when even a low level of natural enemy attack combined with moderate plant resistance is likely to achieve a far better yield. However, the interaction of resistance and natural enemies may not be a simple one, as pointed out by Wellings and Ward (1994) and such interactions urgently deserve further study. Nevertheless, the fact remains that, when integrated appropriately with plant resistance and other measures, even comparatively low levels of attack by natural enemies can lead to disproportionately large improvements in pest control.

Although the major focus of the dossiers has been on the applicability of the information to biological control in Southeast Asia, much has far wider applicability. In particular, a great deal is relevant to classical biological control in the oceanic Pacific which, until the past few decades, has received almost all its important insect pests from Southeast Asia. A brief tabulation of the distribution and importance of each pest in the Pacific is, therefore, given at the beginning of each dossier. The key to Pacific Country abbreviations is: Fr P, French Polynesia; FSM, Federated States of Micronesia; Kiri, Kiribati; Mar Is, Marshall Islands; N Cal, New Caledonia; PNG, Papua New Guinea; A Sam, American Samoa; Sam, Western Samoa; Sol Is, Solomon Islands; Tok, Tokelau; Tong, Tonga; Tuv, Tuvalu; Van, Vanuatu; W&F, Wallis and Futuna. The key to Southeast Asian countries is: Myan, Myanmar (Burma); Thai, Thailand; Laos; Camb, Cambodia; Viet, Vietnam; Msia, Malaysia; Sing, Singapore; Brun, Brunei; Indo, Indonesia; Phil, Philippines.

In any biological control program it is essential that appropriate procedures are adopted in relation to the selection of suitably host-specific natural enemies, the gaining of approval for introduction and release from the national authorities and safe procedures for eliminating unwanted fellow travellers. Simple *Guidelines for biological control projects in the Pacific* (Waterhouse 1991) are available from the South Pacific Commission, Noumea and FAO has a *Draft Code of Conduct for the Import and Release of Biological Control Agents (1993).*

Because there is a considerable lack of uniformity in the names applied to many of the insects involved, a separate index is included listing the preferred scientific names. These have been used in the text, replacing where necessary those used by the authors quoted. Where the name of an insect used in a publication is no longer preferred by taxonomists, the superseded name, x, is shown thus (= x), but this usage is not intended to convey any other taxonomic message. Indeed, the superseded name may still be valid, but simply not applicable to the particular species referred to by the author.

I am most grateful for assistance from many colleagues during the preparation of this book. It is not possible to name them all, but special thanks are due to a number of CSIRO colleagues, in particular to Dr K.R. Norris for editorial assistance, Dr M. Carver for valuable advice on the *Aphis* dossiers, J. Prance for bibliographic assistance and to several taxonomists, including Dr M. Carver (Hemiptera), Dr P. Cranston (Diptera), E.D. Edwards (Lepidoptera), Dr I.D. Naumann (Hymenoptera) and T. Weir (Coleoptera). Others who have provided valuable information include D. Smith (Queensland Department of Primary Industries), Dr P. Cochereau (ORSTOM, Noumea) and Dr C. Klein Koch (Chile).

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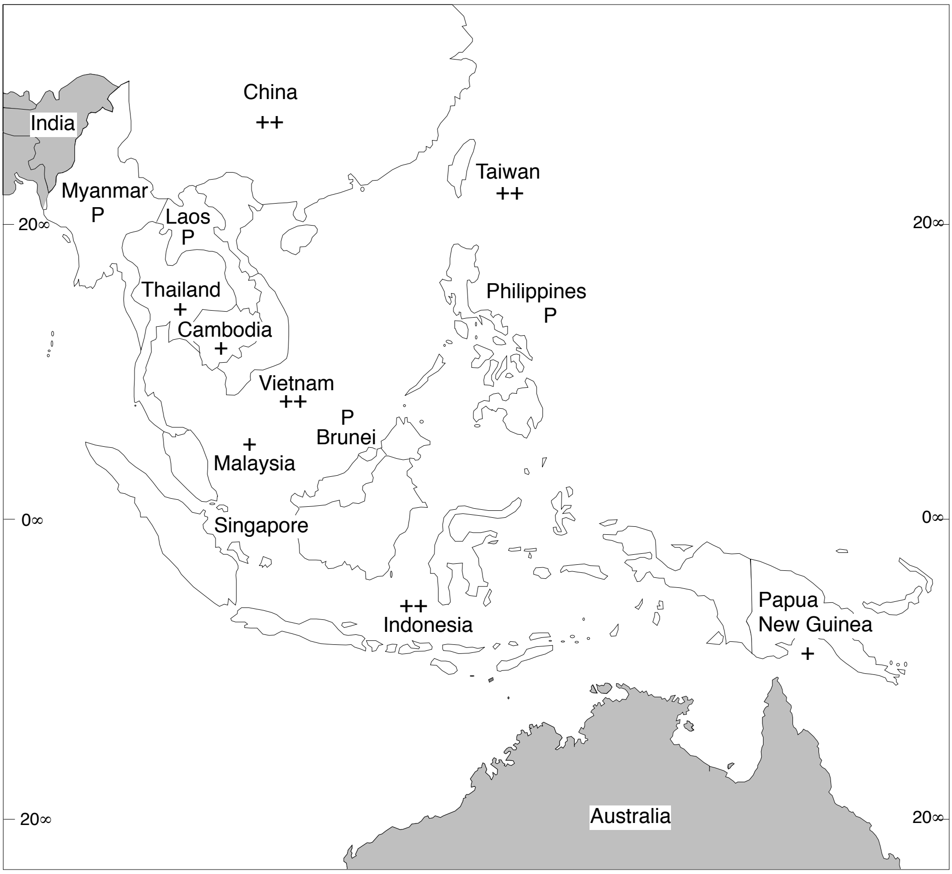
It is again a pleasure to acknowledge, warmly, the expert assistance of Mrs Audra Johnstone in converting my manuscripts into presentable form.

It would certainly not have been possible to continue with these biological control activities long into retirement without the unfailing support, encouragement and forbearance of my wife, to whom my very special thanks are due.

4 Target insect pests

4.1 Agrius convolvuli



The moth *Agrius convolvuli* is widespread in the tropics and subtropics, except for the Americas where it does not occur.

It is an important pest, sporadically, of sweet potato and also attacks several important legumes. For most of the time its populations are maintained at subeconomic levels, apparently by several trichogrammatid egg parasitoids. These could be considered for introduction as biological control agents where they do not already occur. The cause of sporadic outbreaks is unknown.

Agrius convolvuli (Linnaeus)

Lepidoptera: Sphingidae
sweet potato hawk moth, sweet potato hornworm
Synonym: *Herse convolvuli*

Rating

Southeast Asia			China	Southern and Western Pacific		
	++	Viet, Indo	++		+	N Cal, PNG
7	+	Thai, Camb		2		
		Msia				
	P	Myan, Brun			P	Widespread

Origin

Very widespread in tropical and subtropical areas of the world, except for the Americas.

Distribution

Southern Europe: Azores, Crete, Malta, Sicily, Yugoslavia. **Africa**: Algeria, Angola, Benin, Burundi, Cape Verde Is, Congo, Egypt, Ethiopia, Ghana, Ivory Coast, Kenya, Libya, Madagascar, Madeira, Mali, Mauritius, Morocco, Mozambique, Niger, Nigeria, Rwanda, St Helena, Senegal, Seychelles, Sierra Leone, Somalia, South Africa, Sudan, Swaziland, Tanzania, Togo, Tunisia, Uganda, Upper Volta, Zambia, Zimbabwe. **Asia**: Andaman Is, Bangladesh, Bhutan, Cambodia, China, Christmas Is, Cyprus, India, Indonesia, Iran, Iraq, Israel, Japan, Laos, Malaysia, Myanmar, Pakistan, Philippines, Saudi Arabia, Singapore, Sri Lanka, Syria, Thailand, Turkey, Vietnam. **Australasia and Pacific Islands**: Australia, Cook Is, Fiji, Hawaii, Kiribati, Mariana Is, Marquesas Is, New Caledonia, New Zealand, Niue, Norfolk Is, Papua New Guinea, Samoa, Solomon Is, Tonga, Tuvalu, Vanuatu (CIE Map No 451, 1983).

Biology

The smooth eggs are laid singly on stems and leaves and, in common with most other Lepidoptera, *A. convolvuli* larvae have 5 instars. There is a green, a black and a brown form of larvae, which have, at the posterior end, a uniformly curved, tapering, smooth dorsal horn. Fully grown larvae attain a length of 9 cm. Pupation occurs in earthern cells several centimetres below the soil surface. The pupa has a very characteristic proboscis, which is enclosed in a looped tube not fused to the body (Kalshoven 1981; Common

1990). The mean development period at 25°C in Japan was 21.2 days (Setokuchi et al. 1985). In Egypt at 30°C and 61% RH average developmental periods were: larvae 14.4 days, prepupae 1.9 days and pupae 13 days (Awadallah et al. 1976). The moths often enter houses in the evening and, when at rest, resemble pieces of bark. There are at least two generations during summer, and winter is passed as a pupa.

An artificial diet containing powdered sweet potato leaf has been developed (Kiguchi and Shimoda 1994). On this at 27°C and with a day length of 16 hours, *A. convolvuli* larvae moulted to the 5th instar 12 to 14 days after hatching, pupated at 21 to 26 days and adults emerged at 36 to 41 days. The 5th instar larvae grew to 8 cm in length and 11 to 12 g in weight (Shimoda et al. 1994). Consumption of sweet potato leaves was greatest at 30°C, the last instar eating 88% of the total dry weight (5 g) consumed (Setokuchi et al. 1986).

Host plants

The main commercial host is sweet potato (*Ipomoea batatas*), but larvae also attack other *Ipomoea* species [e.g. *I. pescapreae*, *I. cairica*, *I. indica* (morning glory) *I. hederifolia*, (Moulds 1981)] and other Convolvulaceae [e.g. *Merremia dissecta*; bindweed, *Convolvulus arvensis*; Awadallah et al. 1976; (Moulds 1981)]. Several pulses are attacked [e.g. wild mung, *Vigna vexillata* (Govindan et al. 1989); moth bean, *V. aconitifolia* (Bhat et al. 1990); mung bean, *V. radiata* and urd bean, *V. mungo* (Shaw et al. 1989); and also *Phaseolus* spp. (Nagarkatti 1973)]. A strain of moth bean (IPCMO 131) showed good resistance to attack (Bhat et al. 1990). In Papua New Guinea taro is also recorded as a host (Smee 1965).

Damage

A. convolvuli larvae can defoliate sweet potato vines and, even when damage is less severe, harvest is delayed, increasing the likelihood of major attack by the sweet potato weevil, *Cylas formicarius*. Defoliation of pulses results in partial or complete crop failure.

Natural enemies

These are shown in Table 4.1.1.

Table 4.1.1 Natural enemies of *Agrius convolvuli*

Species	Country	Reference
DIPTERA		
PHORIDAE		
Megaselia rufipes	Ireland	Flemying 1918
TACHINIDAE		
Sturmia dilabida	Zimbabwe	Cuthbertson 1934
Zygobothria (= *Argyrophylax* = *Sturmia*) *atropivora*	Malaysia	Corbett & Miller 1933
	Zimbabwe	Cuthbertson 1934
Zygobothria ciliata (= *Sturmia macrophallus*)	Indonesia	Baranoff 1934
	Oman	Whitcombe & Erzinclioglu 1989
	Philippines	Kalshoven 1981
HYMENOPTERA		
BRACONIDAE		
Apanteles spp.	China	Wu 1983
EULOPHIDAE		
species	China	Wu 1983
ICHNEUMONIDAE		
Amblyteles fuscipennis	Central Europe	Fahringer 1922
	England	Morley & Rait-Smith 1933
Charops bicolor	China	Wu 1983
Hadrojoppa cognatoria	Japan	Uchida 1924, 1930
Trogus exaltatorius	England	Morley & Rait-Smith 1933
SCELIONIDAE		
Telenomus sp.	India	Nagarkatti 1973

Table 4.1.1 (cont'd) Natural enemies of *Agrius convolvuli*

Species	Country	Reference
HYMENOPTERA		
TRICHOGRAMMATIDAE		
Trichogramma achaeae	India	Nagarkatti 1973
Trichogramma agriae	India	Nagarkatti 1973
Trichogramma australicum	India	Nagarkatti 1973
Trichogramma chilonis	Guam	Nafus & Schreiner 1986
Trichogramma confusum	India	Nagarkatti & Nagaraja 1978
Trichogramma ?minutum	Indonesia	Leefmans 1929; Kalshoven 1981
Trichogramma sp.	Philippines	Shibuya & Yamashita 1936
FUNGI		
Entomophthora sp. '*grylli*' type	Japan	Kushida et al. 1975

Attempts at classical biological control

A species of *Trichogramma*, possibly *T. australicum,* (Nagarkatti 1973), has been imported on two occasions (Table 4.1.2) to attack the eggs of pest Lepidoptera, including *Agrius convolvuli*, but the resulting impact on populations of the sweet potato hawk moth is not recorded.

Table 4.1.2 Attempts at classical biological control of *A. convolvuli*

Species	From	To	Year	Result	Reference
HYMENOPTERA					
TRICHOGRAMMATIDAE					
Trichogramma ?australicum	USA	Indonesia	before 1929	+	Leefmans 1929; Nagarkatti 1973
Trichogramma ?australicum	Philippines	Japan	1929	+	Shibuya & Yamashita 1936; Nagarkatti 1973

CHINA

In Fujian Province, *A. convolvuli* larvae were parasitised by *Charops bicolor* (Ichneumonidae), *Apanteles* spp. (Braconidae) and eulophid wasps (Wu 1983).

GUAM

A. convolvuli is a minor pest of sweet potato on Guam. When sweet potato was intercropped with maize, *A. convolvuli* eggs were parasitised to the extent of 70 to 100% by *Trichogramma chilonis*. This parasitoid attacks the eggs of a range of sphingids and noctuids, including *Ostrinia furnacalis*, less than 20% of whose eggs on maize were parasitised. *A. convolvuli* colonises new sweet potato plantings as soon as cuttings strike and, by the 4th week, 30 to 60% of its eggs are parasitised. Each large egg produces 13±7 parasitoids, which emerge about 10 days after the host egg is parasitised. It was concluded that *T. chilonis* is a major mortality factor for the sweet potato hornworm (Nafus and Schreiner 1986).

INDIA

A. convolvuli is an occasional pest of sweet potato, *Vigna mungo* and *Vigna radiata*. Eggs are also laid on the leaves of *Colocasia antiquorum* and *Clerodendrum chinense*, but no significant feeding occurs on these latter plants.

Four species of parasitoid attack the eggs of *A. convolvuli* near Bangalore: *Trichogramma australicum*, *T. achaeae*, *T. agriae* and a species of *Telenomus* (Eulophidae). The abundance of each parasitoid varied with the plant species on which the eggs were laid. *T. agriae* was the commonest species in eggs collected on *Colocasia*, followed by *T. achaeae* and

Telenomus sp., up to a total of 43.6%. *T. australicum*, followed by *Telenomus* sp., were the main species emerging from eggs on *Clerodendrum*, up to a total of 63.9%. At no time were *T. achaeae* or *T. agriae* reared from eggs on *Clerodendrum*. Furthermore, *T. australicum* was reared only twice from *Agrius* eggs on *Colocasia*. These results highlight the difficulty of reaching decisions on host specificity on the basis of laboratory trials in a non-natural environment.

Up to 49 *Trichogramma* individuals were reared from a single *A. convolvuli* egg and only in two instances were more than 1 species reared from a single egg. These were 7 *T. agriae* and 4 *T. australicum* on one occasion and 7 *T. achaeae* and 11 *T. australicum* in the second. Eggs parasitised by *Telenomus* sp. usually produced 3 to 5 adults and at no time did a *Trichogramma* emerge from the same egg as a *Telenomus* (Nagarkatti 1973). Later, an additional parasitoid (*Trichogramma confusum*) was recorded from the eggs of *A. convolvuli* on *Clerodendrum chinense* (Nagarkatti and Nagaraja 1978).

Nagarkatti (1973) suggested that the 4 former species might be introduced where *A. convolvuli* is a pest and where they do not already occur.

INDONESIA

Leefmans (1929) reported the parasitisation of *A. convolvuli* eggs by *Trichogramma minutum* imported from America. However, Nagarkatti (1973) suggests that, from the distribution of *T. minutum* at that time, it must have been *T. australicum* or some other species of *Trichogramma*.

IRELAND

An adult *A. convolvuli* produced, soon after capture, many small puparia, from which 76 *Megaselia rufipes* (Diptera, Phoridae) emerged (Flemying 1918).

JAPAN

A species of *Trichogramma* that parasitises the eggs of *Chilo suppressalis* (= *C. simplex*) was imported in 1929 from the Philippines. It was shown to parasitise also the eggs of *A. convolvuli* and 10 other species of Lepidoptera belonging to several families (Shibuya and Yamashita 1936). Nagarkatti (1973) suggests that the species was *Trichogramma australicum*.

OMAN

Adults of the tachinid *Zygobothria ciliata* emerged from puparia from a larva collected on *Ipomoea* (Whitcombe and Erzinclioglu 1989).

SOUTH AFRICA

A. convolvuli is a common pest in the eastern part of South Africa. Although it is generally not abundant, from time to time large areas of sweet potatoes have been almost completely defoliated by it. There are 3 generations a year and overwintering occurs as the pupa. Natural enemies include the white-bellied stork (*Ciconia nigra*) which, on occasion, destroys large numbers of larvae (Anon. 1927).

ZIMBABWE

A. convolvuli larvae on sweet potato were parasitised by the tachinids *Zygobothria atropivora* and *Sturmia dilabida*, both of which are widely distributed in South Africa. The latter parasitoid also attacks larvae of *Spodoptera exigua* (Cuthbertson 1934).

Discussion

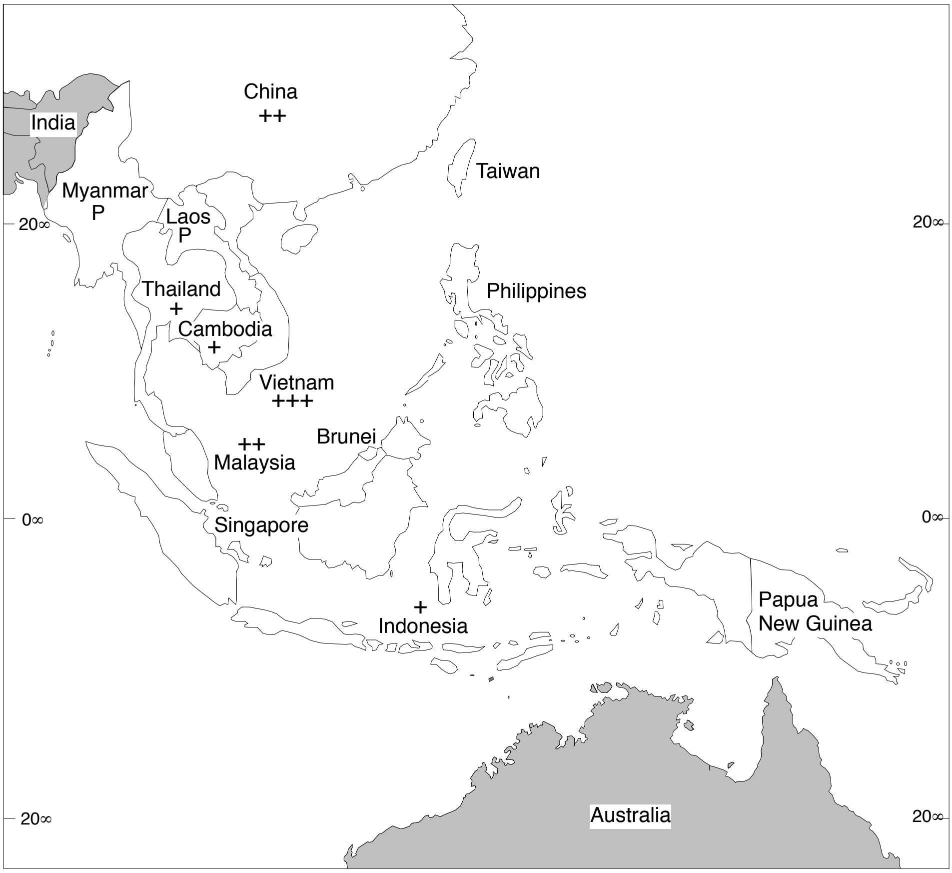
The majority of the parasitoids recorded as attacking *A. convolvuli* also attack the eggs or larvae of a range of other Lepidoptera living in the same environment. Many of these are pest species. Lack of parasitoid specificity is a significant advantage when dealing with a strong flying species, such as *A. convolvuli*, which can travel long distances, since the parasitoids are more likely to be already present on some other host when adult moths arrive to oviposit at a new site. On the other hand, lack of specificity is a disadvantage if the non-target species that are attacked include environmentally important species, the lowering of whose population density is considered undesirable.

In the present instance it is clear, from the information outlined earlier under India that, whereas the *Trichogramma* egg parasitoids involved attack the eggs of a range of species of Lepidoptera, they do so only when the eggs are laid on particular host plants. In this sense they, indeed, display a valuable degree of specificity, which should be taken into consideration when deciding whether or not to proceed with introductions.

With these qualifications it is clear that the establishment, in areas where they do not already occur, of any or all of 4 *Trichogramma* species (*T. achaeae*, *T. agriae*, *T. australicum*, *T. chilonis*) is highly likely to lead to a reduction to (or at least towards) subeconomic levels in the population of *A. convolvuli*.

The underlying causes of the sporadic outbreaks of *A. convolvuli* are unknown. Comparatively little work also has been carried out on the parasitoids and more detailed studies may well reveal attractive new options to pursue.

4.2 *Anomis flava*



The noctuid moth *Anomis flava* occurs widely in Africa, Asia and Oceania, where its larvae sporadically, but seriously, damage cotton, okra, kenaf and other Malvaceae: its adults are fruit-sucking moths. Its sporadic occurrence suggests that it may be under effective biological control for much of the time.

It is attacked by non-specific predators and by a number of parasitoids. Many of the latter attack other Lepidoptera in the same plant environment and appear to be specific to larvae in that environment rather than to individual species inhabiting it.

Further studies are needed to provide information on what the prospects are for classical biological control.

Anomis flava (Fabricius)

Lepidoptera: Noctuidae: Ophiderinae

cotton semi looper, green semi looper, okra semi looper

Synonyms: *Cosmophila flava*, *Cosmophila indica*. *Cosmophila* is now regarded as a subgenus of *Anomis*. *A. flava* does not occur in the Americas, where its equivalent is *Anomis* (*Cosmophila*) *erosa* (Pearson 1958). Records of *A. erosa* in the Asian continent should be referred to *A. flava*.

Rating

Southeast Asia			Southern China	Pacific
	+++	Viet		
10	++	Msia	++	
	+	Thai, Camb, Indo		
	P	Myan, Laos, Phil		present, but not important

Origin

Unclear: could be Africa or Asia. Information available on specific or reasonably specific parasitoids possibly favours Africa.

Distribution

Africa: Central and southern countries, including Angola, Benin, Cameroun, Chad, Congo, Ethiopia, Gambia, Ghana, Ivory Coast, Kenya, Madagascar, Malawi, Mali, Mauritius, Niger, Nigeria, Senegal, Somalia, Sudan, Tanzania, Togo, Uganda, Upper Volta, Zambia, Zimbabwe. **Asia**: Cambodia, China, India, Indonesia, Japan, Korea, Laos, Malaysia, Myanmar, Pakistan, Philippines, Sri Lanka, Taiwan, Thailand, Vietnam. **Australasia** and **Pacific Islands**: Australia, Cook Is, Fiji, Mariana Is, Marquesas, New Caledonia, Papua New Guinea, Samoa, Solomon Is., Tonga, Vanuatu (CIE 1978), Rapa Is, Hawaii (Common 1990).

Biology

Most *A. flava* eggs are laid on the undersurface of leaves, the young larvae are green, those of the last instar measure up to 35 mm in length and bear short, lighter-green longitudinal lines and spots. Young larvae skeletonise leaves, older larvae consume narrow leaf (roselle) cotton leaves and eat irregular holes in broader leaves. Larval survival and growth are greater on hirsutum than on desi cotton (Sidhu and Dhawan 1979; Kalshoven 1981). Pupation occurs in a cocoon spun between leaves. Development times have been recorded on a number of occasions (for examples see Table 4.2.1, also Schmitz 1968; Yu and Tu 1969), egg to adult taking about 3 weeks or a little longer and the number of eggs laid ranging from 158 to 476, depending, in part, upon the larval food plant. Groups of larvae normally pass through 5 moults whereas, when reared singly, up to 22% pass through 6 moults (Kirkpatrick 1963; Essien and Odebiyi 1991). There are 5 overlapping generations a year in Hunan Province, China, but fewer in some other regions (Chen et al. 1991).

Adults rest in foliage by day and are active in the evening: they are attracted to light.

Host plants

A. flava is a major, but sporadic, pest of cotton. Larvae also attack many other plants, mainly in the family Malvaceae. These include, especially, okra (*Hibiscus esculentus*), but also kenaf or Deccan hemp (*H. cannabinus*), jute (*H. sabadariffa*), bele (*H. manihot*), muskmallow an important medicinal plant (*H. abelmoschus*), shooflower (*H. rosa-sinensis*), hollyhock (*Althaea rosea*), *Arbutilon* spp., *Sida* spp. and *Urena* spp. (all Malvaceae). However they also attack tomato (*Lycopersicon esculentum*: Solanaceae); cowpea (*Vigna unguiculata*) and green gram (*Vigna radiata*): Fabaceae; sweet potato (*Ipomoea batatas*): Convolvulaceae; as well as melon (*Citrullus lanatus*), *Macadamia*, *Ricinus*, *Leea* and *Amaranthus* spp. (Kalshoven 1981; Yein and Singh 1981; Croix and Thindwa 1986; Gatoria and Singh 1988; Essien and Odebiyi 1991).

Okra and hemp (kenaf) were the most favoured larval food plants, whereas cotton and okra were the most favourable in terms of pupal weight and adult fecundity (Rao and Patel 1973).

Damage

When abundant, *A. flava* larvae are capable of causing serious damage by destroying the leaves and buds of cotton and other Malvaceous crops. *A. flava* belongs to the subfamily Ophiderinae of noctuids, the adults of which are often fruit-piercing species. In southern China, *A. flava* is reported to be a serious pest of citrus fruit (Li et al. 1997) and, in Korea, *A. flava* is one of a group of fruit-sucking moths observed to damage grapes and pears (Lee et al. 1970).

Table 4.2.1 Average figures (days) for development of *Anomis flava*

	Author				
Stage	**Rao & Patel 1973**	**Kalshoven 1981**	**Ferino et al. 1982a**	**Chen et al. 1991**	**Essien & Odebiyi 1991**
egg development	2		2–3	4–5	2–7
1st instar larva	3				2.4
2nd	1.8				1.8
3rd	1.9		11	12–16	2.2
4th	2				2.2
5th	3				2.3
prepupa	1				1.4
pupa	6.2		6–11		7
egg–adult	21.1	21	19–23	22–29	28
female longevity	31	28	10	4–7	19.8
number of eggs	158	350	492		476
pre–oviposition	1.25		3		3.3
oviposition	6		7		12.4

A. flava is regarded as of only minor importance in the Pacific, which is not surprising since none of its major larval host plants is of much economic importance there.

Natural enemies

Those reported in the literature are listed in Table 4.2.2.

Egg parasitoids are *Trichogramma* spp., which on occasion can be effective: in Mali, 92% parasitisation by *Trichogramma* sp. was recorded in untreated cotton (Pierrard 1970), 12.1% to 15% in the Philippines (Ferino et al. 1982a) and 60 to 80% of eggs on cotton were attacked by *T. dendrolimi* in China (Wang et al. 1985, 1988).

As for larval parasitoids, *Apanteles anomidis* parasitised 27.5% in China (Xie 1984), *Aleiodes aligharensi* and *Aleiodes* sp. together 5.2% in Chad (Silvie et al. 1989), *Charops bicolor* 10.2% in China (Xie 1984), *Meteorus pulchricornis* 4.9% in China (Xie 1984), *Meteorus* sp. 50 to 69.4% in Nepal (Neupane 1977) and *Winthemia dasyops* 2.5% in Chad (Silvie et al. 1989). Most other records did not indicate effectiveness or, if they did, it was lower than 2.5% parasitisation.

A. flava pupae are attacked by at least 5 species of *Brachymeria* (Chalcididae). In Madagascar, *B. multicolor* and *B. tibialis* parasitised 98% of pupae in some fields (Steffan 1958).

Further details are provided in the country summaries. It is not easy to discern a pattern from these although, under some conditions, parasitoids are clearly able to have a major impact on *A. flava* populations.

Less is known about the effectiveness of predators, although pentatomid, carabid, coccinellid, vespid and spider predators have been reported and the Indian mynah bird consumed large numbers of larvae when they were abundant (Khan 1956).

Unexplained disappearance of larvae is often attributed to predation, although heavy rainfall may sometimes be responsible.

Bacillus thuringiensis has been recorded in the field from *A. flava* larvae (Yin et al. 1991) and has given promising control on a number of occasions (Angelini and Couilloud 1972; Delattre 1973; Anon 1976b; Wilson 1981; Chen et al. 1991).

Both granulosis and polyhedrosis viruses have been recorded in the field (Table 4.2.2) and it is possible that virus preparations might be used for control.

Table 4.2.2 Natural enemies of *Anomis flava*

Species	Country	Reference
DERMAPTERA		
CARCINOPHORIDAE		
Euborellia pallipes	China	Yang 1985a
HEMIPTERA		
ANTHOCORIDAE		
Orius minutus	China	Wu et al. 1981
LYGAEIDAE		
Geocoris sp.	China	Wu et al. 1981
NABIDAE		
Nabis sinoferus	China	Wu et al. 1981
PENTATOMIDAE		
Cermatulus nasalis	Australia	Kay & Brown 1991
Eucanthecona (= Cantheconidia) furcellata	China	Wu et al. 1981
Oechalia schellembergii	Australia	Wilson 1981
NEUROPTERA		
CHRYSOPIDAE		
Chrysopa sp.	China	Wu et al. 1981
DIPTERA		
TACHINIDAE		
?Isyropa	India	Maheswariah & Puttarudriah 1956
Cadurcia (= Sturmia) auratocaudata	Nigeria, Gold Coast	Curran 1934
Camplyocheta (= Elpe) sp.	Cameroun	Deguine 1991
Carcelia (= Zenilla) cosmophilae	Australia	Curran 1934, 1938
Carcelia kockiana	India	Sohi 1964
Carcelia illota (= Zenilla noctuae)	Australia	Curran 1934, 1938; Kay & Brown 1991
Cylindromya (= Ocyptera) sp.	Senegal	Risbec 1950

Table 4.2.2 (cont'd) Natural enemies of *Anomis flava*

Species	Country	Reference
DIPTERA		
TACHINIDAE (cont'd)		
Exorista apicalia	India	Sohi 1964
Exorista sorbillans	Australia	Kay & Brown 1991
Palexorista inconspicua (= Sturmia bimaculata)	Africa	Pearson 1958
Palexorista quadrizonula	Africa	Crosskey 1970
	Tanzania	Robertson 1973
Sericophoromyia marshalli	South Africa	Taylor 1930
unidentified	Chad	Silvie et al. 1989
	Philippines	Ferino et al. 1982a
Winthemia dasyops	Chad	Silvie et al. 1989
Zygobothria ciliata (= Sturmia macrophallus)	India	Thompson 1944; Sohi 1964
HYMENOPTERA		
BRACONIDAE		
Aleiodes aligharensi	Chad	Silvie et al. 1989; Silvie 1991
Aleiodes sp.	Chad	Silvie et al. 1989; Silvie 1991
	Philippines	Ferino et al. 1982a
Apanteles anomidis	China	
	Vietnam	Xie 1984; Xiong et al. 1994; van Lam 1996
Apanteles spp.	India	
	Philippines	Maheswariah & Puttarudriah 1956; Sohi1964; Ferino et al. 1982a
Apanteles syleptae	Chad	Silvie et al. 1989; Silvie 1991
Cotesia (= Apanteles) ruficrus	China	Woo & Hsiang 1939
	Fiji	Lever 1943
	Philippines	Ferino et al. 1982a

Table 4.2.2 (cont'd) Natural enemies of *Anomis flava*

Species	Country	Reference
HYMENOPTERA		
BRACONIDAE (cont'd)		
Disophrys lutea	Tanzania	Robertson 1973
Meteorus pulchricornis (= M. japonicus)	China	Chu 1934; Xie 1984
Meteorus sp. *nr fragilis*	Nepal	Neupane 1977
Nyereria sp.	Chad	Silvie et al. 1989
Parapanteles sp.	Chad	Silvie et al. 1989
Protomicroplitis sp.	Chad	Silvie et al. 1989
Sigalphus nigripes	China	He & Chen 1993
CHALCIDIDAE		
Brachymeria nr *aliberti*	Chad	Silvie et al. 1989
Brachymeria lasus (= B. obscurata)	China	Chu & Hsia 1935; Woo & Hsiang 1939
	Philippines	Ferino et al. 1982a
	Vietnam	van Lam 1996
Brachymeria madecassa	Mauritius	Vaissayre 1977
Brachymeria multicolor	Madagascar	Steffan 1958
Brachymeria paolii	Tanzania	Robertson 1973
Brachymeria sp.	Australia	Kay & Brown 1991
Brachymeria tibialis	Madagascar	Steffan 1958
EULOPHIDAE		
Euplectrus manilae	Philippines	Ferino et al. 1982a; Otanes & Butac 1935; Otanes 1935
Tetrastichus howardi (= T. ayyari)	India	Maheswariah & Puttarudriah 1956, Sohi 1964

Table 4.2.2 (cont'd) Natural enemies of *Anomis flava*

Species	Country	Reference
HYMENOPTERA		
EUMENIDAE		
Delta (= Eumenes) pyriforme	Philippines	Ferino et al. 1982a
Eumenes campaniformis	Philippines	Ferino et al. 1982a,b
ICHNEUMONIDAE		
Charops bicolor	China	Xie 1984
Charops sp.	Senegal	Risbec 1950
Echthromorpha agrestoria	Australia	Kay & Brown 1991
Enicospilus ?samoana		Kay & Brown 1991
Enicospilus dolosus	Chad	Silvie et al. 1989; Silvie 1991
Enicospilus sp.	Tanzania	Robertson 1973
Mesochorus sp.	China	Xie 1984
Metopius sp.	Vietnam	van Lam 1996
Xanthopimpla punctata	China	Woo & Hsiang 1939
Zacharops narangae	China	Chu 1934; Woo & Hsiang 1939
TRICHOGRAMMATIDAE		
Trichogramma chilonis	Vietnam	Nguyen & Nguyen 1982
Trichogramma dendrolimi	China	Wang et al. 1985, 1988
Trichogramma minutum	India	Maheswariah & Puttarudriah 1956; Sohi 1964
	Philippines	Otanes & Butac 1935
Trichogramma japonicum	Vietnam	Nguyen & Nguyen 1982
Trichogramma sp.	Australia	Twine & Lloyd 1982
sp.	Mali	Pierrard 1970
spp.	Philippines	Ferino et al. 1982b

Table 4.2.2 (cont'd) Natural enemies of *Anomis flava*

Species	Country	Reference
HYMENOPTERA		
VESPIDAE		
Polistes jokahamae	China	Anon. 1976a
Polistes sp.	China	Anon. 1976a
COLEOPTERA		
CARABIDAE		
Calosoma schayeri	Australia	Twine & Lloyd 1982
Lissauchenius venator	Cameroun	Deguine 1991
COCCINELLIDAE		
Coccinella septempunctata	China	Wu et al. 1981
ARACHNIDA		
Erigonidium graminicolum	China	Wu et al. 1981
Misumenops tricuspidatus	China	Wu et al. 1981
sp. (Oxyopidae)	Philippines	Ferino et al. 1982a
sp. (Thomisidae)	Philippines	Ferino et al. 1982a
NEMATODA		
MERMITHIDAE	India	Mundiwale et al. 1978
not specified	Chad	Silvie 1991
BACTERIA		
Bacillus thuringiensis wuhanensis	China	Yin et al. 1991
VIRUSES		
Granulosis	China	Yin et al. 1991
Polyhedrosis	Australia	Bishop et al. 1978
	Cameroun	Delattre 1973
	China	Liang et al. 1981
	Mali	Atger & Chevalet 1975
	Vietnam	van Cam et al. 1996
AVES		
Acridotheres tristis	India	Khan 1956

Attempts at classical biological control

There appear to have been only two attempts (Table 4.2.3). The pentatomid bug *Podisus maculiventris*, a general predator of lepidopterous larvae, was introduced from USA (where *A. flava* does not occur) and liberated in Anhui Province, China in 1984. However, it failed to become established, possibly due to adverse climatic conditions (Wang and Gong 1987). *Trichogramma minutum* from USA was established, in the Philippines in 1934, but its impact is not recorded (Otanes and Butac 1935).

Table 4.2.3 Attempts at biological control of *Anomis flava*

Species	From	To	Year	Result	Reference
HEMIPTERA					
PENTATOMIDAE					
Podisus maculiventris	USA	China	1984	–	Wang & Gong 1987
HYMENOPTERA					
TRICHOGRAMMATIDAE					
Trichogramma minutum	USA	Philippines	1934	+	Otanes & Butac 1935

AUSTRALIA

Regular releases of *Trichogramma* nr *praetiosum* at the rate of 50000 adults/ha were made from November to March on 8 ha of cotton in south eastern Queensland. The resulting mean rate of egg parasitisation (49.4%) was inadequate to control damage by *Helicoverpa* spp. and the few eggs of *A. flava* collected were not parasitised, although high levels of parasitisation had been reported following the release of the same *Trichogramma* species in northern Western Australia (Twine and Lloyd 1982). Good control on cotton in northern New South Wales was obtained with a mixture of *Bacillus thuringiensis* and chlordimeform at a time at which, except for coccinellids, natural enemies were scarce, although low numbers of spiders and of the pentatomid predator *Oechallia schellembergii* were present (Wilson 1981).

A. flava is one of two major pests of kenaf in northern Queensland and the Ord Irrigation Area of Western Australia, although natural enemies can produce valuable control (Kay and Brown 1991). The tachinids *Carcelia cosmophilae*, *C. illota* and *Exorista sorbillans* attack larvae of *A. flava* and other noctuids. Larvae are also attacked by the predator *Cermatulus nasalis* (Pentatomidae) and the parasitoids *Brachymeria* sp. (Chalcididae), *Echthromorpha agrestoria* and *Enicospilus* ?*samoana* (both Ichneumonidae) (Curran 1938; Kay and Brown 1991).

CHAD

Eleven species of parasitoid, 3 species of hyperparasitoid and nematodes were reared from *A. flava* larvae on cotton (Silvie et al. 1989; Silvie 1991). Total parasitisation never exceeded 25% and, in 1987, 15.7% of 485 *A. flava* larvae were parasitised. Details are shown in Table 4.2.4. The commonest parasitoid was *Aleiodes aligharensi* which, together with *Aleiodes* sp. accounted for nearly a third of all larvae parasitised. Three hyperparasitoids were recorded, about half emerging from species of *Aleiodes*. The most abundant was *Mesochorus (= Stictopisthus) africanus* (Ichneumonidae) followed by *Nesolynx phaeosoma* (Eulophidae) and *Eurytoma syleptae* (Eurytomidae). All three species were also reared from parasitised larvae of other host species (Silvie et al. 1989; Silvie 1991).

Table 4.2.4 Natural enemies of *A. flava* larvae on cotton in Chad

Species	% of total larvae parasitised	Other hosts
Primary parasitoids		
DIPTERA		
TACHINIDAE		
Winthemia dasyops	15.8	*Chrysodeixis acuta*
HYMENOPTERA		
BRACONIDAE		
Aleiodes aligharensi	32.9	*Earias* sp.
Aleiodes sp.		*Helicoverpa armigera*
Apanteles syleptae	1.3	*Syllepte derogata*
Nyereria sp.	1.3	*Syllepte derogata*
Parapanteles sp.	5.3	
Protomicroplitis sp.	3.9	
CHALCIDIDAE		
Brachymeria nr *aliberti*	1.3	
ICHNEUMONIDAE		
Enicospilus dolosus	9.2	
NEMATODA	1.3	
Hyperparasitoids		
ICHNEUMONIDAE		
Mesochorus (= Stictopisthus) africanus	4.0	
Dead parasitoids	23.7	

CHINA

Since 1970 the cultivation of bluish dogbane (*Apocynum venotum*) has increased greatly in Zhejiang Province, where *A. flava* is its most important pest and 43.7% of semilooper larvae were parasitised. There were two braconids, *Apanteles anomidis* (27.5% parasitisation) and *Meteorus pulchricornis* (4.9%); two ichneumonids, *Charops bicolor* (10 to 15%) and *Mesochorus* sp. (2.4%); and an unidentified species (0.54%). *Mesochorus* sp. acted as a hyperparasitoid of *Apanteles anomidis*, but itself parasitised about 1% of *A. flava* larvae (Xie 1984).

Trichogramma chilonis was reared from the eggs of *A. flava* on cotton in Shanxi (Huo et al. 1988). Inoculative releases of *T. dendrolimi* in vegetable gardens adjacent to cotton fields infested with *A. flava* resulted in 61 to 81% parasitisation of its eggs. By comparison, in pesticide-treated fields nearby, parasitisation ranged from 2.5 to 30%. Inundative releases directly in cotton fields led to 30 to 80% parasitisation and no additional control measures were required (Wang et al. 1985, 1988).

Polistes jokahamae and *Polistes* sp. were observed in Hunan Province preying on *A. flava*, the late instar larvae being preferred (Anon. 1976a).

In Hubei Province, the earwig predator *Euborellia pallipes* was reported to reduce *A. flava* larval populations by 38 to 65% (Yang 1985a).

INDIA

Although *A. flava* is generally a minor pest, serious outbreaks occur sporadically. In Hyderabad State more than 1.5 million acres of cotton were affected in one outbreak, with up to 30 larvae per plant consuming everything except branches and bolls. Large numbers of the common mynah were reported eating the larvae (Khan 1956). In Mysore 70% of *A. flava* larvae on cotton in the field were parasitised by tachinid flies and *Apanteles* spp. In the laboratory, eggs were attacked by *Trichogramma minutum* and pupae by *Tetrastichus howardi* (Maheswariah and Puttarudiah 1956).

MADAGASCAR

The non-specific *Brachymeria multicolor* was recorded as producing more than 95% parasitisation of *A. flava* larvae on cotton (Steffan 1958; Delattre 1973). *B. madecassa* was also credited with 50 to 90% parasitisation of larvae in 1956 and 1957 (Vaissayre 1977).

NEPAL

The most important parasitoid of *A. flava* larvae, *Meteorus* sp. nr *fragilis* (Braconidae), was responsible for 50 and 69.4% parasitisation in 1973 and 1974 respectively. There were no pupal parasitoids (Neupane 1977).

PHILIPPINES

High temperatures inhibited and moderate rainfall favoured high populations of *A. flava* on seed cotton, yield being significantly reduced only at densities of 6 to 8 larvae or greater per plant or at damage rates involving at least 60% defoliation. Ten species of natural enemies were recorded, the most important being 2 *Trichogramma* egg parasitoids, a eulophid larval parasitoid, a larval and pupal predator (*Delta* (= *Eumenes*) *pyriforme*) and a pupal parasitoid (*Brachymeria lasus*). Larval disappearance was attributed to predators, including *Eumenes campaniformis* and 2 species of spiders. Egg and pupal parasitisation were generally high during the wet season, whereas larval and pupal predation were higher in the dry season. The major mortality occurred during the larval stage, followed by pupal mortality, with egg mortality being least important. Larval disappearance, suspected to be due to predation, was more important than parasitisation (Ferino et al. 1982a,b).

TAIWAN

A. flava larvae feed on the leaves and buds of kenaf and heavy infestation reduces top growth. There are 3 generations a year, of which the 3rd occurs in July and is the most injurious. In Taiwan the main hosts are cotton and kenaf, although other Malvaceae are attacked (Yu and Tu 1969). The biology of *Eucanthecona furcellata*, a pentatomid predator of *A. flava* larvae, was studied by Chu and Chu (1975).

TANZANIA

Four species of parasitoid were reared from *A. flava* larvae collected from cotton and kenaf. In 1963, 7% and, in 1964, 13.8% of larvae were parasitised. The species involved were the tachinid fly *Palexorista quadrizonula,* which produced 1 to 5 puparia from each parasitised larva and had an average pupal period of 8 days; the ichneumonid *Enicospilus* sp. producing 1 pupa, with an average pupal period of 13 days; and, of lesser importance, the braconid *Disophrys lutea* (1 pupa, 5 days) and the chalcid *Brachymeria paolii* (1 pupa, 11 days). *Palexorista quadrizonula* was also reared from *Spodoptera exigua*, *S. littoralis* and *Xanthodes graellsii* (all Noctuidae); *Enicospilus* sp. from *Helicoverpa armigera;* and *Disophrys lutea* from *Earias biplaga*, *Spodoptera exigua* and *S. littoralis* (Robertson 1973).

VIETNAM

Control of *A. flava* is particularly good in some years due to two naturally occurring egg parasitoids, *Trichogramma chilonis* and *T. japonicum*, 93% parasitisation of eggs being reported (Nguyen and Nguyen 1982; Nguyen 1986).

Major natural enemies

Apanteles anomidis Hym.: Braconidae

A. anomidis is an important endoparasite of *A. flava* in China. It has one generation a year. A mated female lays an average of 109 eggs and prefers to lay in 1st to 3rd instar host larvae. Adults fed on 10% aqueous sugar solution lived about 1.5 days at 29°C (Xiong et al. 1994). An average of 13.7 pupae of *A. anomidis* were obtained from each parasitised *A. flava* larva (Xie 1984).

Palexorista quadrizonula Dip.: Tachinidae

This parasitoid was the most important of 4 species attacking *A. flava* in Tanzania. It is widespread in Africa south of the Sahara and occurs also in the Seychelles and St Helena. It attacks a range of lepidopterous larvae, especially species belonging to the Noctuidae, but also to the Arctiidae, Geometridae, Pyralidae and Tortricidae. In *A. flava* it produces 1 to 5 puparia from each larva, with an average developmental period of 7.9 days (Crosskey 1970; Robertson 1973).

Discussion

Many natural enemies of *A. flava* have been reported, although there have been few studies detailed enough to indicate their true effectiveness. Most of the parasitoids are unlikely to be specific to *A. flava*, but to attack also other lepidopterous larvae feeding on the same host plants. Most of these other hosts are themselves pest species, whose abundance it is desirable to lower. Specificity in these circumstances is rather to lepidopterous larvae in a particular habitat and the parasitoids may thus be sufficiently restricted in their attack on non-target species to be seriously considered as agents for classical biological control. Indeed, for a sporadic pest such as *A. flava*, it is highly desirable that there should be readily available a reservoir of natural enemies present continuously, so as to be in place when populations of *A. flava* start to increase.

The reasons for sporadic outbreaks have not been identified, although Brader (1966) suggested that it might well be due to the application of insecticides resulting in the death of natural enemies.

Table 3 Aggregated ratings of the major invertebrate pests of agriculture in the region.

Order	No. of +s	Pest and + scores	No. times in top 10	Dossier available?	Any biological control successes?	Attractiveness as a target
		30 and over				
1.	41	*Bactrocera* spp.	13	+	+	+
2.	35	*Cosmopolites sordidus*	4	+	+	+ +
3.	34	*Spodoptera litura*	4	+	–	–
4.	32	*Aphis gossypii*	6	+	+	+ + +
5.	31	*Cylas formicarius*	7	+	–	–
6.	30	*Plutella xylostella*	9	+	+	+ + + +
		25–29				
7. =	29	*Crocidolomia pavonana*	4	+	–	+
7. =	29	*Liriomyza* spp.	4	+	+	+ +
9.	27	*Othreis fullonia*	8	+	+	+ + + +
10.	27	*Helicoverpa armigera*	4	+	+	+
11.	26	*Pentalonia nigronervosa*	4	+	–	+
12.	25	*Epilachna* spp.	4	+	+	+ +
13.	25	*Aulacophora* spp.	2	+	–	–
		20–24				
14. =	24	*Nacoleia octasema*	3	+	+	+ +
14. =	24	*Maruca vittrata*	3	+	–	+
16.	24	*Polyphagotarsonemus latus*	1	+	–	–
17.	22	*Agonoxena argaula*	5	+	+	+ + +
18.	22	*Brontispa longissima*	4	+	+	+ + + +
19.	21	*Tarophagus proserpina*	3	+	–	+ + + +
20.	20	*Aleurodicus dispersus*	3	+	+	+ + + +
		15–19				
21. =	18	*Phyllocnistis citrella*	2	+	+	+ + +
21. =	18	*Unaspis citri*	2	–	+	+ + +
23.	17	*Papuana* spp.	5	+	–	+
24.	17	*Adoretus versutus*	4	+	–	–
25.	17	*Dysmicoccus brevipes*	–	+	+	+ +
26.	16	*Euscepes postfasciatus*	3	–	–	–
27.	16	*Halticus tibialis*	2	–	–	–
28.	15	*Oryctes rhinocerus*	3	+	+	+ + + +
29.	15	*Thrips palmi*	3	(+)[a]	–	–
30.	15	*Coccus viridis*	1	–	?	+ +

[a] Walker 1993.

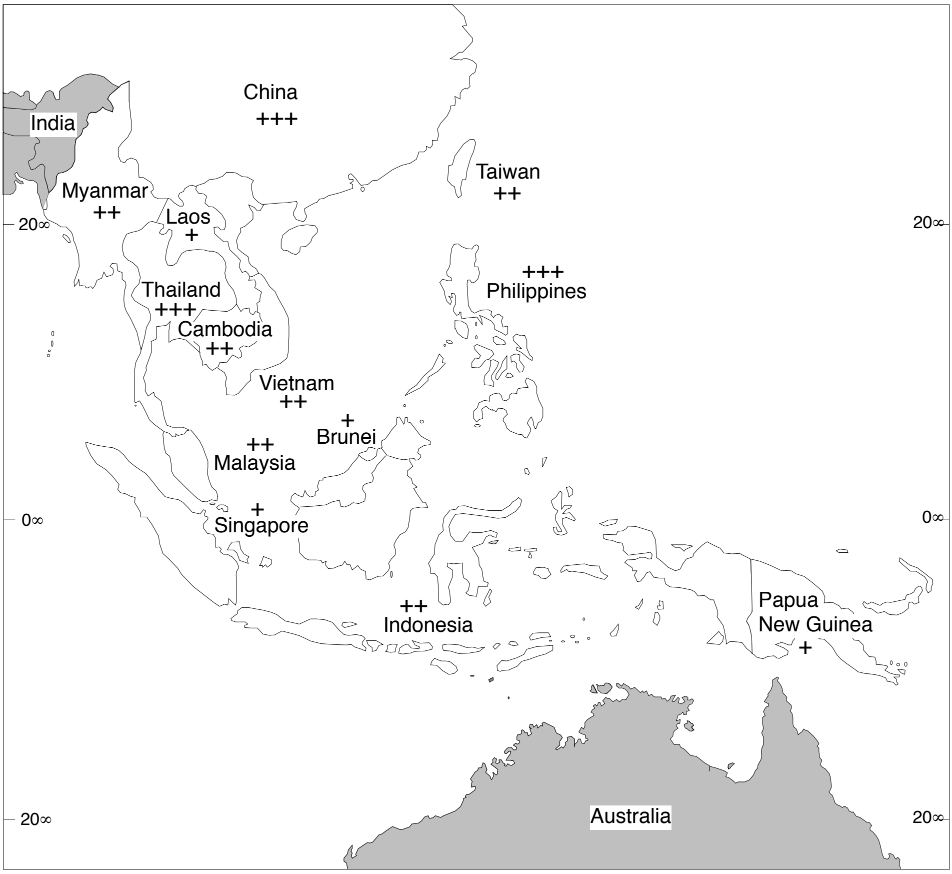
(cont'd over)

Table 3 (cont'd) Aggregated ratings of the major invertebrate pests of agriculture in the region.

Order	No. of +s	Pest and + scores	No. times in top 10	Dossier available?	Any biological control successes?	Attractiveness as a target
		10–14				
31.	14	*Achatina fulica*	2	+	+	+ + + +
32.	14	*Phyllocoptrupa oleivora*	–	–	–	–
32. =	14	*Hellula spp.*	–	+	–	–
32. =	14	*Nezara viridula*	–	+	+	+ + + +
35.	13	*Aspidiotus destructor*	2	+	+	+ + + +
36. =	12	*Graeffea crouanii*	2	+	+	+ + +
36. =	12	*Planococcus pacificus*	2	–	–	+
38.	12	*Earias vittella*	1	–	–	–
39.	11	*Aphis craccivora*	1	+	+	+ +
40.	11	*Tetranycus lambi*	–	–	–	–
41.	10	*Bemisia tabaci*	3	(+)[b]	+	+
42.	10	*Ceroplastes rubens*	1	–	+	+ + +
43. =	10	*Hippotion celerio*	–	–	–	–
43. =	10	*Rhabdoscelus obscurus*	–	–	+	+ +
43. =	10	*Tetranycus marianae*	–	–	–	–
		Still invading				
46.	9	*Bemisia argentifolii*	3	(+)[b]	+	+

[b] De Barro 1995.

4.4 *Aphis gossypii*



The comments under the map of *Aphis craccivora* apply also to *A. gossypii*.

4.4 *Aphis gossypii* Glover

Hemiptera: Aphididae

cotton aphid, melon aphid

Rating

Southeast Asia			**China**	**Southern and Western Pacific**		
	+++	Thai, Phil	+++		+++	Fiji, Guam, Tong, Van
19	++	Myan, Camb, Viet, Msia, Indo		32	++	Cook Is, FSM, Fr P, Kiri, Niue, Sam, Tuv
	+	Laos, Sing, Brun			+	N Cal, PNG, A Sam, Sol Is, Tok, W & F
	P				P	Tuv, Van

Origin

Unclear. Starý (1967a) suggests 'probably steppe areas of the Palaearctic region', possibly inferring southeastern Europe and adjoining regions. The taxonomic status of *A. gossypii* is complex and there are a number of biotypes.

Distribution

A. gossypii is now very widespread throughout warm temperate, subtropical and tropical regions of the world.

Biology

The cotton aphid varies greatly in colour, usually from light green or dark green to almost black but, for older, overcrowded larvae (nymphs) and at high temperatures it is yellow to almost white and the aphids are smaller than on young growth. Wingless females (apterae) vary from 0.9 to 1.8 mm in length and winged females (alatae) 1.1 to 1.8 mm.

In Europe, there is no sexual reproduction, but there is in East Africa, USA, China and Japan. However, in Japan, there are also parthenogenetic overwintering populations (Komazaki 1993). The young generally moult 4 times (range 3 to 5). Their rate of development is influenced by the host plant, cotton being superior to squash. On cotton and squash it takes an average of 4.5 and 6.7 days respectively to the adult stage at about 27°C: there is then a period of about 2 days before nymphs are produced. In this series of experiments females on cotton produced an average of 27 nymphs (range 9 to 43), whereas those on squash produced an average of 14 (range 2 to 35) (Khalifa and Sharaf 1964). Life history data on cucumber is provided by van Steenis and El Khawass (1995).

In U.K., apterae lived 16 days and each produced about 40 offspring. In founding colonies without competition, the 40 progeny could be produced in about 7 days and the total population increased about 10 fold each subsequent week. The rate was reduced as crowding occurred and only then was it possible for the rate of parasitoid increase to exceed that of the aphid (Hussey and Bravenboer 1971).

Host plants

A. gossypii is widely polyphagous. Cotton, in particular, can carry very heavy infestations, as also can various cucurbits (e.g. cucumber, squash, watermelon). In many parts of the world it is one of the most serious of the aphids on citrus. *A. gossypii* also infests beans, egg plant, guava, mango, okra, paprika, potato, taro and numerous ornamentals. In Central and South America it also damages coffee and cocoa.

Damage

As its common and scientific names imply, cotton can be seriously damaged by *A. gossypii*. It can be a major problem and even cause death of the plant at early stages of growth; and a further serious attack may occur when the plant is near maturation and copious production of honeydew can contaminate the cotton lint.

On all of its many hosts, severely attacked leaves curl and young growth is stunted. As populations build up, the upper surface of leaves and fruit becomes contaminated with honeydew, leading to growth of sooty moulds, which is unsightly and interferes with photosynthesis.

For many crops, virus transmission is far more important than direct damage, since even small numbers of migrating aphids can cause serious problems, whereas even large colonies may cause only moderate leaf deformation (Barbagallo and Patti 1983). Although, formerly, it was not an effective vector of citrus tristeza virus, it has now become a dangerous one in USA and Israel. Both adults and nymphs can transmit the virus (Komazaki 1993). *A. gossypii* is also an important vector of a very wide range of other plant viruses.

Natural enemies

Two groups of hymenopterous parasitoids attack (but are restricted to) aphids, a larger one consisting of species belonging to the family Aphidiidae and a smaller group belonging to the family Aphelinidae. Both groups occur worldwide as solitary endoparasitoids. Although many of the species are recorded as having an extensive host range, there is almost always a significant degree of host restriction. Hosts are frequently some (but not all) of the species in a particular aphid genus or several closely related genera. There is good evidence that there are biotypes within some parasitoid species, since populations from some hosts or some areas parasitise a narrower range of hosts than the species as a whole. There may also be differences between biotypes in their preference for the host aphid when feeding on a particular host plant or in a particular habitat. When a parasitoid is abundant on a preferred host it may occasionally attack a nearby non-preferred host, as with *Diaeretiella rapae*, a major parasitoid of the cabbage aphid *Brevicoryne brassicae*, which has occasionally been recorded from both *A. craccivora* and *A. gossypii*, but for which it exhibits a low preference (Dhiman et al. 1983). There are some species (or biotypes of species) that have been found capable of generally causing high levels of parasitisation of *A. craccivora*. Those selected by Starý (1967a, b) are shown in bold italics in table 4.4.1 and might be considered first as potential species for biological control introductions to areas where they do not already occur. Valuable reviews of the effectiveness of aphid parasitoids are provided by Carver (1989), Hagen and van den Bosch (1968) and Hughes (1989).

Although many coccinellids, syrphids, chrysopids, hemerobiids and a few predator species from other insect families attack aphids, their impact in regulating populations is generally regarded as disappointing, although they must certainly at times limit economic damage. The efficiency of a predator depends upon its searching ability and effectiveness in capturing prey. The numbers of predators seem to be greatest when aphid numbers are already declining after a peak in abundance and, thus, their apparently great impact at that time may actually have little significance in population regulation. Predators can increase rapidly in numbers only after their prey has become sufficiently abundant, so there is an important time lag between prey and predator numbers (Hemptinne and Dixon 1991).

Coccinellids have been used successfully for the biological control of several, relatively sessile, coccid pests, whereas results have generally been poor against aphids. One of the reasons is that adult coccinellids and their larvae are poor at capturing other than first instar aphids (Dixon 1989). Indeed, the survival of newly-hatched beetle larvae is very dependent upon the abundance of young aphids, so there is a need for coccinellids to lay eggs very early in the development of aphid colonies. Oviposition late in aphid population development may result in older larvae starving from lack of food and the comparatively poor searching ability of coccinellids for low aphid populations aggravates the situation (Hemptinne and Dixon 1991). Another reason is that coccinellids disperse when prey populations fall to low levels.

Adults of most aphidophagous syrphids are attracted to, and lay their eggs in or close to, large aphid colonies, the number of eggs deposited increasing as aphid density increases (Chandler 1967). Syrphid larvae also generally become abundant when the aphid colony is already declining. The larvae of the aphidophagous cecidomyiid *Aphidoletes aphidimyza* appear to have adequate host specificity to be acceptable for biological control introductions. The species has a high degree of density dependence, kills more aphids than it consumes and is less affected than many other predators by insecticides (Meadow et al. 1985).

Chrysopids and hemerobiids are more effective than many other predators at capturing prey and are likely to be more efficient predators at low aphid densities.

A particular problem with most predators is that they are highly polyphagous. They will almost always attack a very wide range of non-target insects, some of which are likely to be of environmental concern. Regulatory authorities responsible for approving import permits to a country are becoming increasingly reluctant to do so, unless an adequate degree of specificity has been demonstrated and this is occasionally possible.

For the above reasons, no attempt has been made to assemble lists of the many generalist predators recorded as attacking (or probably attacking) *A. craccivora* or *A. gossypii* in the field, although a few facts about their activities are recorded in the segments dealing with individual countries in order to provide an entry into the literature. Abstracts of many additional papers are available in CABI's Review of Agricultural Entomology and its predecessor Review of Applied Entomology, Series A. The major parasitoids of *A. gossypii* are listed in Table 4.4.1.

Table 4.4.1 Parasitoids of *Aphis gossypii*

	Country	Reference
HYMENOPTERA		
APHELINIDAE		
Aphelinus abdominalis	China	Shi 1980
(= †*Aphelinus* sp. nr *flavipes*)	Guam	Fulmek 1956
	India	Ramaseshiah & Dharmadhikari 1969
(= *Aphelinus flavipes*)	Shanghai	Shi 1980
Aphelinus asychis	Italy	Ferrari & Nicoli 1994
Aphelinus chaoniae	Italy	Ferrari & Nicoli 1994
Aphelinus gossypii (= *Aphelinus kashmiriensis*)	Australia	Carver et al. 1993
	Cook Is	Walker & Deitz 1979
	Hawaii	Timberlake 1924; Yoshimoto 1965
	India	Bhat 1987
	Japan	Takada & Tokomaku 1996
	Tonga	Carver et al. 1993; Stechmann & Völkl 1988
Aphelinus humilis	Australia	M. Carver pers. comm.
Aphelinus mali	China	Shi 1985
	India	Ramaseshiah & Dharmadhikari 1969
	Senegal	Risbec 1951; Fulmek 1956
	Shanghai	Shi 1980
	Taiwan	Takada 1992
	Trinidad	Bennett 1985
Aphelinus paramali	Israel	Zehavi & Rosen 1988
Aphelinus semiflavus	USA	Hartley 1922; Spencer 1926; Oatman et al. 1983b; Trumble & Oatman 1984
Aphelinus varipes (= *A. nigritus*)	Transcaucusus	Fulmek 1956
	USA	Wharton 1983

Table 4.4.1 (cont'd) Parasitoids of *Aphis gossypii*

	Country	Reference
HYMENOPTERA		
APHELINIDAE (cont'd)		
Aphelinus sp.	Colombia	Ramirez & Zuluaga 1995
2 × spp.	India	Ramaseshiah & Dharmadhikari 1969
	Japan	Takada 1992
APHIDIIDAE		
†****Aphidius colemani***	Angola	Starý & van Harten 1972
	Argentina	Starý 1967a, 1972
	Australia	Carver & Starý 1974; Room & Wardhaugh 1977
	Chile	Prado 1991, Starý 1975
	China	Xi & Zhu 1984
	Egypt	Selim et al. 1987
	India	Starý 1972; Agarwala et al. 1981
	Japan	Starý 1967a
	Kenya	Starý & Schmutterer 1973
	Mozambique	Starý & van Harten 1972
	Pakistan	Starý 1975
	Réunion	Starý 1975
	Tonga	Carver et al. 1993
	Uruguay	Starý 1975
	Venezuela	Cermeli 1989
†*Aphidius ervi*	Morocco	Fulmek 1956
	Uzbekistan	Starý 1979
Aphidius floridaensis	USA, West Indies	Starý 1967a,b

Table 4.4.1 (cont'd) Parasitoids of *Aphis gossypii*

	Country	Reference
HYMENOPTERA		
APHIDIIDAE (cont'd)		
****Aphidius gifuensis***	China	Shi 1980; Takada 1992
	Hawaii	Mackauer & Starý 1967; Takada 1968
	India	Raychaudhuri 1990
	Japan	Mackauer & Starý 1967; Takada 1968, 1992
	Korea	Mackauer & Starý 1967; Takada 1992
	Taiwan	Mackauer & Starý 1967
Aphidius urticae (= *Aphidius lonicerae*)		Börner et al. 1957
Aphidius matricariae (= *Aphidius phorodontis*)	Brazil	Starý 1967a
	Canada	Starý 1967a
	Chile	Prado 1991
	Germany	Mackauer 1962b
	India	Agarwala et al. 1981; Agarwala 1983
	Italy	Starý 1976
	Lebanon	Tremblay et al. 1985
	Pakistan	Starý & Ghosh 1983
	Peru	Starý 1967a
	Tunisia	Halima-Kamel 1993
	USA	Starý 1967a
		Börner et al. 1957
Aphidius picipes	China	Li & Wen 1988; Xi & Zhu 1984
Aphidius similis	India	Agarwala et al. 1981
Aphidius sonchi		Börner et al. 1957
†*Aphidius uzbekistanicus*	India	Raychaudhuri 1990; Takada 1992

Table 4.4.1 (cont'd) Parasitoids of *Aphis gossypii*

	Country	Reference
HYMENOPTERA		
APHIDIIDAE (cont'd)		
†*Aphidius* spp.	India	Agarwala et al. 1981
Cristicaudus nepalensis	India	Raychaudhuri 1990; Takada 1992
†*Diaeretiella rapae*	India, Japan	Agarwala et al. 1981; Takada 1992
	Tunisia	Halima-Kamel 1993
	USA	Starý 1967a
	Uzbekistan	Starý 1979
†*Ephedrus nacheri*	China, Japan, Europe	Takada 1968, 1992
†****Ephedrus persicae***	India	Agarwala et al. 1981, Takada 1992
	Iraq	Al-Azawi 1970
	Korea	Takada 1972b; Chou 1981; Paik 1975
	Lebanon	Tremblay et al. 1985
	Taiwan	Chou 1981b
	USA	Schlinger & Hall 1960
	USSR	Starý 1970
†*Ephedrus plagiator*	India	Raychaudhuri 1990
	Uzbekistan	Starý 1979
	Japan,	Takada 1992
	Korea, Taiwan	Paik 1975; Chou 1981b
	USSR	Starý 1970
****Lipolexis gracilis***	China	Shi 1980; Xi & Zhu 1984; Takada 1992,
	Europe	Starý 1970
	Hong Kong	Takada 1992
	India	Raychaudhuri 1990
	Japan	Takada 1992
	Lebanon	Tremblay et al. 1985
	Shanghai	Shi 1980
	Taiwan	Chou 1981b, Takada 1992

Table 4.4.1 (cont'd) Parasitoids of *Aphis gossypii*

	Country	Reference
HYMENOPTERA		
APHIDIIDAE (cont'd)		
†*Lipolexis scutellaris* (= *Lipolexis pseudoscutellaris*)	Hong Kong	Takada 1992
	India	Starý & Ghosh 1975; Agarwala et al. 1981; Pramanik & Raychaudhuri 1984; Raychaudhuri 1990; Takada 1992
	Malaysia	Ng & Starý 1986; Takada 1992;
	Philippines	V.J. Calilung pers. comm. 1995
	Vietnam	Starý & Zelený 1983
Lysaphidus schimitscheki	India	Raychaudhuri 1990
****Lysiphlebia japonica***	China, Japan Korea, Taiwan	Takada 1968, 1992; Paik 1975; Chou 1981; Tian et al. 1981; Xi & Zhu 1984
Lysiphlebia mirzai	Vietnam	Starý & Zelený 1983; Takada 1992
†****Lysiphlebus fabarum*** (= *Lysiphlebus ambiguus* = *Lysiphlebus cardui* = *Lysiphlebus confusus*)	Algeria, Bulgaria, Corsica, Israel, Italy	Starý et al. 1975; Starý 1976
	Egypt	Selim et al. 1987
	Europe	Starý 1970
	Greece	Santas 1978
	Iraq	Al-Azawi 1966
	Japan	Takada 1992
	Lebanon	Tremblay et al. 1985
	Morocco	Starý 1967a
	Pakistan	Hamid et al. 1977
	Tunisia	Halima-Kamel 1993
	USA	Starý 1967a
	USSR	Starý 1967a; Lyashova 1992
	Uzbekistan	Starý 1979
Lysiphlebus shaanxiensis	China	Chou & Xiang 1982

Table 4.4.1 (cont'd) Parasitoids of *Aphis gossypii*

	Country	Reference
HYMENOPTERA		
APHIDIIDAE (cont'd)		
†****Lysiphlebus testaceipes***	Chile	Prado 1991
	Colombia	Fulmek 1956; Vergara & Galeano 1994
	Cuba	Starý 1967b, 1981
	France	Starý et al. 1988a,b
	Guadeloupe	Starý et al. 1987
	Haiti	Fulmek 1956
	Hawaii	Starý 1967a
	Italy	Tremblay & Barbagallo 1982
	Mexico	Starý & Remaudière 1982
	Spain	Starý et al. 1988a,b;
	Portugal	Costa & Starý 1988; Starý et al. 1988c
	Trinidad	Bennett 1985
	USA	Spencer 1926; Schlinger & Hall 1960; Starý 1970; Oatman et al. 1983b; Trumble & Oatman 1984
	Venezuela	Cermeli 1989
	West Indies	Starý 1967b
Lysiphlebus sp.	Argentina	Fulmek 1956
	Colombia	Ramirez & Zuluaga 1995
	Hawaii	Fulmek 1956
	India	Agarwala et al. 1981
	Pakistan	Mohyuddin & Anwar 1972, 1973
	Portugal	Boelpaepe et al. 1992
	USA	Fulmek 1956
†*Praon abjectum*	India	Raychaudhuri 1990; Takada 1992
Praon absinthii	India	Agarwala et al. 1981
†*Praon exsoletum*	Uzbekistan	Starý 1979

Table 4.4.1 (cont'd) Parasitoids of *Aphis gossypii*

	Country	Reference
HYMENOPTERA		
APHIDIIDAE (cont'd)		
Praon myzophagum	India	Agarwala et al. 1981
†*Praon volucre*	Lebanon	Tremblay et al. 1985
	Tajikistan, Uzbekistan	Starý 1979
†*Praon* sp.	India	Agarwala et al. 1981
	Uzbekistan	Starý 1979
Toxares macrosiphophagum	India	Raychaudhuri 1990; Takada 1992
†*Trioxys acalephae*	China	Takada 1992,
	India	Agarwala et al. 1981
†*Trioxys angelicae*	Corsica, Greece, Iraq, Italy,	Starý 1976; Santas 1978
	Israel, Morocco	Al-Azawi 1970
	Israel	Rosen 1967b
	Lebanon	Hussein & Kawar 1984; Tremblay et al. 1985
	Tunisia	Halima-Kamel 1993
†*Trioxys asiaticus*	Iran, Tajikistan, Uzbekistan	Starý 1979
†*Trioxys auctus*	USSR	Fulmek 1956; Mackauer & Starý 1967
	Uzbekistan	Starý 1979
Trioxys basicurvus	India	Agarwala et al. 1981; Raychaudhuri 1990; Takada 1992
Trioxys communis	China	Shi 1980, 1985
	Japan, Korea, Taiwan	Paik 1976; Chou 1981a; Lu & Lee 1987; Takada 1992
	Philippines	V.J. Calilung pers. comm. 1995
Trioxys complanatus	Uzbekistan	Starý 1979
Trioxys equatus	India	Samanta et al. 1985; Raychaudhuri 1990

Table 4.4.1 (cont'd) Parasitoids of *Aphis gossypii*

	Country	Reference
HYMENOPTERA		
APHIDIIDAE (cont'd)		
†****Trioxys indicus***	China	Tian et al. 1981, Xi & Zhu 1984
	India	Starý & Ghosh 1975; Agarwala et al. 1981; Agarwala 1983,1988; Raychaudhuri 1990; Takada 1992
	Taiwan	Chou 1981b, Takada 1992
Trioxys nr *pallidus*	Morocco	Fulmek 1956
Trioxys rietscheli	China, India	Shi 1980; Raychaudhuri 1990
Trioxys rubicola	India	Agarwala et al. 1981
Trioxys sinensis	Pakistan	Mohyuddin et al. 1972
†*Trioxys* sp.	Portugal	Börner et al. 1957; Boelpaepe et al. 1992
	Taiwan, USA	Fulmek 1956
ENCYRTIDAE		
Aphidencyrtus sp.	Malaysia	Yunus & Ho 1980
PTEROMALIDAE		
Pachyneuron aphidis	China	Shi 1987
DIPTERA		
CECIDOMYIIDAE		
Aphidoletes aphidimyza	Chile, Europe, Nth America	Harris 1973; Kocourek et al. 1993, Meadow et al. 1985; Prado 1991
Endaphis maculans	Trinidad	Kirkpatrick 1954
	USA	Tang et al. 1994; Yokomi et al. 1994

Table 4.4.1 (cont'd) Parasitoids of *Aphis gossypii*

	Country	**Reference**
ACARINA		
TROMBIDIIDAE		
Allothrombium pulvinum	China	Dong et al. 1992 Xu et al. 1993 Zhang et al. 1993; Zhang & Chen 1993

*Starý (1967a, 1970) selected these species (bold type) for possible introduction to areas where they do not occur.

†Also recorded from *Aphis craccivora*

Under humid conditions, high aphid mortality may result from fungal infection. The two species commonly reported are *Neozygites fresenii* and *Cephalosporium* (= *Verticillium*) *lecanii* (Table 4.4.2), although about a dozen species may be involved (Hagen and van den Bosch 1968). Effective use of the above fungi has been made under glasshouse conditions and *V. lecanii* is available commercially for this purpose. However, in Florida this fungus has performed poorly on *A. gossypii* compared with against *Myzus persicae* (Osborne et al. 1994).

Table 4.4.2 Fungi attacking *Aphis gossypii* and/or *A. craccivora*

	Country	**Reference**
Arthrobotrys sp.	USA	O'Brien et al. 1993
Beauveria bassiana	USSR	Pavlyushin & Krasavina 1987
Cephalosporium lecanii	Japan	Masuda & Kikuchi 1992;
	Netherlands	Saito 1988
	USA	Yokomi & Gottwald 1988; Sopp et al. 1990; Vehrs & Parrella 1991; Schelt 1993
	USSR	Cermeli 1989
	Venezuela	Pavlyushin & Krasavina 1987
Entomophthora exitialis	India	Kranz et al. 1977
Entomophthora sp.	Chile	Prado 1991
Neozygites fresenii	Australia	Milner & Holdom 1986
	Chad	Silvie & Papierok 1991
	China	Zhang 1987
	Cuba	Hernandez & Alvarez 1985
	USA	Steinkraus et al. 1991, 1995, 1996; O'Brien et al. 1993; Steinkraus & Slaymaker 1994; Smith & Hardee 1996
Paecilomyces fumosoroseus	USSR	Pavlyushin & Krasavina 1987

Attempts at biological control

There have been many intentional and unintentional transfers of aphid parasitoids, which have influenced the populations of *A. craccivora* and *A. gossypii* in different regions of the world. However, the majority of intentional transfers have been aimed at other target aphid pests. Some deliberate attempts against these two species have been unsuccessful (Table 4.4.3). Overall, however, there is little doubt that, where parasitoids have become established, the situation is better, sometimes significantly better, than if they were not present, even if the level of control may not be as effective as is desirable. There is little doubt that, in many regions, an improved situation is likely to occur if additional parasitoid species are established.

AUSTRALIA

Aphidius colemani is capable of producing rapid decreases in populations of *A. gossypii* on cotton and, of carrying this to extinction in association with high densities of *Harmonia octomaculata* (= *Coccinella arcuata*) and *Coccinella transversalis* (= *C. repanda*) (Room and Wardhaugh 1977). Three species of parasitoid were imported in the hope that, as polyphagous species, they would contribute to the biological control of several species of pest aphid. The principal target for two of the species was *A. craccivora*, which is very sporadic in occurrence in Australia. It was hoped that, in the unpredictable absence of *A. craccivora*, the parasitoids would continue to breed and survive in other hosts.

Lysiphlebus testaceipes (from *Aphis nerii* in California) and *L. fabarum* (from Greece and Turkey) were imported as biological control agents of *A. craccivora* on legumes, mass reared, and released in 1982 and 1983 in New South Wales and Victoria. Both parasitoids readily parasitised *A. craccivora*, *A. gossypii* and some other aphid species in the laboratory. The releases coincided with a prolonged drought during which there were no *A. craccivora* available on legume crops. Releases were, therefore, made on *A. gossypii* infesting *Hibiscus* bushes. No parasites were recovered the following year from either *A. craccivora* or *A. gossypii*, although *L. testaceipes* became established in *Aphis nerii* on oleander (*Nerium*) (Hughes 1989). *L. fabarum* was not recovered. It was concluded that the parasitoids must have been unsuitable biotypes (Carver 1984, 1989).

Table 4.4.3 Releases for the biological control (inter alia) of *Aphis craccivora* and/or *A. gossypii*

Parasitoid	From	To	Year	Result	Reference
Aphelinus varipes	South Carolina	California		+	Wharton 1983
Aphelinus abdominalis	India	U.K.		+	Hussey & Bravenboer 1971
Aphidius colemani	S. Brazil	France	1982	+	Rabasse 1986
	Australia	Tonga	1990	+	Carver et al. 1993; Wellings et al. 1994
Lysiphlebus fabarum	France, Italy, Greece, Turkey	Australia	1982, 1983	-	Carver 1984, 1989
Lysiphlebus testaceipes	USA	China	1983	+	Zheng & Tang 1989
	USA	Hawaii	1923	+	Beardsley 1961
	USA	India	1966	?	Ramaseshiah et al. 1969; Sankaran 1974
	USA	Australia	1982	+	Carver 1984; Hughes 1989
	Cuba	France, Italy	1973	+	Rabasse 1986; Starý et al. 1988a,b
	Czechoslovakia	Tonga		-	Stechmann & Völkl 1988; Völkl et al. 1990
	Hawaii	Pakistan	1972	?	Anwar 1974; Mohyuddin & Anwar 1972, 1973, Mohyuddin et al. 1971
	Mexico	USSR	1989	+	Shiiko et al. 1991
	USA	China	1983	+	Zheng & Tang 1989
Trioxys indicus	India	Australia	1986	-	Carver 1989; Sandow 1986

Praon volucre was imported from the Mediterranean area for the biological control of *Hyperomyzus lactucae*, a vector of lettuce necrotic yellows. It was mass reared and released in 1981 and 1982, mainly in New South Wales and Victoria. It has not been recovered from mainland Australia, but is reported to be present in Tasmania. In laboratory trials it successfully parasitised a number of pest aphids that occur in Australia, including *A. craccivora*.

In 1986 *Trioxys indicus* was introduced from India and released in Western Australia, Victoria and New South Wales against *A. craccivora* (Carver 1989), but establishment did not occur.

Although he gives no further details Mohammad (1979) states that parasitisation of *A. craccivora* in Adelaide soon after colonisation frequently prevented the establishment of a colony.

CHINA

Zhang (1992) recorded for *A. gossypii* on cotton in China more than 48 species of natural enemy (belonging to 19 families in 9 orders). Coccinellids, spiders and lacewings were the most important predators of this and other pests in cotton fields. Nan et al. (1987) record attack on *A. gossypii* and other cotton pests by 5 species of pentatomid, 9 species of coccinellid, 4 species of lacewing and 36 species of spider. The dominant predators studied by Wu (1986) were found to vary according to the season and included the coccinellids *Coccinella septempunctata*, *Hippodamia variegata*, *Propylea japonica*, *Harmonia axyridis*, the lacewings *Chrysopa* (= *Chrysoperla*) *sinica, Chrysopa formosa*, *C. pallens* (= *C. septempunctata*), *C. intima* and the spiders *Erigonidium graminicolum*, *Misumenops tricuspidatus* and *Xysticus croceus*. Zhang (1985) carried out laboratory tests on the daily consumption of *A. gossypii* by *Scymnus hoffmanni*, *Chrysopa sinica* and the spider *Erigonidium graminicolum*. Ma and Liu (1985) reported on the effectiveness and seasonal fluctuations of *Propylea japonica* and Yang (1985b) on its laboratory rearing. Ding and Chen (1986) examined the predation pattern of *Chrysopa sinica*. *Propylea japonica*, *Scymnus hoffmanni* and spiders (especially *Theridion octomaculatum* and *Erigonidium graminicolum*) were major enemies of *A. gossypii* on cotton in Hunan Province. The spiders (2.6 to 26 per 100 plants) were present from late June to late August and were relatively unaffected by the weather. Coccinellid populations fluctuated somewhat with the season. Reproduction of *A. gossypii* was inhibited and its damage reduced when the ratio of total natural enemies to aphids was 1:50 or the ratio of coccinellids was 1:140. Since 1978, cotton fields over large areas have not been treated with insecticides before August, in order to safeguard the natural enemies which now hold the aphids in check (Mao and Xia 1983). Zhao et al. (1989) report that the lycosid spider *Pardosa astrigata* is an important predator in cotton fields and Dong (1988) that the coccinellid *Harmonia axyridis* was an effective natural enemy when present in adequate numbers. Other predators include the anthocorid bug *Orius minutus* (Miao & Sun 1987), the coccinellids *Scymnus hoffmanni* (Zhao and Holling 1986), *Propylea japonica* and *Harmonia axyridis* (Zou et al. 1986; Lei et al. 1987).

The aphidiid *Aphidius picipes* (= *A. avenae*) parasitised more than 80% of *A. gossypii* individuals on Chinese cabbage growing near cotton fields (Li & Wen 1988). Laboratory studies showed that *Trioxys communis* was more effective than *Aphelinus mali* in suppressing *A. gossypii* populations (Shi 1985). Of the 5 species of parasitoid recorded by Xi and Zhu (1984) on *A. gossypii* on cotton in Jiangsu Province, *Lysiphlebia japonica* and *Trioxys indicus* were dominant and each accounts for about 45% of all parasitoids. In the laboratory, female *L. japonica* laid an average of 120 eggs and produced a parasitisation rate of up to 14%. In the field it overwinters as larvae inside *A. gossypii*, *A. craccivora* or *Myzus persicae*. In an earlier study Tian et al. (1981) recorded the same two parasitoids on both *A. craccivora* and *A. gossypii* with a combined parasitisation rate of 13%. This did not provide effective control and it was pointed out there was heavy attack by hyperparasitoids, such as *Aphidencyrtus* sp. (Encyrtidae).

Larvae of the mite *Allothrombium pulvinum* have been observed attacking *A. gossypii* in cotton fields (Zhang and Chen 1993; Zhang et al. 1993).

COLOMBIA

Aphelinus sp. caused 2.2% and *Lysiphlebus* sp. 0.3% parasitisation of *A. gossypii* on cotton in the field (Ramirez and Zuluaga 1995).

CUBA

Aphis craccivora is a common pest of vegetables and many other crops and also occurs on wayside trees, such as *Gliricidia*. In beans and other annual crops it occurs for a short period only, whereas on wayside trees it is present more or less continuously. The native parasitoid *Lysiphlebus testaceipes* parasitises the aphid heavily on *Gliricidia*, but poorly or not at all on young beans. This appears to be primarily a matter of the relative rates of dispersal of the aphid and its parasitoid (Starý 1970).

EAST ASIA

A list of parasitoids recorded from *A. gossypii* in East Asia is shown in table 4.4.1 in which most entries from this region are based on Takada (1992). The most comprehensive information within this region is available from Taiwan (Starý and Schlinger 1967; Tao and Chiu 1971; Chou 1984), Japan (Takada 1968; Takada and Yamauchi 1979; Takada unpublished) and India (Raychaudhuri 1990). For Southeast Asia, there are two records from

Vietnam and one from Malaysia. In so far as one can argue from such scanty data, the principal parasitoids of *A. gossypii* in the Far East (*Trioxys communis*, *Lysiphlebia japonica* and the particular species involved of *Aphelinus*) do not occur in India (Takada 1992). According to Takada, the principal species attacking *A. gossypii* in India is *Trioxys indicus*, which is recorded from Taiwan, but apparently not from Japan. Another species attacking *A. gossypii* in India is *Lipolexis scutellaris*, which also occurs in Vietnam, Malaysia and Hong Kong, but is not recorded elsewhere in the Far East (Takada 1992). Two widely distributed and effective parasitoids that attack *A. gossypii* in other parts of the world (*Aphidius colemani* and *Lysiphlebus testaceipes*) do not yet seem to be present in Southeast Asia, although *A. colemani* is recorded from the field in Pakistan (Starý 1975). Takada (1992) comments on the habitat specialisations in Japan of parasitoids of *A. gossypii*, which occurs in both open and lightly wooded habitats: *Trioxys communis*, and *Aphelinus* species prefer the open habitat, whereas *Lysiphlebia japonica*, *Ephedrus nacheri*, *E. persicae* and *E. plagiator* prefer the lightly-wooded habitat. Thus, the parasitoid complex on *A. gossypii* on cucumber, egg plant or taro is quite different from that on *Hibiscus* or *Rhamnus* in a garden.

FRANCE

Starý et al. (1973) reviewed the parasitoids of aphids in France. A South American strain of *Aphidius colemani,* which is adapted to warm subtropical conditions and is highly polyphagous, was introduced from southern Brazil and released against *Toxoptera aurantii* in France near Antibes in 1982. It is reported to be established (Rabasse 1986; Tardieux and Rabasse 1986). In 1973–74 *Lysiphlebus testaceipes* was introduced into France and released near Antibes and in Corsica. It was recovered soon after, and later in Italy. It was also sent to eastern Spain where it established and spread to become the predominant parasitoid in the regions where it occurs. It attacks *A. gossypii* on citrus and a number of other aphids on other host plants (Starý et al. 1988a).

INDIA

Including the widespread *Trioxys indicus*, 14 parasitoids were recorded from *A. gossypii* (a preferred host) and 8 from *A. craccivora* (Agarwala 1983). *Ephedrus persicae* is reported to be confined in India to *A. craccivora* and 3 parasitoids, *Praon absinthii*, *Trioxys basicurvus* and *T. rubicola* confined to the *A. gossypii* complex (Agarwala et al. 1981).

The impact of the widespread parasitoid *Trioxys indicus* on *A. craccivora* feeding on pigeon pea was studied in the laboratory and the field. The parasitoid had a high searching ability and exhibited a density dependent relationship with its host. A single female oviposited in 100 to 150 aphids in 3 to 5 days after emergence and the life cycle occupied 15 to 20 days. Early in the season 9.4% of the aphids were parasitised, rising to a peak of 64.6% two months later and resulting in suppression of the aphid population. *Trioxys indicus* has a relatively narrow host range, which includes *A. gossypii, A. craccivora* and the oleander aphid *A. nerii*. Up to 2.4% of the parasitoids were hyperparasitised by a cynipoid wasp. Singh and Sinha (1983) concluded from these studies that *T. indicus* had most of the necessary attributes of a potentially effective biological control agent for *A. craccivora* and *A. gossypii*.

Ramaseshiah and Dharmadhikari (1969) found *Aphelinus abdominalis* (= *A. flavipes*) to be one of the important parasitoids of *A. gossypii* in India; furthermore, that *Aphelinus* sp. nr *abdominalis* had *A. craccivora* as a preferred host, but also attacked *A. gossypii*.

Many generalist predators attack *A. gossypii* and other aphids in India, and Agarwala and Saha (1986) record 8 species attacking it there on cotton. Seven species of predatory coccinellid, 2 syrphids and a chrysopid were recorded preying on *A. gossypii* on potatoes. *Coccinella septempunctata* and *Cheilomenes* (= *Menochilus) sexmaculata* were the most important (Raj 1989). *A. gossypii* was reported to be controlled on sunflower by coccinellids (Goel and Kumar 1990). The aphidophaghous coccinellid *Micraspis discolor* showed a preference for *A. craccivora* (Agarwala et al. 1988).

The biology of the predatory *Leucopis* species (Diptera) attacking both *A. craccivora* and *A. gossypii* on chrysanthemums is described by Kumar et al. (1988). Larvae of *Chrysopa orestes* had a substantial effect on *A. gossypii* on eggplant (Bhagat and Masoodi 1986).

Raychaudhuri et al. (1979) record three predatory spiders: *Cyclosa insulana* (Araneidae) attacking *A. craccivora* and *A. gossypii*; *Theridion* sp. (Theridiidae) attacking *A. craccivora;* and *Uloborus* sp. (Uloboridae) attacking *A. gossypii*.

IRAQ

A. gossypii is parasitised on melons, cotton and okra by *Lysiphlebus fabarum* which, in turn, is attacked by the hyperparasitoids *Pachyneuron aphidis* (Pteromalidae), *Dendrocerus* (= *Lygocerus*) sp. (Megaspilidae), *Aphidencyrtus* sp. (Encyrtidae) and *Alloxysta* (= *Charips*) sp. (Charipidae) (Al-Azawi 1966).

ISRAEL

A. gossypii occasionally infests citrus in the vicinity of cotton fields. Based on small samples, it was found to be attacked by only one parasitoid, *Trioxys angelicae* (Rosen 1967a,b).

ITALY

A. gossypii in particular, but also *A. craccivora*, are two of the 10 aphid species attacking citrus. Eleven species of aphidiine parasitoids provide a considerable measure of biological control (Tremblay 1980). *Lysiphlebus testaceipes* (particularly) and *L. fabarum* are the commonest species and together may attain a parasitisation rate of 90% to 100%.

The most important predators are coccinellids, of which *Scymnus* spp. are common amongst colonies of *A. gossypii*. Together with *Coccinella septempunctata* and other natural enemies, they may quickly suppress a cotton aphid population. Chrysopid, syrphid and cecidomyiid larvae are less effective although, in the absence of coccinellid larvae, syrphid larvae may be important. *A. gossypii* is under biological control on citrus in orchards where pest management procedures are adopted (Barbagallo and Patti 1983; Starý 1964). Recent papers on natural enemies of *A. gossypii* in Italy have been published by Ferrari and Burgio (1994) and Ferrari & Nicoli (1994).

JAPAN

Amongst numerous predators reported on *A. gossypii* by many authors are *Coccinella septempunctata* (Nozato and Abe 1988) and *Scymnus hoffmanni* (Kawauchi 1987).

KOREA

The consumption of *A. gossypii* by larvae of the coccinellid *Harmonia axyridis* was studied by Choi and Kim (1985).

Eight species of parasitoid (and 6 of hyperparasitoid) of *A. craccivora* were reported by Chang and Youn (1983). The more important species (and rates of parasitisation) were *Lysiphlebus fabarum* (31.6%), *Lipolexis scutellaris* (18.8%), *Lysiphlebia japonica* (16.7%) and *Adialytus salicaphis* (11.4%). Of 509 field collected, mummified aphids 44.8% produced parasitoids and 43.8% hyperparasitoids giving an overall parasitisation rate of 88.6%.

MALAYSIA

The only record of parasitoids of *A. craccivora* or *A. gossypii* appears to be that of Ng and Starý (1986). *Lipolexis scutellaris*, an oriental species with a wide distribution in India and extending to Vietnam, southern China and Taiwan, was recorded from both aphid hosts. *Trioxys communis*, also an oriental species, was rarely found, but only on another aphid species (*Aphis spiraecola*). At least 3 unidentified species of aphelinids were bred and in large numbers, but no other information on these is provided.

NETHERLANDS

A valuable review of the biological control of *A. gossypii* in glasshouses, with special reference to the situation in the Netherlands, is provided by van Steenis (1992). van Steenis (1995) evaluated 4 aphidiine parasitoids for biological control of *A. gossypii* on glasshouse cucumbers. *Aphidius colemani* performed the best (72 to 80% parasitisation), followed by

Lysiphlebus testaceipes (26%), *Ephedrus cerasicola* (23%) and *Aphidius matricariae* (less than 5%). The general principles of selection and establishment of species are relevant elsewhere, although only the first of the three species selected (*Lysiphlebus testaceipes*, *Aphidius matricariae*, *Ephedrus cerasicola*) would appear to be particularly relevant to Southeast Asia or the Pacific.

PAKISTAN

In investigations from 1967 to 1970, 6 parasitoid species and 22 predator species were recorded attacking *Aphis craccivora* on a range of leguminous crops and weeds in 5 climatologically different zones of Pakistan (Hamid et al. 1977). Alate *A. craccivora* were found on soybean (*Glycine max*), but colonies of apterous aphids never developed, possibly due to the presence of abundant plant hairs.

Aphelinus abdominalis (= *A. basalis*), which was widespread and active throughout the year, parasitised from 0.6% to 17.6% of *A. craccivora*, the level depending upon host plant, location (hills, foothills or plains) and season. Perhaps due to its small size, *A. abdominalis* was the only parasite that attacked *A. craccivora* under the covering of hairs on *Phaseolus aureus*. The period from oviposition in the aphid to mummy formation was 3 to 4 days and adult wasps then emerged in 5 days. *Trioxys ?sinensis* parasitised up to 21.3% of aphids. Development from oviposition in the aphid to mummy formation took 14 to 16 days and adults emerged 4 to 7 days later. *Lysiphlebus fabarum* parasitised between 1.3% and 72.9% of available hosts, *Ephedrus* nr *cerasicola* 1.3% to 1.4% and *Aphidius absinthii* 11%. A low level of attack on most of the parasitoids was recorded by the hyperparasitoids *Alloxysta* sp. and *Pachyneuron* sp.

Ants (*Monomorium indicum* and *Pheidole* sp.) were associated with over 90% of the aphid colonies. The size of *A. craccivora* on *Vicia faba* nursed by ants was far greater than those not attended and aphid mortality was higher when ants were absent. The most abundant of 22 predator species (Table 4.4.2) were *Cheilomenes sexmaculata*, *Coccinella septempunctata* and *Syrphus* spp.

In the same environment *Trioxys sinensis* and *Lysiphlebus fabarum* parasitised *Aphis gossypii* on cucumbers and on *Hibiscus esculentus* (Hamid et al. 1977).

PHILIPPINES

A. craccivora is commonly attacked by *Lipolexis scutellaris;* and *A. gossypii* by this species and also *Trioxys communis*. Both parasitoids also attack other species of aphids, but not the banana aphid *Pentalonia nigronervosa* (V.J. Calilung pers. comm. 1995).

RÉUNION

A. craccivora is parasitised by *Aphidius colemani* on *Gliricidia maculata* and by *Aphelinus* sp. on *Vigna unguiculata*. In turn *Aphelinus* sp. is parasitised by *Syrphophagus africanus* and *Pachyneuron vitodurense*. *A. craccivora* is also attacked by the coccinellid predators *Scymnus constrictus* and *Platynaspis capicola* (Quilici et al. 1988).

SHANGHAI

The main parasitoids of *A. gossypii* on cotton were *Trioxys communis*, *T. rietscheli* and *Lipolexis gracilis*. Next in importance was *Aphidius gifuensis*, and there was occasional attack by *Aphelinus abdominalis* and *A. mali*. The highest total parasitisation recorded was about 27%. Parasitoids constituted 22.7% of the emergences from aphid mummies and the hyperparasitoids *Syrphophagus aphidivora* 45.2%, *Alloxysta* sp. 15.1%, *Pachyneuron aphidis* 14.7% and *Dendrocerus* 2.3%. The number of parasitoids only exceeded that of hyperparasitoids during the first half of August (Shi 1980, 1987).

TONGA

Aphidius colemani and *Lysiphlebus testaceipes* were introduced from cultures in Czechoslovakia for the biological control of the banana aphid *Pentalonia nigronervosa* (Stechmann and Völkl 1988, 1990; Völkl et al. 1990), but there is no indication that they became established. *A. colemani* from a culture originating from a garden in Canberra was introduced again in 1990 and recovered in 1992 from *Aphis gossypii* on taro, but not from the banana aphid. The further introduction of Aphidiidae, which are obligate parasitoids of aphids, was recommended since they could assist in the control of pest aphids and not pose a threat to non-target insects (Carver et al. 1993). Although 15 aphid species are recorded in Tonga including *A. craccivora*, by 1993 no aphids other than *A. gossypii* had been recorded as hosts of *A. colemani*, although recent monitoring has not been possible. Two other primary parasitoids were recorded, *Aphelinus gossypii* (from *Aphis gossypii*) and *Lipolexis scutellaris*, from a single female, free on a banana sucker (Carver et al. 1993; Wellings et al. 1994).

Three common and widespread aphid predators were recorded (the syrphid *Ischiodon scutellaris*, the coccinellid *Harmonia octomaculata* and the hemerobiid *Micromus timidus*) in addition to 11 tramp species of ants (Carver et al. 1993).

USA

Lysiphlebus testaceipes parasitised 74.5% of *Aphis gossypii* on strawberries and *Aphelinus semiflavus* a smaller number. Seven hyperparasitoids were reared (Oatman et al. 1983b). *L. testaceipes* was considered by Schlinger and Hall (1960) to be the most effective aphid parasitoid in southern California and to give excellent control there of *Aphis gossypii*. At least 8 hyperparasitoid species were also reared (Schlinger and Hall 1960).

Entomopathogen infection was the primary cause of a reduction in *A. gossypii* population that occurred during the week after peak aphid abundance on cotton in Mississippi and continued pathogen activity, combined with predation, maintained aphids at a low density for the remainder of the season. Early in the season parasitisation and predation may have reduced aphid population growth (Weathersbee and Hardee 1993, 1994).

In untreated cotton plots small predators (spiders and *Geocoris* spp.: Hemiptera, Lygaeidae) had the greatest impact on *A. gossypii* populations and the parasitoid *Lysiphlebus testaceipes* was never abundant. Fungi killed many aphids and constituted the most important natural enemy factor in insecticide treated plots (Kerns and Gaylor 1993). Fungi attacking *A. gossypii* in USA include *Neozygites fresenii* (Steinkraus et al. 1992, 1993a,b,c; Sanchez-Pena 1993, Smith and Hardee 1993) and *Cephalosporium* (= *Verticillium*) *lecanii* (Sopp et al. 1990, Yokomi and Gottwald 1988). The coccinellid predators *Hippodamia convergens* and *Scymnus louisianae*, the chrysopid *Chrysoperla carnea*, and *Syrphus* sp. were effective in reducing populations of *A. gossypii* in Texas (Vinson and Scarborough 1989). In Alabama the hemerobiid *Micromus posticus* is an important predator (Miller and Cave 1987).

USSR

In southern USSR coccinellid beetles are important predators of aphids. Adult *Coccinella undecimpunctata* and larvae of *Hippodamia variegata* are the most voracious and prefer *A. gossypii*, whereas *Coccinella septempunctata* prefers *A. craccivora* (Belikova and Kosaev 1985).

There are many papers dealing with the control of *A. gossypii* and associated pests in glasshouses. The lacewing *Chrysoperla carnea* was effective only when released at a predator: aphid ratio of 1:20, whereas *Chrysopa sinica* was effective at 1:50 (Shuvakhina 1983). Other predators utilised include *Chrysopa perla* (Ushchekov 1989) and the cecidomyiid *Aphidoletes aphidimyza* (Begunov and Storozhkov 1986). Under conditions of high humidity, high aphid mortality was caused by the fungi *Cephalosporium lecanii*, *Beauveria bassiana* and *Paecilomyces fumosoroseus* (Pavlyushin and Krasavina 1987).

VIETNAM

A. gossypii was one of four aphids surveyed for parasitoids by Starý and Zelený (1983), but the number of aphidiid species found (2) was surprisingly low. *Lipolexis scutellaris* was commoner than *Lysiphlebia mirzai*. The former parasitises a number of other *Aphis* species, including *Aphis spiraecola* (= *A. citricola*), *A. craccivora* and *A. nerii*. Some unidentified aphelinid parasitoids were also present.

Starý and Zelený (1983) suggest that *Lipolexis scutellaris* may be a valuable species for transfer elsewhere and also that Vietnam would benefit from the introduction of additional parasitoid species.

The major parasitoid species

General features of the Aphidiidae

Different populations of many Aphidiidae have differing biological properties and are often known as biotypes, i.e. contrasting groups, each consisting of individuals of the same species. Biotypes are recognised by biological function rather than morphology and consist of those individuals that behave similarly as far as our immediate interests are concerned (Mackauer and Way 1976).

The members of this family attack aphids exclusively and are probably the most commonly observed cause of aphid mortality in the field. In Europe, many, if not all, aphid colonies come to include some mummified individuals (i.e. dead aphids containing a fully-grown parasitoid larva or pupa) (Starý 1970). Aphidiidae may hibernate as prepupae within host mummies. All are solitary endoparasitoids. All aphid stages are attacked except the eggs, but alatae are least often attacked. The parasitoid egg is usually inserted anywhere in the aphid abdomen. The preferred aphid larval instar varies with the parasitoid species, but younger instars are usually chosen. If adult aphids are parasitised the parasitoid larva may not complete its development before the insect dies, so that the parasitoid perishes also. Oviposition into an aphid does not ensure the successful development of a parasitoid, since the host may be unsuitable or it may already be parasitised: defence and immune responses are common. However parasitised hosts are usually distinguished by the parasitoid and receive no further eggs.

If an aphid is parasitised during the last larval instar, a mummy is formed after it moults to the adult. The first and second instars of aphidiid parasitoids generally feed on haemolymph, but the last instar attacks the alimentary canal and other organs, ultimately killing its host. The parasitoid larva then spins a cocoon and pupates inside the empty aphid skin. The adult emerges through a small circular hole usually cut dorsally or apically near the posterior of the mummy. Aphidiid mummies are round and usually straw-coloured to brown and in some genera (e.g. *Ephedrus*) always black and parchment-like. Aphelinid larvae do not spin cocoons, and their mummies are usually slender and black (Takada 1992).

The chain of events that determines host specificity includes, in sequence, host habitat finding, host finding, host acceptance by the parasitoid and host suitability.

The last larval instar of some parasitoids provokes their aphid hosts to move away from the plant on which they were feeding. With *Lysiphlebus fabarum*, *Ephedrus plagiator* and *Trioxys angelicae* this migration of pre-mummies is connected with diapause (under conditions of a short day) or with aestivation (under conditions of a long day). Parasitoids usually emerge without delay from aphids which become mummies where they have been feeding (Behrendt 1968).

Starý (1970) provides additional details of many of the species of Aphidiidae that follow below and Hågvar and Hofsvang (1991) a comprehensive review of their biology, host selection and use in biological control.

Aphelinus abdominalis (= A. flavipes) Hym.: Aphelinidae

This species is widespread in Europe and is recorded also from USSR, India, Australia and Israel. It is extensively distributed in India as one of the important parasitoids of *Myzus persicae* and *A. gossypii*. It becomes active in late May and is abundant during June and July. The incubation time for eggs is 2 days and adults emerge after 13 days in September (Ramaseshiah and Dharmadhikari 1969).

When an Indian strain was liberated in a U.K. glasshouse at 23°C, one week after artificially infesting plants with *A. gossypii*, it was unable to overtake the pest population because the rate of increase of the pest was scarcely affected by the parasitoid. Only when aphid overcrowding occurred and rate of increase was self-limited, did the parasite's rate of increase (6 × per week) exceed that of the aphid. Reducing the glasshouse temperature to 19°C slowed the rate of aphid increase and permitted the parasitoids to contain the pest before severe leaf-distortion occurred. On the other hand, when parasitoids were present at the time that *A. gossypii* was introduced, aphid reproduction was suppressed and effective control resulted (Hussey and Bravenboer 1971).

Aphelinus gossypii Hym.: Aphelinidae

This species was described from Hawaii and is recorded from Australia, New Zealand, India, Japan and also from Tonga, where it was reared in abundance from *Aphis gossypii* on taro (*Colocasia esculenta*). It is probably present elsewhere under other names (Carver et al. 1993). *Aphelinus gossypii* lays in some host eggs encountered, but also kills many others by probing and then feeding on exuding fluids (Takada and Tokumaku 1996). Parasitisation is reduced when the host is protected by the presence of ants (Stechman et al. 1996). *Aphelinus gossypii* was parasitised in Tonga to the extent of 30% to 60% by the cynipoid hyperparasitoid *Alloxysta darci*. This parasitises species of *Aphelinus*, but not of Aphidiidae so it is most unlikely to parasitise *Aphidius colemani*, a recently established parasitoid attacking *Aphis gossypii* there. *Alloxysta darci* was earlier incorrectly identified as *Alloxysta brevis* (Carver 1992; Carver et al. 1993). *Aphelinus gossypii* is an effective parasitoid at low *A. gossypii* density and hence an important candidate for consideration for introduction (P. Wellings, pers. comm.).

Aphelinus mali Hym.: Aphelinidae

This well known North American parasitoid of above-ground stages of the woolly apple aphid *Eriosoma lanigerum* has been introduced intentionally or inadvertently into almost every country where its host has established itself as a pest. It is a very effective parasitoid in moderately warm climates (Rosen 1967b) and has occasionally been reported from other hosts, including *Aphis gossypii,* although in such instances it has probably been confused with the very similar *Aphelinus gossypii* (M. Carver pers. comm.). The life cycle occupies almost 20 days in summer (egg 3, larva 10 to 12 and pupa 6 to 7 days respectively). Parasitised aphids have a strong tendency to seek sheltered places before death (Clausen 1978).

Aphelinus semiflavus Hym.: Aphelinidae

This species has a wide host range and occurs in USA, Hawaii, India and Europe. It overwinters as a pupa in its host. Single eggs are laid, generally in the dorsal surface of the host abdomen. Young aphids are preferred hosts, but even adults are parasitised, in which case fewer young are produced by the aphid before it is killed. Over 600 eggs may be produced by a female which often feeds on haemolymph exuding from oviposition punctures. Males are rare and females can produce offspring parthenogenetically. Developmental periods are: egg 3 days, larva 6 to 11 days and pupa 7 to 8 days. Although *Myzus persicae* is preferred, *A. semiflavus* also parasitises *Aphis gossypii* as one of 15 or so other hosts. In USA it was attacked by 3 hyperparasitoids, *Asaphes lucens* (= *A. americana*) (Pteromalidae), *Alloxysta* sp. (Charipidae) and *Syrphophagus aphidivora* (= *Aphidencyrtus aphidiphagus*) (Encyrtidae) (Hartley 1922; Ramaseshiah and Dharmadhikari 1969; Schlinger and Hall 1959).

Aphidius colemani Hym.: Aphidiidae *(= A. platensis, = A. transcaspicus)*

Starý (1975) postulated that this species originated in India or nearby (possibly the Eastern Mediterranean). It is now widely distributed in Mediterranean Europe, Asia Minor, Central Asia, India, Pakistan, Africa, South America, Australia, New Zealand and New Caledonia (Starý 1972). In addition there have been intentional introductions to California, U.K., Czechoslovakia, Kenya (Starý1975) and Tonga (Carver et al. 1993). It is rather strange, if it originated in India, that it appears to be absent from Japan, China and possibly some of Southeast Asia (Starý 1975; Takada 1992). *A. colemani* is restricted to the family Aphididae. Hosts consist of at least 9 species of *Aphis,* including *A. craccivora* and *A. gossypii* and at least 30 species in other genera (Elliott et al. 1994; Starý 1975).

In the field in Australia *A. colemani* is known to parasitise many species in the aphid tribes Aphidini and Myzini, but rarely species in the Macrosiphini and even more rarely species in other subfamilies (Carver et al. 1993).

There are significant differences between countries both in the range of hosts attacked by *A. colemani* and the preference for particular host species (e.g. Messing and Rabasse 1995). This indicates that the species that is known as *A. colemani* is a complex of closely-related species or biotypes. For example, *A. colemani* parasitises *Melanaphis donacis* and *Hyalopterus pruni* in Mediterranean Italy and France, but none of the many other aphids present; in Central Asia only the latter aphid is attacked and in Iraq both aphids are attacked, in addition to *Aphis zizyphi* and *A. punicae*. An Italian population from *Hyalopterus pruni* was successfully reared on both *Aphis craccivora* and *A. fabae* in the laboratory. Furthermore, a French population from *Melanaphis donacis* was readily reared in the laboratory on *Aphis craccivora*, *A. fabae* and *Myzus persicae* (Starý1975). As another example, a strain (from Brazil) of *Aphidius colemani* successfully parasitised the oleander aphid *Aphis nerii* in France whereas another strain (from France) failed to do so (Tardieux and Rabasse 1986, 1988). In Mediterranean regions *A. colemani* parasitised *A. gossypii* successfully at 20°C, but at temperatures above 27° it frequently failed to do so (Guenaoui 1991). The number of eggs laid per female *A. colemani* was 302 at 20°C and 388 at 25°C and development time to adult was 12.7 days and 10.0 days respectively. The intrinsic rate of increase of the parasitoid was similar to that of *A. gossypii*, suggesting that it is a promising parasitoid (van Steenis 1993). The optimum scheme for introducing *A. colemani* into glasshouses for control of *A. gossypii* on cucumbers has been investigated by van Steenis et al. (1996). Chou (1984) recorded *A. colemani* from Taiwan—the first record of this species from east Asia—with *H. pruni* as its only host.

The care needed in selecting a biotype appropriate to the target pest is also illustrated by the following example. *A. colemani* from *Aphis nerii* mummies on a garden plant (*Tweedia coerulia*) in Canberra was readily reared for some generations in an insectary on the banana aphid *Pentalonia nigronervosa* before release in Tonga for biological control of that species. It has not been recovered from the banana aphid, but is now well established on *A. gossypii* attacking cucurbits (Carver et al. 1993; Wellings et al. 1994). When *P. nigronervosa* colonies are small they are mainly located deep in the leaf sheaths and they only extend into more exposed areas as they increase in size. Stadler and Völkl (1991) found that *Lysiphlebus testaceipes* searched mainly in exposed areas for hosts, whereas *A. colemani* searched both exposed and concealed areas. This suggests that *A. colemani* would be the more appropriate of the parasitoids for hosts in concealed situations and, interestingly, it has been reported from *P. nigronervosa* in the field in northern New South Wales (M. Carver pers. comm.), where it is rare and was not encountered in recent searches (P.W. Wellings pers. comm.).

A. colemani (often under one of its synonyms) has been introduced to several countries for the biological control of a range of aphid species (Starý 1975).

Aphidius gifuensis Hym.: Aphidiidae

This species is native to the Oriental region. Details of its fecundity, oviposition period and longevity are provided by Fukui and Takada (1988).

Aphidius matricariae Hym.: Aphidiidae *(= A. phorodontis)*

This species is native to the temperate zones of the Palearctic region and has been recorded from more than 40 aphid species in Europe, North Africa, the Middle East, Israel, Mongolia and North and South America. It has a preference for the green peach aphid *Myzus persicae* in Israel (Rosen 1967a,b) and California (Schlinger and Mackauer 1963). After contact with honeydew or an aphid host the time spent in searching that region for hosts increased (Masum 1994).

Ephedrus persicae Hym.: Aphidiidae

This is an almost cosmopolitan species, which is probably native to the Middle East or Central Asia, and now occurs in the Far East, Europe, South Africa, Madagascar, Australia and North America. It prefers leaf-curling aphid hosts, mainly belonging to the Myzinae and, less frequently, to the Aphidinae (*Aphis* spp.) (Mackauer 1963, 1965; Starý 1966). A review of the taxonomy and biology of *Ephedrus persicae* and *E. plagiator* is provided by Gärdenfors (1986).

Ephedrus plagiator Hym.: Aphidiidae

This aphid is native to the far eastern deciduous forests and steppes of the Palearctic region and is widely distributed in India. It has many hosts amongst species of *Aphis* and *Myzus* (Starý 1967a).

Lipolexis gracilis Hym.: Aphidiidae

This is a European or Far Eastern species with hosts in a number of aphid genera, including *Aphis* (Starý 1967a).

Lipolexis scutellaris Hym.: Aphidiidae

This is an oriental species (Raychaudhuri 1990) and is known from southern China, Japan and Taiwan and also from India, Pakistan and Tonga. It has a wide host range and an apparent preference for *Aphis* species (Carver et al. 1993).

Lysiphlebia japonica Hym.: Aphidiidae

This is native to the Far East and is probably a well-adapted species for tropical climates. It typically occurs in forest or open woodland environments on many species in the genus *Aphis* in addition to those in a number of other related aphid genera (Starý 1967b).

Lysiphlebia mirzai Hym.: Aphidiidae

This species was described from India and is known also from Vietnam and China.

Lysiphlebus fabarum Hym.: Aphidiidae
(= Lysiphlebus confusus, L. ambiguus)

This is a Palaearctic species (Europe, Asia Minor, Caucasus, Central Asia), which is now widespread and occurs also in Israel, a number of African countries and USA. It is the most abundant parasitoid of the black citrus aphid *Toxoptera aurantii* in Italy (Starý 1964) and Israel (Rosen 1967a,b). In some countries it is biparental but, in Israel, only females are known (Rosen 1967a,b). It is recommended by Starý (1967b) as a species useful for biological control. *L. fabarum* is both biparental and parthenogenetic (Carver 1984) and 15 to 16 generations a year have been recorded in Italy (Tremblay 1964). It has a very extensive host range, with records from at least 144 species of aphids in 36 genera, 81 (56%) of these species belonging to the genus *Aphis* (Carver 1984).

There is little doubt that *L. fabarum* refers to a complex of closely related sibling species or at least of host-specific biotypes. For example, in the laboratory *L. fabarum* bred from *Aphis* species readily parasitised other *Aphis* species, but not *Brachycaudus* sp.. However, in the field, colonies of *Brachycaudus cardui* heavily parasitised by *L. fabarum* shared the same host plants as unparasitised *Aphis fabae* (Mackauer 1962a). The influence of temperature and humidity on the development of *L. fabarum* in *A. gossypii* and *A. craccivora* has been reported by Davletshina and Gomolitskia (1975) and methods for its mass production by Tregubenko and Popushoi (1987).

Lysiphlebus testaceipes Hym.: Aphidiidae

This parasitoid has a natural range extending from North America through Central America to the northern parts of South America. It is now known also from Hawaii, Australia, Europe and East Africa. It is the commonest native parasitoid of aphids in Mexico (Starý and Remaudière 1982). It has a very wide host range, having been reported from at least 79 aphid species (32 in the genus *Aphis*) in 32 genera (Carver 1984).

Oviposition generally occurs in the abdomen of half grown and unparasitised hosts and, when hosts are scarce, more than one egg may be deposited (Sekhar 1957). Up to 254 eggs may be laid. It is heavily attacked by hyperparasitoids in its natural range (eg. 6 species when attacking *Aphis gossypii* (Schlinger and Hall 1960) or 7 species (Oatman et al. 1983b)).

L. testaceipes was present in Australia (New South Wales and South Australia) prior to its introduction as a biological control agent and attacked an indigenous aphid *Aphis acaenovinae* (Starý and Carver 1979).

There are many examples to demonstrate that *L. testaceipes* consists of biotypes. Thus, Californian *L. testaceipes* is unable to complete its development on *Aphis spiraecola*, whereas a Cuban strain does so successfully. The Californian strain did not attack *Aphis nerii* after introduction to Hawaii, although a Mexican strain subsequently introduced did so (Starý 1970). Then again, the biotype from *A. craccivora* on *Robinia pseudacacia* does not parasitise this same aphid on *Phaseolus vulgaris*; another biotype prefers *A. gossypii* on squash to this same aphid on hibiscus (Sekhar 1960; Tremblay and Barbagallo 1982). The effectiveness of *Lysiphlebus testaceipes* as a parasitoid on *A. gossypii* is thus significantly affected by the host plant on which the aphid is feeding (Steinberg et al. 1993).

L. testaceipes is reported to attack *A. gossypii* in Cuba (Starý 1981), Mexico (Starý and Remaudière 1982) and, after introduction to Europe, in Spain, France and Italy. In Europe it now attacks more than 26 aphid species including *A. craccivora* and *A. gossypii*, often with high levels of parasitisation (Starý et al. 1988a,b,c).

Lysiphlebus testaceipes was successfully introduced in 1923 from California to Hawaii for the biological control of aphids, including *Aphis craccivora* and *A. gossypii*. It soon spread widely throughout the islands, attacking these and other aphid species. In 1965, a further introduction from Mexico was made to control the oleander aphid *Aphis nerii* which had previously escaped attack. By 1927 several hyperparasitoids were recorded as attacking *L. testaceipes* breeding in *Rhopalosiphum maidis,* an important virus vector on sugarcane (Timberlake 1927). According to Starý (1970), the introductions were partially to substantially effective, but importation of additional species was recommended. *L. testaceipes* from Cuba was introduced to Czechoslovakia for the biological control of aphids in greenhouses and also of some pest aphids in some subtropical areas (Starý 1970). *L. testaceipes* was introduced in 1956 and 1960 from Hawaii to the Philippines, but no recoveries have been recorded (Baltazar 1963). *L. testaceipes* was introduced in 1973 from Cuba into France and Corsica (Italy) to reduce the numbers of citrus aphids (Starý et al. 1988b). It became well established, heavily parasitising *Aphis gossypii* and several other aphids (Rabasse 1986).

Although there do not seem to be comparable data for *A. gossypii*, Hall and Ehler (1980) found that *L. testaceipes* averaged 79.5% parasitisation of *Aphis nerii* populations on oleander, with an average density of 12.4 aphids per shoot. When natural enemies were excluded, an average of 32.6 aphids were present per shoot, a clear indication that parasitisation was having a significant effect. A hyperparasitoid *Pachyneuron* sp. was active, but appeared to be generally unimportant in aphid population regulation. The average fecundity of *L. testaceipes* was found to be 128.2 eggs at 20°C and 180 eggs at 25°C. Development from egg to female adult was completed in 12.9 days at 20°C and 9.5 days at 25°C; and the life span of females was 2.7 and 2.6 days at 20 and 25°C respectively. At 20°C the intrinsic rate of increase was slightly lower than that of *Aphis gossypii*, but was the same at 25°C. It was concluded that, at temperatures below 25°C, *L. testaceipes* might not be able to overtake an established population of *A. gossypii* (van Steenis 1994). Earlier Schlinger and Hall (1960) concluded that *L. testaceipes* was capable of producing excellent control of both *A. craccivora* and *A. gossypii.*

Praon volucre Hym.: Aphidiidae

This is a palearctic species and is known from the Middle East, North Africa, India and Central Asia. It has an extensive and diverse host range, having been recorded from at least 90 aphid species in 35 genera. There is good evidence that *P. volucre* exists as a complex of host-specific biotypes or sibling species (Mackauer 1959, 1962a,b). Its biology has been studied by Beirne (1942). As in other *Praon* spp., pupation takes place under the empty mummy of the parasitised host. *P. volucre* females have been observed to use their front legs to hold the host aphid during oviposition (Beirne 1942). Although it has been recorded from *A. craccivora* in the field (Starý 1967a) and the laboratory (Carver 1984), it does not seem to have been reported from *A. gossypii.*

Trioxys angelicae Hym.: Aphidiidae

This is widely distributed in Europe, Asia Minor and North Africa and has been reared from a wide range of hosts (Rosen 1967a,b).

Trioxys communis Hym.: Aphidiidae

This very important parasitoid of *A. gossypii* in China has been studied in a series of papers by Shi (1984, 1985, 1986). It develops in 8 days at 30°C and in 16 days at 20°C. When 4th instar *A. gossypii* are parasitised they mummify in the adult stage, having produced very few offspring. It is hyperparasitised by the pteromalid *Pachyneuron aphidis*.

T. communis has also been recorded from *A. gossypii* in Japan, Korea, Taiwan and India and has been taken rarely in Malaysia from *Aphis spiraecola* (= *A. citricola*), but apparently not from other aphids (Ng and Starý 1986).

Trioxys indicus Hym.: Aphidiidae

A valuable review of the biology, ecology and control efficiency of this parasitoid is presented by Singh and Agarwala (1992). Its biology has been studied by Subba Rao and Sharma (1962) and later in a long series of papers from India (e.g. Singh et al. 1979; Sinha and Singh 1980a,b; Singh and Sinha 1980a,b,c, 1982a,b; Pandey et al. 1982, 1984; Kumar et al. 1983; Singh and Pandey 1986; Singh and Srivastava 1988a,b, 1991, Singh and Agarwala 1992). Ghosh and Agarwala (1982) provide host, host plant records and information on its distribution in India.

Recorded hosts of *T. indicus* belong to 24 species of aphids in 14 genera, of which species of *Aphis* are best represented. The majority of host aphids are polyphagous, 6 are oligophagous and 1 monophagous. *T. indicus* prefers hosts on cultivated and wild shrubs to those on herbaceous and woody plants. *A. craccivora* is parasitised to the extent of 87% on pigeon pea (Singh and Tripathi 1987) and *A. gossypii* to the extent of 60% on both bottle gourd (Singh and Bhatt 1988) and eggplant (Subba Rao and Sharma 1962), and 30% on cotton (Agarwala 1988).

Based on extensive field observations, the three main hosts of *T. indicus* are *A. craccivora*, *A. gossypii* and *A. nerii*, each of which is parasitised by a range of other polyphagous parasitoids.

The native range of *T. indicus* is largely the Indian subcontinent, although it has also been recorded from Taiwan (Starý and Schlinger 1967). It is most abundant in tropical and subtropical regions, where its numbers are comparatively low in summer and in rainy months and higher in the cooler months (Agarwala 1988).

T. indicus females prefer to oviposit in second and third instar host nymphs. Probing without oviposition is common with first and second instars, leading to high aphid mortality (up to 80% for first instars). Hosts that are already parasitised are generally avoided. Fecundity varies, but the figure of 143 offspring per female is quoted. The average time from oviposition to emergence is 10 days at 24 to 27°C on *A. gossypii* (Subba Rao and Sharma 1962) and 16 to 18 days at 24 to 26°C on *A. craccivora*. *T. indicus* lives less than 10 days in the laboratory (Pandey et al. 1982). Augmentation of *T. indicus* early in the season in pigeon pea fields in India was sufficient to control *A. craccivora* (Singh and Agarwala 1992). Extracts of *A. craccivora* sprayed on pigeon pea increased the fecundity of *T. indicus* and reduced the population doubling time (Singh and Srivastava 1991).

A density-dependent relationship between *T. indicus* and its hosts has been reported by several authors (Subba Rao and Sharma 1962; Singh and Sinha 1980a; Saha and Agarwala 1986; Bhatt and Singh 1991a,b).

Eleven hyperparasitoids of *T. indicus* are known (Singh and Agarwala 1992) and these should be rigorously excluded in any biological control transfers.

Singh and Agarwala (1992) conclude that *T. indicus* is a very important parasitoid, especially of several species of *Aphis* in India, that it possesses most of the desirable attributes of a successful biological control agent and is therefore a promising natural enemy for introduction elsewhere against relevant pest aphids. It is also of value for inundative releases (Singh and Rao 1995).

Diptera

Endaphis maculans Dip.: Cecidomyiidae

This aphid endoparasitoid attacked *Toxoptera aurantii* freely, but *A. gossypii* only lightly. It was seldom found in *A. craccivora* (Kirkpatrick 1954). *E. maculans* lays its eggs on aphid-infested leaves and, upon hatching, the larva searches for aphids. When a host is encountered the larva penetrates the aphids dorsum and develops as an endoparasitoid, leaving as a mature larva via the aphid’s anus. Average development time from egg to adult at 25° to 26°C was 19.1 days (Tang et al. 1994).

An aphid-specific predator

Aphidoletes aphidimyza Dip.: Cecidomyiidae

This is a common and widely distributed species throughout the northern hemisphere. It has been recorded from Japan, USSR, Czechoslovakia, Austria, Germany, Finland, France, Netherlands, U.K., Italy, Israel, Egypt, Sudan, Canada, USA and Hawaii. It is not recorded from Australia or New Zealand.

Larvae of *Aphidoletes* reportedly feed exclusively as predators on aphids and are hence more host-specific than many of the other predators: *A. aphidimyza* is the best known of the cecidomyiid predators. Adults emerge during the day from pupae in the soil. They generally fly between sunset and sunrise. Orange-coloured eggs are laid singly or in clusters of up to 40, usually on plants near aphid colonies. Females live up to 14 days in the laboratory and lay about 100 eggs. These hatch after 3–4 days and first instar larvae immediately seek out and attack aphids. They usually attack by piercing a leg joint or some other joint. A toxin is perhaps injected, since the aphid is rapidly immobilised before its body fluids are extracted. The shrivelled bodies of some aphids remain attached to the plant by the stylet. Larval development involves 3 instars and takes 7 to 14 days (Harris 1973). On the other hand, Herpai (1991) reports 21 days from egg to adult (egg 3 days, larva 8 days, pupa 10 days).

Roberti (1946) gave a figure of 60 to 80 *Aphis gossypii* attacked per day. Predator larvae usually drop to the soil to pupate. They construct small silk cocoons in the top few millimetres of soil, but occasionally cocoons may be spun on plants. Larvae pupate within a few days of cocoon construction and adults emerge after 1–3 weeks depending upon temperatures. The life cycle can be completed in about 3 weeks at temperatures above 21°C (Harris 1973; Herpai 1991).

Harris (1973) does not record it from *A. craccivora*. Two hyperparasitoids of *A. aphidimyza* are known in Africa, the platygasterid *Synopeas rhanis* and an unidentified braconid (Harris 1973).

Comments

There are many reports in the literature that natural enemies play an important role in reducing (and probably regulating) the abundance of pest aphids. More than 100 biological control programs have been mounted against at least 26 aphid species and 48% of them have reported success (Hågvar and Hofsvang 1991). Twenty three species of aphidiid parasitoids have been used in classical biological control of aphids and the parasitoids became established in 32 out of 55 attempts (Greathead 1989). Most pest aphids are attacked in their native range by many parasitoids and predators and by a few pathogenic fungi. However, many of the natural enemies have not accompanied their aphid hosts when these have spread into new regions. Indeed, they may not even be present throughout the presumed native range of their host. Since both the direct and indirect damage caused by aphids seem to be proportional to their numbers, any reduction is potentially beneficial. Even in the case of virus transmission, where the feeding (or probing) of single infected aphids on a crop may lead to substantial loss, reduction in aphid numbers will more than proportionally reduce the probability of flying aphids migrating to an uninfected plant (Wellings 1991), because reduced crowding of aphids usually results in a lower number forming wings. As indicated above, there have been a number of attempts at classical biological control of aphids, and there are at least 7 well-documented successes up to 1988 (Hughes 1989). None of these, however, involved *A. craccivora* or *A. gossypii* as the main target. These latter species have, however, been subjected to important attack by parasitoids introduced primarily against another pest aphid in the same general environment. For example, although *Aphidius colemani* failed to establish on *Pentalonia nigronervosa* in Tonga, it did so very successfully there on *A. gossypii*. Although *A. craccivora* is also present in Tonga, *Aphidius colemani* has not yet been recorded from it (Carver et al. 1993), but monitoring has been minimal.

The best predictor of success in biological control is previous success with a natural enemy in a similar environment. If this experience is unavailable, the best chances appear to be with a climatically adapted, adequately host-specific, natural enemy that is known to attack the pest in its native or expanded range. Parasitic wasps appear to be the best natural enemies available for aphids, because they are generally far more host specific than predators and are often more efficient at searching for hosts at low aphid densities (Hughes 1989). Predators can be very effective in reducing aphid numbers at certain times of the year, but are often unable to prevent damage. Furthermore, their general lack of host specificity makes most of them unattractive to authorities responsible for approving introductions, so they have not been dealt with in any detail in this dossier.

A feature that makes it difficult to generalise—and even to make clear recommendations—is that many of the identifications of some of the parasitoids are incorrect, particularly the earlier ones, but even some of the more recent ones made by non-specialists. The selection of appropriate natural enemies for an aphid biological control program requires a detailed knowledge of the ecology of the target aphid and often of other potential aphid hosts in the environment where it is causing problems; also of where to obtain parasitoid biotypes with appropriate host specificity and habitat adaptation. If an apparently good species fails to establish or, if established, to become effective, it is probably worth seeking the same enemy from a potentially more appropriate source, such as one with a better climate match; or a biotype that exhibits a special preference for the target aphid; or the first generation from field-collected material, rather than employing individuals bred for many generations in the laboratory (Hughes 1989).

Both *A. craccivora* and *A. gossypii* are now almost cosmopolitan in their occurrence throughout the temperate, subtropical and tropical regions of the world and both are polyphagous. At least *A. gossypii* exists as a series of biotypes with different spectra of host preferences and both it and *A. craccivora* owe a considerable amount of their economic importance to their ability to transmit an extensive range of important plant viruses.

Both aphids are attacked by a wide range of parasitoids and share a number of these species. The majority of these parasitoids are polyphagous and attack many other (but not all) species of the genus *Aphis* and some species in related aphid genera. Two important parasitoids are the American *Lysiphlebus testaceipes* and the Indian *Aphidius colemani*. These parasitoids both exist in a number of biotypes with different host spectra and abilities to attack *A. craccivora* and *A. gossypii* on some plants, but not on others. Thus, when biological control is attempted, care must be taken to select a parasitoid biotype that is appropriate for the aphid biotype, the host plant and the prevailing environmental conditions. Laboratory comparison of the impact on *A. gossypii* of *Aphidius colemani*, *Lysiphlebus testaceipes* and *Aphidius matricariae* indicated that *A. colemani* was the most and *A. matricariae* the least effective (van Steenis 1992). The polyphagous nature of many effective parasitoids has the advantage that, in any region, a number of other aphid species will be parasitised—and hence serve as valuable reservoirs of parasitoids when the target pest population falls to a low level. The aims of aphid biological control are (i) as far as possible to maintain densities below those at which alates are formed due to crowding and (ii) if possible, to depress densities still further, so that sap removal, volume of honeydew produced and plant deformation become unimportant.

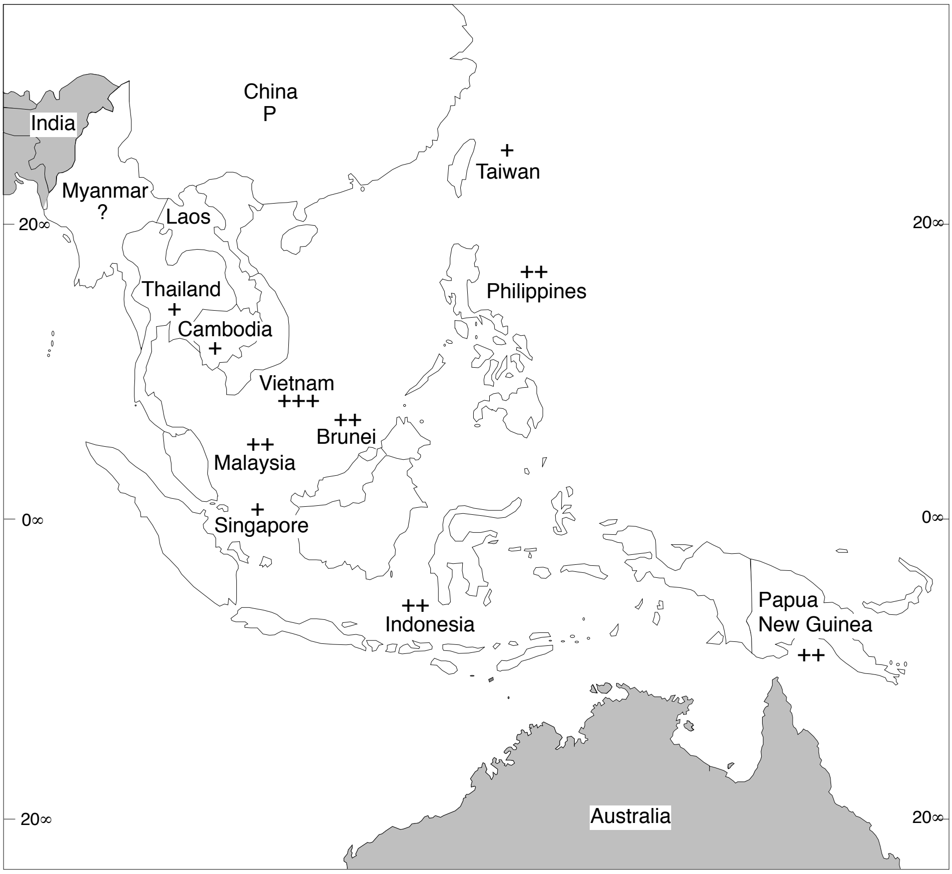
Takada (1992) points out that the aphid parasitoid fauna in Far East Asia is quite different from that in India. Thus, the most important parasitoids of *A. gossypii* in the Far East are *Trioxys communis*, *Lysiphlebia japonica* and *Aphelinus* sp., none of which occurs in India. On the other hand, the dominant parasitoid of *A. gossypii* in India is *Trioxys indicus,* which is present in Taiwan, but not in Japan or Korea. Another Oriental species, *Lipolexis scutellaris* occurs in Hong Kong, Vietnam and Malaysia. It appears that Indian parasitoids, rather than Far East Asian species are present in Southeast Asia. However inadequate information is available in Southeast Asia on the natural enemies of *A. craccivora* and *A. gossypii* present in the many different crop systems and environments in which these aphids occur. Even within a single country, it is necessary to examine the aphid population in the particular situations and the crops where they are causing important problems. This can be illustrated by the parasitoid complex of *A. gossypii* in Japan where it occurs in habitats ranging from open fields with low vegetation to garden habitats with low shrubs. In both situations it is attacked by specialised and generalist parasitoids. Of the two specialised parasitoids, *Trioxys communis* prefers the open field whereas *Lysiphlebia japonica* the garden habitat. Of the generalist parasitoids *Aphelinus* sp. prefers the open field and *Ephedrus* sp. the garden habitat. Thus the parasitoid complex of *A. gossypii* on cucumber, eggplant or taro in an open field is quite different from that on *Hibiscus* or *Rhamnus* in a garden (Takada 1992). Hence, in any country, the aim would be to determine whether there are gaps in the range of parasitoids present that might be filled with species known to be effective elsewhere. If there appear to be important gaps, there are good reasons for believing that there could be considerable advantages in filling them. Nevertheless, there are greater complexities than for many other pests in making clear recommendations, largely because of the range of biotypes that exist in both aphid hosts and their parasitoids.

Although it is not possible to make specific recommendations for any country without knowing what parasitoids are already present and the crop(s) on which control is desired the following parasitoids merit consideration:

Aphelinus gossypii
Aphidius colemani
Aphidius gifuensis
Ephedrus persicae
Lipolexis scutellaris
Lysiphlebia japonica
Lysiphlebus fabarum
Lysiphlebus testaceipes
Trioxys communis
Trioxys indicus

Even if any of these species is already in a country, but not attacking either *A. craccivora* or *A. gossypii*, a host-adapted strain should be considered for introduction. It is possible that some of the parasitoid species will compete directly with species that are already present. If this happens and one parasitoid species is displaced from an aphid host in some situations or on some crops, the final result will almost always be a lower overall aphid density.

4.5 Cosmopolites sordidus



The banana weevil borer *Cosmopolites sordidus* is native to the Indo-Malaysian region.

There have been many attempts at biological control, involving three predatory beetles, but the results have generally been disappointing. Many predators attack *Cosmopolites* larvae in their native range, especially the histerid beetles *Plaesius javanus* and *Plaesius laevigatus* in Indonesia and *Dactylosternum hydrophiloides* in Malaysia. The first two species have been established in Fiji, with some reduction in *Cosmopolites* abundance, but it remains an important pest there. In Cook Is, they appear to have had little impact. Unless beneficial effects from *P. javanus* and *P. laevigatus* can be demonstrated in Fiji or other countries, there would seem to be little point in introducing these species to any additional countries. In Kenya, Koppenhöfer et al. (1992) recorded two important predatory beetles, *Dactylosternum abdominale* and *Thyreocephalus interocularis*, capable of reducing larval abundance by 40% to 90%. In Cuba, the ant *Tetramorium bicarinatum* is reported to keep *C. sordidus* under control. This ant is widespread, but there is no information on its effectiveness elsewhere.

It would be highly desirable to investigate whether the weevil is indeed absent or of very minor importance in some areas (e.g. Myanmar, southern China) and, if so, what part is played by resistant cultivars, cultural methods or natural enemies. Ants might be evaluated for their effects in the Solomon Is where *Cosmopolites* is unimportant or in Papua New Guinea where it is of local importance only.

Cosmopolites sordidus (Germar)

Coleoptera: Curculionidae
banana weevil borer

Rating

Southeast Asia			China	Southern and Western Pacific		
	+++	Viet			+++	Cook Is, Fr. P, Fiji, Guam, New Cal, Niue, A Sam, Tong
13	++	Msia, Brun, Indo, Phil		35	++	PNG, Sol Is, Sam, Van, W & F
	+	Thai, Sing			+	FSM
	P	Camb	P		P	Kir
	?	Myan, Laos				

This account brings up-to-date the chapter on *C. sordidus* in Waterhouse and Norris (1987) and increases its relevance to Southeast Asia.

Origin

According to Purseglove (1972) the genus *Musa* has a centre of diversity in the Assam-Burma-Thailand area and it probably originated there. The banana weevil borer is also stated to be a native of the Indo-Malaysian region (Zimmerman 1968; Clausen 1978). Although this region seems a likely centre of origin of the weevil, and those investigating its biological control have consistently assumed so, there had already been, by the time of Germar's 1824 description based on material from India, centuries of intercontinental travel by Europeans, by means of which the weevil could have spread to many other lands in infested plants, thus obscuring its origin.

There are only two species in the genus *Cosmopolites*, the lesser known *C. pruinosus* occurring in Borneo and the Philippines and, after introduction, in Micronesia (Zimmerman 1968).

Distribution

C. sordidus is present in virtually all banana-growing areas of the world, including most, if not all, of Southeast Asia and most of the Pacific. Exceptions in the Pacific are Marshall Is, Tuvalu and Tokelau (Anon. 1979b; Waterhouse and Norris 1987; Waterhouse 1997). In Southeast Asia no information is available from Laos and the situation in Myanmar is unclear. A recommendation was made in the standard work on the 'Insect Pests of Burma' (Ghosh 1940) to guard against the introduction to that country of *C. sordidus* and neither N. von Keyserlingk nor G. Pierrard (pers. comm.

1992) were able to establish, when based in Yangon, that the species occurred in Myanmar. Its uncertain status in Myanmar and Laos and its status of ‘present, but unimportant’, in Cambodia and China clearly merits further investigation.

Biology

The ovoid, 2 mm long, white eggs are laid singly, usually between the leaf-sheath scars on the crown of the banana rhizome, in small cavities chewed out by the female just above the ground surface. Laying also occurs on the pseudostems of fallen plants. The eggs hatch in about 8 days in summer and the larvae tunnel into the tissues. On reaching maturity, after about 20 days feeding in warm weather (Jepson 1914), the larvae tunnel to near the surface of the corm and form an oval chamber in which they pupate. The period from egg to adult may be as short as 29 days in the New South Wales summer or as long as 6 months in the cooler parts of the year (Hely et al. 1982). Fifty days is a more usual maximum for the life cycle in Fiji (Swaine 1971). The nocturnal adults also tunnel in banana tissues. During the day they generally hide in or around the rhizomes or between the leaf sheaths at or just above ground level. They are slow moving and will feign death when disturbed. They seldom fly, but walk over the soil surface and vegetation. Whalley (1957) found that adults dispersed slowly in Uganda. Of 400 marked weevils 35% were recovered over an 8-month period within a radius of 7 m from the release point. In Colombia a few marked adults were recaptured after 2 weeks at a distance of 6 to 8 m, but 23 months after release none were found in another plantation 20 m away (Cardenas and Arango 1986). Male *C. sordidus* release an aggregation pheromone, sordidin (Beauhaire et al. 1995), from the hindgut which attracts both males and females, but females do not produce a pheromone attractive to either sex (Budenberg et al. 1993b; Ndiege et al. 1996). Both sexes were attracted to freshly cut rhizome and pseudostem and females to rotting pseudostem (Budenberg et al. 1993a). Eggs are laid throughout the year at a rate varying with temperature and up to 100 a year. Adults may live as long as 2 years (Swaine 1971). They can survive in captivity for 14 weeks without food (Zimmerman 1968). Laboratory rearing of *C. sordidus* was studied by Afreh (1993) and Koppenhöfer and Reddy (1994).

Damage

The status of *C. sordidus* as one of the most important pests of bananas is often reported (Swaine 1971; Purseglove 1972) and, indeed, many adults and larvae are often present. It is reported to be now the most important pest of bananas in Africa (Nahif et al. 1994; Ortiz et al. 1995). However, in order to place these reports in context, it is necessary to outline the stages of growth of the plant. Bananas are propagated vegetatively by planting rhizomes (corms), which give rise to shoots after a few weeks. As the plant grows, a pseudostem is formed from the sheaths of the leaves which continue to develop internally until a flowering shoot emerges from the top of the pseudostem at a height of 2 to 4 m depending upon the variety. When each bunch of bananas is cut, the pseudostem bearing that bunch is also cut down. At the same time a healthy sucker growing from the same base is selected to succeed and other suckers removed. *C. sordidus* larvae tunnel in the rhizome and the base of the pseudostem, but do not attack the roots. This tunneling may kill young plants and greatly increases the susceptibility of mature plants to wind damage. Adults cause little damage and feed mainly on rotting banana tissue. Injury by larvae to the rhizome can interfere with root initiation and sap flow within the plant and grossly infested plants may bear small bunches of undersized fruit (Wright 1976). Much of the damage attributed to *C. sordidus* is probably caused by rhizome rot or nematodes (Ostmark 1974). In East Africa the combined attack of nematodes and of banana weevil borer is considered to be the main reason for the serious decline in productivity of bananas (De Langhe 1988), but the precise role of the weevil is still to be established. Suckers infested with nematodes were found to be more than four times more likely to be attacked by *C. sordidus* than suckers without nematodes (Speijer et al. 1993). Although the banana weevil borer has occasionally been responsible for severe losses of newly-planted rhizomes, extensive experiments in Central America agree with some reports from Australia (Smith 1993; Wallace 1937) that weevil damage is not as important as frequently claimed since the larvae have a strong preference for rhizomes of harvested plants over healthy rhizomes (Ostmark 1974). There are reports that some banana cultivars are comparatively resistant to attack by *C. sordidus* (Mesquita et al. 1984; Mesquita and Caldas 1987), but the mechanism of such resistance (repellency, toxicity, greater tolerance to damage, etc.) is not known.

In Australia, Braithwaite (1963) concluded that the importance of *C. sordidus* infestation is aggravated by poor culture, but that benefit could be derived from almost complete control with insecticides (Braithwaite 1958). In the same region Loebel (1975) concluded that heavy weevil infestation is a symptom, rather than a cause, of a declining plantation, because 2 years of effective use of chemicals failed to improve growth or yield in his experimental plots. In Costa Rica several insecticides were effective in controlling *C. sordidus* populations, but banana yields were not increased (Nanne and Klink 1975). Nevertheless *C. sordidus* is always likely to be of importance in areas that experience strong winds. The abundance of adult weevils can be estimated by counting the number attracted to cut segments of pseudostem and of larvae by estimating the area damaged and counting the number of galleries exposed by slitting the rhizome or the pseudostem very near to its base (Vilardebo 1973; Delattre 1980; Mesquita 1985; Smith 1993). In spite of this, an adequate relationship between adult and larval abundance and economic loss remains to be established. It must be added, however, that there continues to be a widespread view that *C. sordidus* is a major pest.

Host plants

The weevil attacks all banana (*Musa sapientum*) cultivars, including plantain, and also Manila hemp (*Musa textilis*). It has been recorded in earlier days (but not in recent years) from plants in other Orders, but these reports are almost certainly in error.

Natural enemies

Although many predators are known to attack *C. sordidus* eggs, larvae and pupae (Table 4.5.1), it is extraordinary that, with one possible exception, not a single parasitoid of any life history stage has been recorded. That exception is the early report from the Philippines of Cendana (1922), who found a chalcidid wasp in one of his *C. sordidus* breeding cages, but it may not have been parasitising the weevil. It is, perhaps, less surprising that the heavily sclerotised adult weevil has very few enemies. It is true that some weevils are effectively attacked by hymenopterous parasitoids and that some tachinid parasitoids are able to attack certain weevils by laying eggs in their food or beneath their mouth when they are feeding (Jacobs and Renner 1988), but neither has been observed for *C. sordidus*. Koppenhöfer (1993a,b) estimated that 58% of the eggs were accessible to predators and presumably at least as many should be available to parasitoids if there were any. Most eggs were found in the surface layer of rhizomes, particularly in the crown, but some are also laid at the base of pseudostems and in the walls of abandoned larval tunnels in both pseudostems and rhizomes. As soon as eggs hatch the young larvae immediately tunnel deeper into the plant tissue and thus become far less available to natural enemies.

Table 4.5.1 Insect predators of *Cosmopolites sordidus*

Insect	**Stage attacked**	**Country**	**Reference**
DERMAPTERA			
LABIIDAE			
Carcinophora (=*Psalis*) *americana*	larvae	Jamaica Puerto Rico	Edwards 1934 Anon. 1939
Euborellia (= *Anisolabis*) *annulipes*	egg, larva	Jamaica Kenya	Edwards 1934 Koppenhöfer et al. 1992; Sirjusingh et al. 1992
Labia borellii	egg, larva	Kenya	Koppenhöfer et al. 1992
Labia curvicauda	egg, larva	Kenya	Koppenhöfer et al. 1992
HEMIPTERA			
CYDNIDAE			
Geotomus pygmaeus	egg	Malaysia, widespread	China 1935
MIRIDAE			
Fulvius nigricornis	egg	Malaysia	China 1935
NABIDAE			
Phorticus pygmaeus	egg	Malaysia, Papua New Guinea	China 1935
REDUVIIDAE			
Physoderes curculionis	larva	Malaysia	China 1935
COLEOPTERA			
CARABIDAE			
Abacetus? *optimus*		Kenya	Koppenhöfer et al. 1992
Galerita (=*Propagalerita*) *bicolor*			Sirjusingh et al. 1992
Scarites sp.			Sirjusingh et al. 1992

Table 4.5.1 (cont'd) Insect predators of *Cosmopolites sordidus*

Insect	Stage attacked	Country	Reference
COLEOPTERA			
ELATERIDAE			
unidentified spp.		Australia,	Froggatt 1928a
		New Caledonia	Jacques 1931
HISTERIDAE			
Hister niloticus	larva	Kenya	Koppenhöfer et al. 1992
Hololepta (= *Lioderma*) *quadridentata*		Malaysia	Clement 1944
		Trinidad	Pea & Duncan 1991
Hololepta striaditera	larva, pupa	Kenya	Koppenhöfer et al. 1992
Hololepta sp.		St Vincent	Sirjusingh et al. 1992
Lioderma sp.			Sirjusingh et al. 1992
Plaesius (= *Hyposolenus*) *laevigatus*		Indonesia	Froggatt 1928b
Plaesius javanus	larva, pupa	Malaysia	Froggatt 1928b; Clement 1944;
		Indonesia	Jepson 1914
		Thailand	Charernsom 1992
Platysoma abrupta	larva	Malaysia	Corbett 1936; Lamas 1947
Platysoma sp.			Corbett 1936
unidentified histerid sp.	egg, larva, pupa	Kenya	Koppenhöfer et al. 1992
HYDROPHILIDAE			
Dactylosternum abdominale	larva	Kenya, Philippines	Corbett 1936; Edwards 1939, Koppenhöfer et al. 1992
D. hydrophiloides	larva	Indonesia, Malaysia	Corbett 1936
D. intermedium	larva	Guinea	Cuillé 1950
D. profundus		San Thomè	Beccari 1967
D. subdepressum		Trinidad	Cock 1985
D. subquadratum	larva	Malaysia	Corbett 1936
Omicrogiton insularis	larva	Malaysia	Corbett 1936

Table 4.5.1 (cont'd) Insect predators of *Cosmopolites sordidus*

Insect	Stage attacked	Country	Reference
COLEOPTERA			
SILVANIDAE			
Cathartus sp.	larva	Indonesia	Jepson 1914
STAPHYLINIDAE			
Belonuchus ferrugatus	larva	Indonesia	Jepson 1914; Cuillé 1950
B. quadratus	larva	Malaysia	Corbett 1936; Lamas 1947
Charichirus sp.	egg. larva	Kenya	Koppenhöfer et al. 1992
Eulissus sp.		Kenya	Reddy 1988
Hesperus? sparsior	egg, larva	Kenya	Koppenhöfer et al. 1992
Priochirus (= *Leptochirus*) *unicolor*	larva	Indonesia	Jepson 1914, Cuillé 1950
Thyreocephalus? interocularis	egg, larva	Kenya	Koppenhöfer et al. 1992
TENEBRIONIDAE			
Eutochia pulla	egg	Kenya	Koppenhöfer et al. 1992
DIPTERA			
RHAGIONIDAE			
Chrysopilus ferruginosus	larva	Indonesia, India, Philippines	Froggatt 1928b; Beccari 1967 Jepson 1914
Chrysopilus sp.		Brazil	Sirjusingh et al. 1992
HYMENOPTERA			
FORMICIDAE			
Anochaetus sp.		Kenya	Reddy 1988
Pheidole megacephala	egg, larva	Cuba	Castineiras et al. 1991a
Tetramorium bicarinatum (= *T. guineense*)	egg, larva	Cuba	Roche & Abreu 1983

Because of the reported existence of natural enemies of *C. sordidus* in Indonesia and nearby countries, Jepson (1914) was sent from Fiji to investigate the situation in Java. The histerid beetle *Plaesius javanus* was commonly found preying on *C. sordidus* and other insects in the soil and leaf litter. Two staphylinid beetles *Belonuchus ferrugatus* and *Priochirus* (= *Leptochirus*) *unicolor* and a silvanid beetle *Cathartus* sp. were also shown to attack *C. sordidus* larvae, but they were not nearly as voracious. The predatory larvae of the rhagionid fly *Chrysopilus ferruginosus* attacked *C. sordidus* larvae in the laboratory, but not in the field.

A later investigation in Java (Froggatt 1928b) failed to reveal any egg parasites, but *P. javanus* and *C. ferruginosus* were recorded, as well as two other species of Histeridae, one probably *Plaesius* (= *Hyposolenus*) *laevigatus*, one or two species of Staphylinidae and two species of Hydrophilidae (all Coleoptera). Several species of Dermaptera were fairly common in the rotting banana plant. In southern China (Yunnan Province) two Dermaptera (one a forficulid) are reported to eat *C. sordidus* larvae and pupae, and a mite to attack larvae and adults; also a white muscardine fungus to infect 1% of larvae and pupae (Sun 1994).

The only detailed study in recent times of the natural enemies of *C. sordidus* is that of Koppenhöfer et al. (1992) in Kenya. Not surprisingly, the species (of predators) recorded were all polyphagous, since many were native species that had come to include an introduced pest amongst their prey. Twelve predators of eggs, larvae and pupae of *C. sordidus* were found. None of these attacked adults and no parasitoids were recorded (Koppenhöfer et al. 1992). Of these predators, the hydrophilid beetle *Dactylosternum abdominale* reduced weevil numbers in suckers by up to 50% and in residual stumps of harvested suckers by 39%. In spent pseudostems, *D. abdominale* reduced numbers by 40% to 90% at different predator densities and the large staphylinid predator *Thyreocephalus interocularis* reduced numbers by 42%. Other predators (Table 4.5.1) were unimportant (Koppenhöfer and Schmutterer 1993).

These particular predators are clearly non-specific, since they are native to East Africa and *C. sordidus* is not. Thus, although they may be attractive candidates for introduction (and *Plaesius javanus* was in this same category), the widely held view now is that, because of their impact on non-target organisms, very careful consideration should be given before any highly non-specific predators are introduced to a new region.

Extensive testing has been carried out of fungi (*Metarhizium anisopliae* and *Beauveria bassiana*) and of entomopathogenic nematodes (*Heterorhabditis* spp. and *Steinernema* spp.) as biological ‘pesticides’ against *C. sordidus*. Laboratory or field trials showed that strains of both fungi were capable of killing adults and larvae (Delattre and Jean-Bart 1978; Filho et al. 1987; Busoli et al. 1989; Castineiras et al. 1991a,b; Pea and Duncan 1991; Ponce et al. 1992; Brenes and Carballo 1994; Carballo and de Lopez 1994; Pea et al. 1995). In the field the best results were obtained with application of fungi twice a year at a dose of 10^{13} conidia per ha. This reduced trap catches of adults by 52% and rhizome damage by 65%, leading to a 25% yield increase. Parallel experiments with 9 colonies per ha of the predatory ant *Pheidole megacephala* yielded similar results (Castineiras et al. 1991a,b).

Early laboratory tests in Guadelupe by Laumond et al. (1979) showed that *C. sordidus* is susceptible to the entomopathogenic nematode *Steinernema carpocapsae* (= *S. feltiae*), an observation since widely confirmed in Central America for this and other nematode species (e.g. Figueroa 1990; Pea and Duncan 1991). However, the most extensive recent work has been carried out in Australia and Tonga. Twenty-one different species of *Steinernema* and *Heterorhabditis*, 7 strains of *Steinernema carpocapsae*, 2 of *S. feltiae*, 4 of *H. bacteriophora* and 2 of *H. zealandica* were tested against adult banana weevils. The best of these, *S. carpocapsae* BW strain, gave 85% infection in the laboratory (Parnitzki et al. 1990, 1998; Treverrow et al. 1991). Adult *C. sordidus* are highly resistant to entomopathogenic nematodes, due to the difficulty of nematodes entering the host via the mouth or anus. The large spiracles of the first abdominal segment offer an effective site of entry for the nematodes if they are able to pass under the tightly fitting elytra. By adding paraffin oil to the nematode preparation to seal the elytra, the beetle is caused to raise them slightly to respire, simultaneously giving the nematodes access to the spiracles. Adult weevils are strongly attracted to holes or cuts in the rhizome or psuedostem, but they require a thigmotactic stimulus to remain long enough to become infected by nematodes. If a core of tissue is removed from two sites at the base of a residual corm using a desuckering tool, 250000 nematodes (*S. carpocapsae* BW) added to each hole and the core loosely inserted, nearly all adult weevils attracted are killed. In one large scale field trial in New South Wales 8% of plants in untreated plots suffered significant damage, 3% when prothiophos was added to the core, 1% when nematodes were added and 0% when prothiophos was applied to the soil around the base of the plant. It was concluded that control of banana weevil using entomopathogenic nematodes should now be economically feasible (Treverrow and Bedding 1992, 1993a,b). More recently, Treverrow (1994) has found that baiting, and stem injection with very small amounts of insecticide, can reduce treatment costs to less than 1 cent per stool. This makes nematode applications against adults uncompetitive unless market premiums can be obtained for fruit produced in the absence of insecticides. However, targetting the highly susceptible larvae instead of the more resistant adult weevils may significantly reduce the costs of nematode applications. Applications of *S. carpocapsae* with a water-absorbing polyacrylamide gel into cuts or holes made in residual rhizomes gave significant mortality of *C. sordidus* larvae (Treverrow et al. 1991; Treverrow and Bedding 1993b). However, mortality at this stage may have limited effect on abundance, since a survey of 50 properties showed that 70% of adult weevils had already emerged from pre-harvest corms (Treverrow and Bedding 1993a; Treverrow 1994). The importance of correct formulation for the nematodes is highlighted by the disappointing results obtained in Queensland, when an earlier formulation without a water-absorbing gel failed to give effective control of adults, possibly due to the accumulation of excess water in the core holes (Smith 1993).

Attempts at biological control

FIJI

C. sordidus became a very destructive pest of bananas following its introduction about 1901 and this led to the first attempt at its biological control. This consisted of the introduction of the predatory histerid beetle *Plaesius javanus* into Fiji in 1913 from Java (Jepson 1914). This was unsuccessful (Table 4.5.2), but a further introduction in 1918 led to its establishment (Veitch 1926; Bennett et al. 1976). Simmonds (1935) reported a marked reduction in weevil damage, an opinion supported by Anon. (1935), but Pemberton (1954) considered that only partial control had been achieved. It now seems probable that, in addition to *P. javanus*, the similar looking histerid *Plaesius laevigatus* was also introduced, at least to Cook Is (Walker and Deitz 1979).

AUSTRALIA

Cosmopolites sordidus is thought to have become established in Queensland about the end of the 19th century, having arrived possibly from Papua New Guinea, but it was not until about 1914–15 that it reached New South Wales as a result of an accidental introduction from Fiji (Wilson 1960). Following its successful introduction into Fiji, *Plaesius javanus* was introduced from Java and liberated in Queensland from 1921 to 1928, but became established only briefly. It was introduced into New South Wales in 1922 from Java and again in 1934 from Fiji, but again it did not become established. The fly *Chrysopilus ferruginosus* was also introduced from Java, but failed to become established.

Table 4.5.2 Introductions for the biological control of *Cosmopolites sordidus*

Country and species	Liberated	From	Result	Reference
AUSTRALIA				
Plaesius javanus	1921–28	Java	–	Clausen 1978 Weddell 1932
	1934	Fiji	–	Wilson 1960
Chrysopilus ferruginosus	1928	Java	–	Wilson 1960
Dactylosternum hydrophiloides	1939	Malaysia	+	Smith 1944; Wilson 1960
CAMEROON				
Plaesius javanus	1952	Trinidad	–	Bennett et al. 1976
Hololepta quadridentata	1952	Trinidad	–	Bennett et al. 1976
COOK IS				
Plaesius javanus	1937–40	Fiji	+	Walker & Deitz 1979
Plaesius laevigatus	1937–40	Fiji	+	Walker & Deitz 1979
CUBA				
Plaesius laevigatus			–	Sirjusingh et al. 1992
DOMINICA				
Plaesius javanus	1951	Trinidad	–	Cock 1985
	1958–59	?	–	Clausen 1978
Hololepta quadridentata	1951	Trinidad	–	Cock 1985
	1958–59	?	–	Clausen 1978
FIJI				
Plaesius javanus	1913	Java	–	Jepson 1914
	1918	Java	+	Veitch 1926
Plaesius laevigatus	1918	Java	+	Walker & Deitz 1979

Table 4.5.2 (cont'd) Introductions for the biological control of *Cosmopolites sordidus*

Country and species	Liberated	From	Result	Reference
FRENCH POLYNESIA				
Plaesius javanus	1937	Fiji	+	Delobel 1977
GRENADA				
Hololepta quadridentata	1949, 1951	Trinidad	–	Cock 1985
Plaesius javanus	1949, 1951	Trinidad	–	Cock 1985
HONDURAS				
Plaesius javanus	1942	?	–	Greathead 1971
JAMAICA				
Plaesius javanus	1918–19	Java	–	Cock 1985; Edwards 1934
	1937–38	Java via Fiji	+	Cock 1985
			–	Sirjusingh et al. 1992
Dactylosternum hydrophiloides	1918–19	Malaysia	–	Edwards 1934
	1937–38	Malaysia	+	Edwards 1934
Dactylosternum abdominale	1937–38	Malaysia	–	Edwards 1934
MARIANAS				
Plaesius javanus	1947	Fiji	+	Clausen 1978
Hololepta quadridentata	1953	?	–	Clausen 1978
Hololepta minuta	1953	?	–	Clausen 1978
Hololepta sp.	1953	Trinidad	–	Clausen 1978
MAURITIUS				
Plaesius javanus	1959	Trinidad	–	Bennett et al. 1976
	?	Trinidad	–	Gomy 1983
Hololepta quadridentata	1942	Trinidad	–	Bennett et al. 1976
	1959	?	–	Clausen 1978

Table 4.5.2 (cont'd) Introductions for the biological control of *Cosmopolites sordidus*

Country and species	Liberated	From	Result	Reference
MEXICO				
Plaesius javanus	1955	?	+	Barrera & Jiminez 1994; Greathead 1971
NEW CALEDONIA				
Plaesius javanus	1949	Fiji	+	Dumbleton 1957
PALAU IS				
Dactylosternum hydrophiloides	1948	Malaysia	–	Dumbleton 1957
Hololepta sp.	1953	?	–	Dumbleton 1957
PUERTO RICO				
Plaesius javanus	1936	?	–	Greathead 1971
SAMOA				
Plaesius javanus	1957	Fiji	+	Dale and Herring 1959
SEYCHELLES				
Plaesius javanus	1952	Trinidad	–	Greathead 1971
Hololepta quadridentata	1952	Trinidad	–	Greathead 1971
ST LUCIA				
Hololepta quadridentata	1950–1954	Trinidad	–	Cock 1985
Plaesius javanus	1950–1954	Trinidad	–	Cock 1985
ST VINCENT				
Dactylosternum subdepressum	1950–1954	Trinidad	–	Cock 1985
Hololepta quadridentata	1942	Trinidad	+	Bennett et al. 1976
Plaesius javanus	1981	Trinidad	–	Cock 1985

Table 4.5.2 (cont'd) Introductions for the biological control of *Cosmopolites sordidus*

Country and species	Liberated	From	Result	Reference
TAIWAN				
Plaesius javanus	1938	?	–	Greathead 1971
TANZANIA				
Plaesius javanus	1948	?	–	Greathead 1971
TONGA				
Plaesius javanus	1952	Fiji	– +	Dumbleton 1957 O. Fakalata pers. comm.
TRINIDAD				
Plaesius javanus	1942	Jamaica	+ –	Bennett et al. 1976 Sirjusingh et al. 1992
UGANDA				
Plaesius javanus	1934–35	Java	–	Greathead 1971
VANUATU				
Plaesius javanus	?	?	?	Anon. 1979a
WALLIS IS				
Plaesius javanus	1947	Fiji	?	Cohic 1959

The predatory hydrophilid beetle *Dactylosternum hydrophiloides* from Malaysia was liberated in 1939 and has become established but has not had a major effect on weevil abundance (Wilson 1960).

Braithwaite (1958) reports an unusual native predator of *C. sordidus*, a blue planarian worm *Kontikia* (= *Geoplana*) *caerulea*, which lives in moist sheltered situations. It sucks out the body fluids of its prey, leaving the cuticle intact.

CAMEROON, MAURITIUS, SEYCHELLES, UGANDA

Both *P. javanus* and *Hololepta quadridentata* were supplied from Trinidad to Cameroon (1952), Mauritius (1959) and the Seychelles (1950–54) and *P. javanus* from Java to Uganda in 1934–35. Neither species became established (Greathead 1971).

COOK IS

Although only *Plaesius javanus* is recorded as having been introduced from Fiji into the Cook Is during the period 1937 to 1940, voucher specimens (DSIR, NZ) show that *Plaesius laevigatus* was also present in the material liberated and both species still occur in the Cook Is, although the latter does not appear in voucher specimens in Fiji. Unfortunately the banana weevil borer is still an important problem (Walker and Deitz 1979; Waterhouse 1995, 1997).

CUBA

In Cuba the ant *Tetramorium bicarinatum* (= *T. guineense*) was found to be capable of destroying up to 65% of *C. sordidus* in heavily infested plantations. With lower populations, 73.8% and 83.5% control was obtained in successive years. For colonisation of a plantation in 3 to 4 months, ants should be released over 25% to 30% of the area (Roche and Abreu 1983). The ant is a more effective predator during the dry than the wet season (Lopez and Ramos 1986). In countries where this widespread ant is already present (e.g. the Americas, Africa, Papua New Guinea, Australia, the oceanic Pacific) it might well be considered for manipulating *C. sordidus* abundance, but very careful consideration should be given to any proposal to introduce such an agressive broad-spectrum predator into a new country.

INDIA

The predatory beetle *Dactylosternum hydrophiloides* was introduced from Malaysia in 1948, but there is no record of the outcome (Whilshaw 1949).

JAMAICA

Although an initial release in 1918–19 of *Plaesius javanus* from Java was unsuccessful, this predator became established as a result of a further release of Fijian material in 1937–38 (Bennett et al. 1976). More recently Sirjusingh et al. (1992) recorded that it was no longer present.

MYANMAR

There do not appear to be any records in Myanmar of natural enemies of *C. sordidus* which is very uncommon and apparently confined to aromatic and sweet-flavoured banana varieties. Control is achieved by cutting the pseudostems every three years, a practice readily accepted because the stems are used in Mohinga, a popular fish soup (H. Morris pers. comm. 1994).

PAPUA NEW GUINEA

Bananas are grown widely and are the staple food in some areas but *C. sordidus* is not a serious pest. The ant *Tetramorium bicarinatum* occurs there but there is no information on any possible interaction with *C. sordidus* (J.W. Ismay pers. comm. 1985).

TRINIDAD

P. javanus was established in Trinidad in 1942 and, from there, together with a native histerid *Hololepta quadridentata*, it was sent to other islands in the West Indies. Evidence of establishment was not available to Simmonds (1958) but, in 1972, *H. quadridentata* was recovered in St Vincent (Bennett et al. 1976).

OTHER COUNTRIES

Although details are not available, *P. javanus* has been widely distributed and is reported to be established in French Polynesia, Marianas, New Caledonia (where chemical control is still required) (Delobel 1977; Clausen 1978; M. Kauma pers. comm. 1985) and Tonga (O. Fakalata pers. comm. 1985). It is also widespread on Upolu Is, Samoa (T.V. Bourke pers. comm. 1986).

In addition to the records in table 4.5.2, Sirjusingh et al. (1992) list a number of predators for Central or South America (Table 4.5.3). However, it is seldom clear which of these may be introductions (intentional or otherwise) from elsewhere and which are native to the region, as some almost certainly are. Their biological control potential has not been assessed.

Table 4.5.3 Additional natural enemies of *C. sordidus* in Central and South America

Insect	Country	?Native
DERMAPTERA		
LABIIDAE		
Carcinophora (= *Psalis*) americana	Brazil	probably
Euborellia annulipes	Brazil	?
HEMIPTERA		
CYDNIDAE		
Geotomus pygmaeus	Brazil	probably not
MIRIDAE		
Fulvius nigricornis	Brazil	probably not
NABIDAE		
Phorticus pygmaeus	Brazil	probably not
REDUVIIDAE		
Physoderes curculionis	Brazil	probably not
COLEOPTERA		
CARABIDAE		
Galerita bicolor	Florida	probably
Scarites spp.	Florida	probably
HISTERIDAE		
Hololepta spp.	St Vincent	possibly
Lioderma sp.	Brazil	probably
Platysoma abrupta	Brazil	probably not
HYDROPHILIDAE		
Dactylosternum abdominale	Trinidad	probably not
D. hydrophiloides	Trinidad	probably not
D. intermedium	Trinidad	probably not
D. profundus	Trinidad	probably
Omicrogiton insularis	Brazil	probably not
SILVANIDAE		
Cathartus sp.	Brazil	(not established)
STAPHYLINIDAE		
Belonuchus ferrugatus	Brazil	(not established)
B. quadratus	Brazil	probably not
Priochirus (= *Leptochirus*) *unicolor*	Brazil	(not established)
DIPTERA		
RHAGIONIDAE		
Chrysopilus sp.	Brazil	(not established)

Biology of main natural enemies

Dactylosternum abdominale Col.: Hydrophilidae

This is the most effective predator in Kenya. Its larvae are polyphagous predators and consume the contents of *C. sordidus* larvae and at high predator density may become cannibalistic. They also feed on the micro-fauna and micro-flora of decomposing plant tissues. On the other hand, the adults cause significant mortality of *C. sordidus* eggs; although many are laid in inaccessible positions inside the pseudostem and the polyphagous adults do not specifically search for eggs. Adults cannot penetrate the narrow tunnels of young larvae, so can only capture newly hatched larvae: later instar larvae are not attacked (Koppenhöfer and Schmutterer 1993; Koppenhöfer et al. 1992, 1995). Development from egg to adult takes 17 to 33 days, life span is 95 days and females lay an average of 1.7 egg cases per week, each case containing 4 eggs. The preoviposition period is 16.6 days (Koppenhöfer et al. 1995).

Geotomus pygmaeus Hem.: Cydnidae

This predator is recorded from India, Ceylon, Myanmar, Indonesia, Vietnam, China, Japan, New Caledonia, Fiji, Samoa, French Polynesia and Hawaii. Its extensive distribution is probably due to its ready transportation in the soil attached to the roots of cultivated plants. Although reported to attack *C. sordidus* eggs in Malaysia, China (1935) suggests that this species normally is unlikely to be a predator.

Plaesius javanus Col.: Histeridae

The predatory larvae and adults of this Indonesian beetle attack larvae and pupae of *Cosmopolites sordidus* and many other soil and litter-inhabiting insects. Eggs are laid singly in old banana stumps, at the base of the stem and on the rhizome below the soil surface. The eggs hatch in 8 to 9 days, producing active, voracious larvae which feed for 5 to 6 months, older larvae being capable of consuming up to 30 or more *C. sordidus* larvae per day. A prepupal period of 10 to 15 days is passed in a pupation cell constructed in the soil, followed by a pupal stage of about 14 days. The adult remains in the cell for 7 to 10 days before emerging and is then capable of consuming 7 or 8 weevil larvae per day (Clausen 1978; Jepson 1914; Weddell 1932).

Thyreocephalus interocularis Col.: Staphylinidae

This is the second most effective predator on *C. sordidus* larvae in Kenya. Both adults and larvae are polyphagous. In the absence of other hosts adults may prey on their own larvae and larvae are also occasionally cannibalistic (Koppenhöfer and Schmutterer 1993). After a pre-oviposition period of 32 days, females lay an average of 31 eggs in decomposing banana pseudostems and in moist soil below banana mulch. Pupation occurs in the soil. Total development time averages 46 days and adults live an average of 142 days (Koppenhöfer 1994).

Comments

Although weevils, as a group, seem to be poor candidates for biological control, the establishment of *Plaesius javanus* and *P. laevigatus* in Fiji appears to have reduced the pest status of *Cosmopolites sordidus* there. Introductions of *P. javanus* (Table 4.5.2) have resulted in successful establishment (but often not at the first attempt) in Cook Is, French Polynesia, Jamaica, Marianas, Mauritius, New Caledonia, Samoa and Trinidad, but no information is available on the effects it has produced. Introductions have been unsuccessful in Australia, Cameroon, Dominica, Honduras, Mauritius, Mexico, Puerto Rico, Seychelles, St Lucia, St Vincent, Taiwan, Tanzania, Tonga and Uganda (Bartlett 1937; Miwa 1938; Clausen 1978). Based on his observation and that of others, Koppenhöfer (1993a,b, Koppenhöfer and Schmutterer 1993) considered that the biology of *P. javanus* does not enable it to have any greater effect and that studies are necessary of the potential impact of proposed predator species before release. Two other predators have been established, one in Australia and one in Jamaica and St Vincent, but seemingly without much effect.

If the beneficial effects of *P. javanus* (and *P. laevigatus*) in Fiji can be confirmed, it may be worth renewing efforts to establish them in other countries where *C. sordidus* is a major pest. Otherwise, resources available for biological control might be better deployed searching for, and evaluating, other natural enemies.

It is possible that entomopathogenic nematodes (CSIRO 1993; Treverrow and Bedding 1993a) or fungi may hold some promise as biological pesticides. Nematodes generally have far less capability for self-perpetuation and dispersal in the environment than imported arthropod enemies, but they can be highly effective. However, in many tropical countries where bananas are a major staple food the distribution and application of mass-produced biological control agents, such as nematodes or fungi, is often impracticable because of storage and transport problems and lack of suitable equipment for application. In addition, like insecticides, they may be too costly for subsistence farmers who constitute the majority of banana producers. Even if it only leads to a partial (but still significant) reduction in pest status, classical biological control is, under these circumstances, a particularly appropriate approach to reduce losses.

4.6 *Deanolis sublimbalis*

The red banded mango caterpillar, *Deanolis sublimbalis* tunnels in the flesh and seed of the fruit of mango, *Mangifera indica*, and also attacks the fruit of *M. odorata*, *M. minor* and *Bouea burmanica*. It is reported from India eastwards to Southeast Asia, southern China and Papua New Guinea. In this vast region there are scattered reports of damage ranging up to 50 per cent of fruit, but many areas within it from which there are no reports of damage or even of its presence.

The only records of natural enemies are of two trichogrammatid egg parasitoids and a vespid larval predator, all in the Philippines. Further searches would be necessary before the potential of classical biological control could be evaluated, especially for infestation in new areas into which it has spread in recent years.

Deanolis sublimbalis Snellen

Lepidoptera: Pyralidae: Odontinae

red banded mango caterpillar, red banded borer

Synonyms

Long known as *Noorda albizonalis* Hampson 1903 or *Autocharis albizonalis* (Hampson), this species should be referred to as *Deanolis sublimbalis* Snellen, because of the priority of its description (Snellen 1899) (M. Shaffer pers. comm. 1997) from specimens collected in Celebes (now Sulawesi). He also referred to two females from Batavia (now Jakarta). Hampson's type specimen (Hampson 1903), labelled Darjiling, is in the British Museum (Natural History) (BMNH); and the distribution of his species was given as Sikkim; Celebes, Palos B., Dongola (Doherty). Dongola is currently spelt Donggala and is at the southern headland of Palos bay at the head of which is Palu. Doherty's obituary (Hartent 1901) reveals that he collected there in August and September 1896.

Rating

Southeast Asia			**China**			**Pacific**		
3	++	Phil	2	++	Yunnan Province	2	++	PNG
	+	Thai						
	P	Brun, Indo						

Origin

The origin of mango (*Mangifera indica*) is believed to be in the India-Myanmar region, from which it might be inferred that *D. sublimbalis* also evolved within this region, unless it has transferred to *M. indica* from a related plant.

Distribution

India, Myanmar, Thailand, China (Yunnan Province: Li et al. 1997), Brunei, Philippines, Indonesia (Java, Sulawesi, Irian Jaya), Papua New Guinea, Torres Strait (Dauan Is, Saibai Is: AQIS 1991; NAQS 1993) (Fenner 1987; Singh 1987).

It is apparently not known in Pakistan (M.A. Poswal pers. comm. 1997), Sri Lanka (J. Edirisinghe pers. comm. 1997), Nepal (Neupane 1995) or Peninsular Malaysia (Yunus and Ho 1980; Tan Chai-Lin pers. comm. 1997) and does not occur on the Australian mainland or in the oceanic Pacific. It is widely distributed throughout Papua New Guinea coastal mainland and islands (F. Dori pers. comm. 1997).

Specimens in the BMNH carry the following labels

India:	Darjiling (now Darjeeling) Calcutta 22 March, 1945 Orissa March, 1952
Myanmar:	Rangoon March, 1923
Thailand and Philippines:	no dates
Brunei:	12 April, 1973, 5 September 1992
Indonesia:	Java August, 1922 (Koepoedan) Sulawesi (Minahassa, Tomohon). Irian Jaya July, 1936 (Cyclops Mts, Sabron 2000ft)
Papua New Guinea:	Kokoda August, 1933;

and in the Australian National Insect Collection the following labels:

Papua New Guinea:	Finisterre Range 23 June–21 July, 1958 (Gabumi, 2000ft) Telefomin 2 May and 18 June, 1959 (Feramin 4700ft) 2 May–18 June Port Moresby 5 March–12 May, 1963 (Mt Lawes 1300ft)

Biology

Referring presumably to the major (summer) crop of mangos, Fenner (1987) and Golez (1991a) comment that the eggs are oval, waxy white and generally laid in masses near the apex of the developing fruit. However F. Dori (pers. comm. 1997) reports that, in the winter (July) crop near Port Moresby (PNG), eggs were white to crimson. They were laid in groups of 1 to 4 near or on the peduncle at the base of the fruit and sometimes covered by the sepals or deposited in small crevices in the fruit. On hatching, larvae travel to the apex to enter the fruit. Oviposition occurs as early as 45 to 55 days after flower induction and continues up to fruit maturity. After an egg incubation period of 3 to 4 days, larvae hatch and pass through 5 instars in the next 14 to 20 days. The larva has a brown or black head and white body with red segmental bands. It feeds first in the pulp of the fruit (1st and 2nd instars) and later in the seeds. The tunnels formed gradually broaden as the larvae grow to about 2 cm in length. Fruit in all stages of development from marble size upwards are attacked. As many as 11 larvae may be found in a fruit, although there is commonly only one. A pre-pupal stage lasts about 2 to 3 days and pupation occurs in a silk-lined earthern cocoon. In wooden cages in Papua New Guinea, larvae pupated in strongly spun cocoons covered with particles of chewed wood, suggesting that pupation on bark may occur in the field. In India, Sengupta and Behura (1955, 1957) record pupation generally inside the fruit, the moth emerging through an exit hole. The pupal period lasts from 9 to 14 days, so that the total period from egg to adult takes from 28 to 41 days. Adult longevity is 8 to 9 days. Adult males can be distinguished from females by having expanded dark brown, hairy, mesothoracic tibiae (Leefmans and Van der Vecht 1930; Voûte 1936; Kalshoven 1981; Fenner 1987, 1997; Golez 1991a).

Adults are generally nocturnal and, during the day, spend most of their time resting under leaves on the tree. They are seldom attracted to light. Females prefer to oviposit on fruit protected from direct light. Newly hatched larvae stay together and tunnel into the fruit near where the eggs were laid. If later instar larvae are crowded, some may leave by suspending themselves on silken threads, which also facilitate transfer to other fruits. A shorter developmental period was observed for both males and females reared on the pulp than on the seed of carabao mangoes, although those reared on the seeds were larger and lived longer, females producing more eggs. Development differed slightly on different mango varieties (Golez 1991a).

In cages in Papua New Guinea only a small proportion of pupae yielded adults in the several months after pupation, suggesting a pupal diapause which may synchronise the life cycle with the seasonal fruiting of its host (Fenner 1987, 1997).

Host plants

The commonest host, wherever *D. sublimbalis* occurs, is *Mangifera indica*, but there are records also from *M. odorata* in Papua New Guinea and Indonesia from *M. minor* in Papua New Guinea (F. Dori pers. comm. 1997). and from *Bouea burmanica* in Thailand (Beller and Bhenchitr 1936). All four belong to the family Anacardiaceae (Sengupta and Behura 1955; Kalshoven 1981; M. Schaffer pers. comm. 1997). Larvae are unable to develop on parts of the mango tree other than the fruit, or in the fruit of avocado, chico, guava, jackfruit, papaya, santol, sineguelas or star apple (Golez 1991a). However, as the genus *Mangifera* contains many species it is quite possible that further wild hosts will be found (Fenner 1997). Indeed the label data, quoted earlier, on specimens collected well outside the major fruiting season of *M. indica* suggests that this may well be so. The genus *Mangifera* contains about 62 species of tall evergreen trees which are native to the area stretching from India to Papua New Guinea, with the greatest number in the Malay Peninsula. Fifteen species bear edible fruit, but only *M. indica* is widely planted of the 6 species sometimes cultivated. *M. indica* probably originated in the Indo-Myanmar region and grows wild in the forests of India, particularly in hilly areas in the northeast. It has been grown throughout the Indian sub-continent for at least 4000 years. It was probably taken to Malaysia and eastwards further into Southeast Asia between 300 and 400 AD and there are now many commercial varieties (Purseglove 1968).

Damage

Mango fruit in all stages of development are attacked, often leading to premature drop. First and second instar larvae feed on the tissues beneath the skin, making tunnels towards the seed. Larger larvae destroy the seed. Soon after boring starts, secondary infestations of bacteria, fungi, fruit flies (e.g. *Bactrocera ferrugineus*, *B. frauenfeldi*), and other pests occur. Liquid exudes from the skin of attacked fruit at the opening of the entry tunnel and trickles down to the drip point where it accumulates. It rapidly darkens to form a characteristic black spot, often about 1cm in diameter at the tip of the fruit (Fenner 1987). Another common sign of borer damage is the bursting of the apex and longitudinal cracking of the fruit. In Guimaras Province (Philippines), up to 12.5% fruit infestation was recorded by Golez (1991a), with up to 14.5 larvae occurring per kg fruit. In years of serious infestation, yield could be reduced by as much as 40 to 50 per cent (Tipon 1979). In Papua New Guinea, fruit infestation levels of greater than 20% are encountered in the Port Moresby area (F. Dori pers. comm. 1997; T.L. Fenner pers. comm. 1997). In India the seeds are used as human food in times of famine and a flour is made from them (Purseglove 1968).

However, for an insect that can be significantly damaging to mango fruit, it is remarkable that there are so very few references to it in the literature. It is, perhaps, instructive to list those that are directly relevant, so as to contribute to determining (i) whether it has, for many years, frequently been overlooked as a pest, (ii) whether it has spread to new areas in recent times, (iii) whether it has only become a pest of edible mangoes in recent times, (iv) whether suppression by natural enemies is no longer as effective as it once was and/or (v) whether there are other reasons.

D. sublimbalis must have been present in northern India before it was described in 1903 (Hampson 1903), although it was not mentioned in the books by Maxwell-Lefroy and Howlett (1909), Fletcher (1914) or Ayyar (1963) all dealing with insects of agricultural importance in India. It was, however, reported a little later by Wadhi and Batra (1964) who referred to papers by Sengupta and Behura (1955, 1957) and Sengupta and Misra (1956). It was also reported, briefly, by Nair (1975) and, in more detail, by Butani (1979). Strangely, the above Sengupta and Behura (1955) reference lists *D. albizonalis* among *new* records of crop pests in Orissa and then only of grafted mangoes in Puri District, implying that it was not known much earlier there as a damaging species. Furthermore, only recently (Zaheruddeen and Sujatha 1993) was *D. sublimbalis* recorded as having caused serious losses to mango fruits from marble size to maturity in Godavari Districts of Andhra Pradesh.

Although a specimen was collected in Rangoon in 1923 (BMNH), *D. sublimbalis* was not listed by Ghosh (1940) in his major work 'Insect Pests of Burma' or by Yunus and Ho (1980) in Malaysia when dealing with economic pests from 1920 to 1978. This striking absence of records from peninsular Malaysia continues to this day (Tan Chai-lin pers. comm. 1997). Nevertheless, *D. sublimbalis* has been well known in Thailand since 1936 (Beller and Bhenchitr 1936; Cantelo and Pholboon 1965; Wongsiri 1991; Kuroko and Lewvanich 1993).

In the Philippines it was not recorded by Cendana et al. (1984) in 'Insect Pests of Fruit Plants in the Philippines', so it was evidently not generally regarded as a pest at that time, although a paper recording 40 to 50% damage in bad years had been delivered 5 years earlier (Tipon 1979). A comprehensive account of up to 12.5% infestation of fruit in Guimaras Province was published in 1991 by Golez (1991a,b).

In contrast, in Indonesia it was present prior to 1899 (Snellen 1899) and has been well known as a mango pest since 1930 (Leefmans and van der Vecht 1930). Its damaging presence there is also documented by Vote (1936) and Kalshoven (1981).

D. sublimbalis has been known in Irian Jaya since 1936 (BMNH specimen) and was common in mangoes in Jayapura in the early nineties (T.L. Fenner pers. comm. 1997). It was collected in Papua New Guinea (Kokoda) in 1933 (BMNH specimen) and was recorded again in 1958, 1959 and 1963 (ANIC specimens) and is common nowadays in Port Moresby. It was first recorded on Australian islands in Torres Strait (Saibai I) in 1990 and again in October 1996 (at a level of about 1% infestation on Dauan I) (Australian Quarantine Inspection Service).

Natural enemies

Leefmans and van der Vecht (1930) commented that no parasites had been bred in their studies on *D. albizonalis* in Java.

In Luzon (Philippines) the egg parasitoids *Trichogramma chilonis* and *T. chilotraeae* (Table 4.6.1) were recorded by Golez (1991a) who reported, however, that no parasitoids were encountered at that time in the three municipalities of Guimaras, all of which had dry, dusty and windy conditions.

Golez (1991a) reported that predation in Guimaras occurs as larvae leave the fruit, either to migrate to another fruit or to pupate in the soil. The most important predator was the vespid *Rhychium attrisium* which appeared to be the main cause of the high larval disappearance that occurs. *R. attrisium* is abundant in summer, especially during warm sunny days.

Larvae were attacked by a fungus in the laboratory in Indonesia (Leefmans and van der Vecht 1930). The wasp *Evania appendigaster* is reported as a larval/pupal parasite (Golez 1991b), but Fenner (1997) points out that this record needs confirmation since the Evaniidae are reportedly all parasites of cockroach eggs.

A tachinid, *Carcelia* (*Senometopia*) sp., was reared from mango fruit possibly infested with *D. sublimbalis* near Nodup in September 1982 (J. Ismay pers. comm. 1997) and also from a *D. sublimbalis* larva near Rabaul (both Papua New Guinea) in 1984 (F. Dori pers. comm. 1997).

Table 4.6.1 Natural enemies of *Deanolis sublimbalis*

Species	**Location**	**Reference**
DIPTERA		
TACHINIDAE		
Carcelia sp.	Rabaul (PNG)	F. Dori pers. comm. 1997
HYMENOPTERA		
TRICHOGRAMMATIDAE		
Trichogramma chilonis	Philippines	Golez 1991a
Trichogramma chilotraeae	Philippines	Golez 1991a
EVANIIDAE		
Evania appendigaster		Golez 1991b
VESPIDAE		
Rhychium attrisium	Philippines	Golez 1991a

Comment

It is tempting to postulate that the damage that is actually due to the red banded mango caterpillar is commonly attributed to other causes. Perhaps this is due, in part, to the fact that larvae have often left the fruit before the cause of damage is investigated although, with a larval duration of 2 to 3 weeks, this would be surprising, particularly when there is a characteristic dark spot for much of this time at the drip point of the mango fruit.

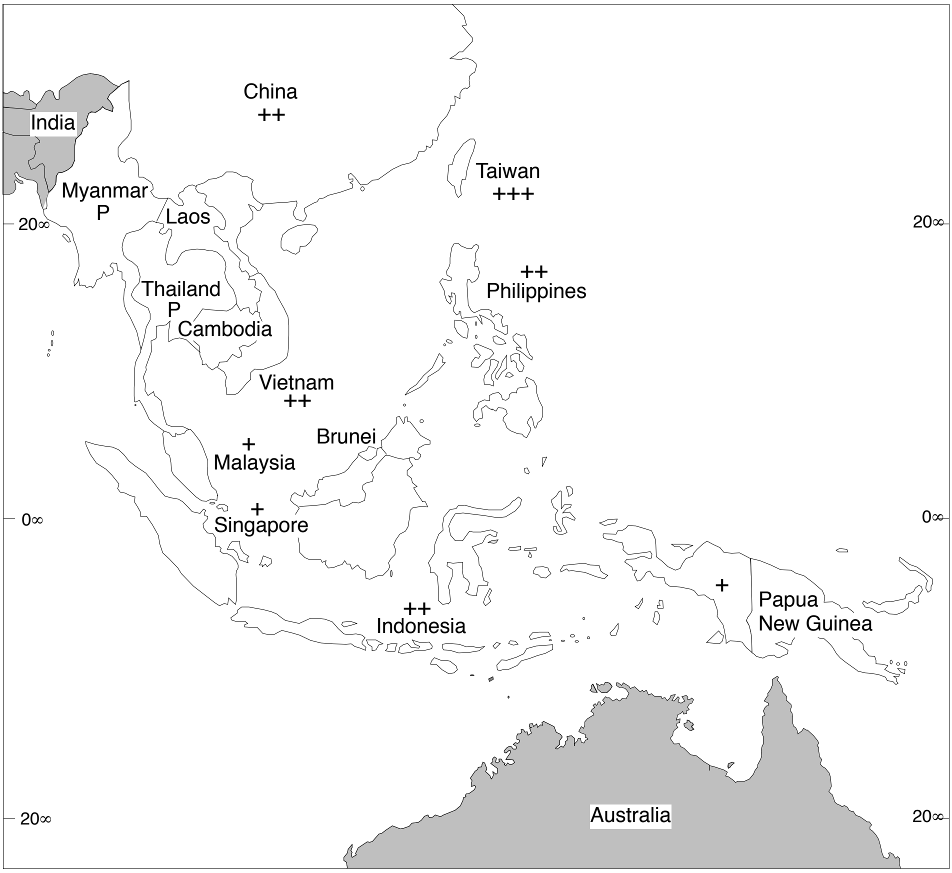
The absence of records of its presence over vast areas within its distribution range suggests that its abundance must be very low (perhaps due to inhospitable host varieties or effective biological control) or, perhaps, that it does not occur there.

The only record of effective chemical control is of 4 applications of cyfluthrin or deltamethrin at 60, 75, 90 and 105 days after fruit induction (Golez 1991a).

Further research for natural enemies attacking eggs, larvae and pupae within its long established range would be necessary to determine whether any are likely to be promising for biological control.

If, as is very probable, *D. sublimbalis* produces a sex pheromone, its availability as a lure would be of great value as a means of monitoring the presence and distribution of the red banded mango caterpillar in mango and other hosts. Its identification, synthesis and availability should have high priority.

4.7 Diaphorina citri



The citrus psyllid *Diaphorina citri* is native to the Indo-Malaysian region, but has spread outside it to Réunion, Mauritius, Saudi Arabia, Honduras, and Brazil. The sap it removes from new flushes of citrus growth is of minor consequence, but it is the vector of a devastating bacterial disease, citrus greening.

Its major controlling factors are high rainfall (washing off eggs and young nymphs) and two parasitoids, *Tamarixia radiata* and *Diaphorencyrtus aligarhensis*. Where these parasitoids are native they are very heavily attacked by hyperparasitoids which diminish their effectiveness. Freed of these hyperparasitoids *T. radiata* has been established in 3 countries where it was not present: Réunion, Madagascar and Taiwan, resulting in excellent biological control. Although *T. radiata* appears to be widespread in Southeast Asia, observations might well disclose regions where it is not present and could be introduced with advantage. The prospects for successful biological control of *D. citri* are good when it invades regions where hyperparasitoids of *T. radiata* are absent or deficient.

Diaphorina citri Kuwayama

Hemiptera, Psyllidae
citrus psyllid, Asian citrus psyllid

Rating

Southeast Asia			China	Southern and Western Pacific
8	++	Viet, Indo, Phil	3+++	absent
	+	Msia, Sing		
	P	Myan, Thai		

These Southeast Asian ratings arose from an earlier survey of country opinions (Waterhouse 1993b) and may not reflect current assessments.

Origin

The Indo-Malaysian region. *D. citri* was described from Punjab, India (Waterston 1922). There is evidence of recent spread into the southeastern and eastern portions of Southeast Asia.

Distribution

D. citri is widespread from Afganistan eastwards through Pakistan, India, Nepal and Bhutan to Southeast Asia, southern China (up to about 30°N, Xie et al. 1988), Taiwan (Catling 1970; Tsai et al. 1984; Aubert 1990) and the Ryuku Is (Japan) (Miyakawa and Tsuno 1989). It has recently become established in Ende (Flores) and Timor and in Irian Jaya (Aubert 1989b, 1990). *D. citri* was collected in June 1993 in the Jayapura area of Irian Jaya and citrus there showed symptoms of greening (Northern Australia Quarantine Strategy 1993). It has been introduced to Réunion, Mauritius, Comoro Is (Hollis 1987), Saudi Arabia (Wooler et al. 1974), Yemen (Bové 1986), Brazil (Silva et al. 1968; Bergmann et al. 1994) and Honduras (Burckhardt and Martinez 1989). In 1990 there were still limited areas free of *D. citri* in east Mindoro (Philippines) and Palau and Tambun (Malaysia). It is not yet recorded from Papua New Guinea and does not occur in Australia, the Oceanic Pacific or North America.

In Réunion it has not colonised citrus plantings above 800 m, where the lowest temperature is 7°C, whereas in Malaysia the height limit is 1200 m with a minimum temperature of 14°C.

Biology

D. citri survives a wide range of temperature extremes from 45°C in Saudi Arabia to –7° to –8°C in China, thereby tolerating cold that will kill citrus (Xie et al. 1989a). Far more than temperature, high humidity and rainfall are important limiting factors, rain by washing off eggs and early instar nymphs and humidity by favouring fungal attack. These two factors are mainly responsible for the low *D. citri* populations on the windward (rainy) side of Mindoro (Philippines) and Réunion (Aubert 1989a).

There have been several studies on the life cycle of *D. citri*, which conform generally with the results in Table 4.7.1, leading to up to 11 generations a year in Fujian Province, China (Xu et al. 1988b, 1994). *D. citri* has a short life cycle and high fecundity and is commonest in hot coastal areas. Mating commences soon after the insects become adult and, after a pre-oviposition period of about 12 days, eggs are laid singly inside half-folded leaves of buds, in leaf axils and other places on the young tender shoots. Average adult lifespan is 30 to 40 days, although overwintering adults had a lifespan of 260 days (Xu et al. 1994).

Table 4.7.1 Bionomics of *D. citri* (average in days) in Fujian Province, China (Xu et al. 1988b)

	Adult life-span		Eggs per female	Incubation	Nymphal development	Egg–adult
	Max	Min				
Spring	96	28.1	17.7	10	31.8	42
Summer	46	19.7	43.8	2	10.3	13
Autumn	59	31.6	22.6	4	16.8	21
Winter	131–165					

The abundance of both eggs and nymphs is correlated with the availability of new growth flushes and breeding is largely suspended when trees become dormant. On its favoured host plant *Murraya paniculata* in Fujian, populations may average 51 adults per young shoot and a 4-year-old plant produces 900–1000 shoots. On mandarin (*Citrus reticulata*) the average colony size is 20 per shoot, with 600 to 650 shoots, and peak abundance occurs about 6 weeks later than on *M. paniculata* (Aubert 1990). *D. citri* nymphs develop well under cool, humid spring conditions, but are seriously affected by fungal infections under hot, humid conditions. On *M. paniculata*, adult numbers were highest on leaf midveins (43%), followed by petioles (30.7%), leaf blades (23.7%) and stems (2.6%) (Tsai et al. 1984).

D. citri nymphs normally lead a sedentary existence clustered in groups, but will move away when disturbed. Adults are 2.5 mm long and jump when disturbed, whereupon they may fly up to 5 m before settling again. Seasonal migratory flights occur when adults fly up to about 7 m above ground level, entering mild winds which may carry them up to 4 km distant (Aubert 1990). Flying adults are attracted to yellow traps, which have been used for sampling (Aubert and Xie 1990). Adult *D. citri* have yellowish-brown bodies, greyish-brown legs and transparent wings. They have white spots or are light brown with a broad, beige, longitudinal, central band.

Host plants

D. citri feeds and breeds on the entire group of horticultural *Citrus*, with additional hosts in eight different genera belonging to the Aurantoidea (Aubert 1990). *D. citri* thus has a wider host range than the greening organism it transmits to citrus (see Damage). An indication of the relative suitability of its various host plants is shown in Table 4.7.2, although there may be local modifications of the groupings. This is probably due to different *D. citri* biotypes. For example, unlike Réunion populations, Malaysian populations breed well on *Bergera koenigii* and, in the Philippines, adults are more attracted by *Clausena anisumolens* than by *Murraya paniculata* (Aubert 1990). Overall, jasmin orange, *Murraya paniculata,* is the preferred host and this plant is widely grown in Southern and Southeast Asia as an ornamental shrub and hedge plant.

Damage

Although sap removal by large populations of *D. citri* can cause young foliage on flushes of growth to wilt, by far the most damaging effect of feeding is due to the transmission of a gram-negative bacterium which is the cause of citrus greening, known as huanglungbin in China (Xu et al. 1988a). Citrus greening is known to affect 3 genera of the subtribe Citrinae, namely *Citrus*, *Poncirus* and *Fortunella* (Aubert 1990). It has also been experimentally transferred from *Citrus* to Madagascar periwinkle (*Catharanthus roseus* (Ke 1987). Once infected with the bacterium, *D. citri* remains infective for its lifetime, but does not pass on the infection transovarially. Amongst citrus, pummelo and lemon are less affected by greening than most other species. *D. citri* is the only known vector of citrus greening in Asia, although several other psyllids attacking citrus have been described: *D. auberti* (Comoro Is: Hollis 1987), *Psylla citricola*, *P. citrisuga* and *Trioza citroimpura* (China: Yang and Li 1984) and *Psylla murrayii* (Malaysia: Osman and Lim 1990).

Table 4.7.2 *Diaphorina citri* host plants (after Aubert 1990)

		Leaf sucking	Egg laying	Nymphal development
Preferred host plant	*Murraya paniculata* (jasmin orange)	+++	+++	+++
Good host plants	*Citrus aurantifolia* (lime)	+++	+++	+++
	Bergera (Murraya) koenigii (curry bush)			
Common host plants	*Citrus limon* (lemon)	++	++	++
	Citrus sinensis (sweet orange)			
	Citrus medica (citron)			
	Citrus reticulata (mandarin)			
	*Microcitrus australisiaca**			
	Citrus maxima var. *racemosa* (pummelo)			
	Citrus hystrix (*Mauritius papeda*)			
	Citrus madurensis			
	Clausena excavata			
	Clausena lansium			
Occasional host plants	*Citrus maxima* (pummelo)	+	+	+
	*Triphasia trifoliata**	+	+	+
	Fortunella sp.* (kumquat)	+	+	+
	*Poncirus trifoliata**	+	+	–
	Clausena anisumolens (anise)	+	+	+
	*Merrillia caloxylon**	+	–	–
	*Toddalia asiatica**	+	–	–

Table 4.7.2 (cont'd) *Diaphorina citri* host plants (after Aubert 1990)

		Leaf sucking	**Egg laying**	**Nymphal development**
Occasional host plants	*Vepris lanceolata**	+	–	–
	*Swinglea glutinesa**	+	unknown	unknown
	Atalantia sp.	+	unknown	unknown
	*Clausena indica**	+	unknown	unknown
	*Murraya exotica**	+	unknown	unknown

Citrus species hosts are, according to the classification of Jones (1990):

+++ very common;
++ usual
+ occasional;
– complete life cycle not observed

*observations on caged insects

In Africa, Réunion, Madagascar and Saudi Arabia another psyllid *Trioza erytreae* transmits a slightly different citrus greening organism (see later under Réunion).

Citrus greening is believed to have originated in northeastern Guangdong Province (Lin and Lin 1990). Amongst other symptoms, the leaves of new green shoots first turn yellow at their base, then often become mottled yellow and drop. The branches remain small, upright and stiff. Diseased trees flower abundantly in the off-season and flowers drop readily or result in small, irregular fruit whose base turns red before the remainder changes from green (Ke 1987). Citrus greening is widespread throughout South and Southeast Asia, where it is almost always the most serious disease of citrus. It is spread to new areas by infected nursery plants or infected budwood and within orchards by *D. citri* (Capoor et al. 1967; Whittle 1992). However, *D. citri* has been intercepted by quarantine in France on citrus imported from Honduras (Burckhardt and Martinez 1989). The tonnage of citrus produced worldwide is second as a fruit crop only to that of grapes (Aubert 1987b). An extremely serious citrus disease which already affects nearly 50 countries in Asia and Africa must, therefore, be regarded as of major importance. It is reported that a total of over a million trees are destroyed each year in China, Thailand, Malaysia, Indonesia and Philippines alone (Aubert 1987a). In Indonesia citrus greening has caused the loss of many millions of trees. Small farmers are frequently reluctant to remove declining trees before they almost cease bearing. This tends to increase *D. citri* populations, which breed on young flush since a symptom of greening is unseasonal flushing (Whittle 1992). The recent history of production in northern Vietnam, where citrus is grown mainly in larger orchards or state farms, is typically cyclical, with the gradual destruction of trees by greening and then wholesale removal and replanting. A new cycle of planting commenced in the late 1980s, but greening is already to be seen in many young orchards, although populations of *D. citri* are still low (Whittle 1992). Only by keeping populations at very low levels by biological control and/or insecticides will the rate of spread of greening be diminished. Insecticides are said to be highly cost effective if used only during a restricted flushing period, but if needed frequently they are very costly and environmentally undesirable. Recent developments with carefully specified, highly refined petroleum oils has given high levels of control of *D. citri* (A. Beattie pers. comm. 1995), with presumably little direct effect on its parasitoids. Whittle (1992) reported that he was unable to find *D. citri* in the vicinity of Ho Chi Minh City (southern Vietnam), a very unusual situation for an area with a fairly long history of citrus cultivation.

The Asian citrus greening bacterium can withstand high temperatures and occurs in China, Southeast Asia, India and Saudi Arabia. On the other hand, Southern African greening, which is transmitted by the psyllid *Trioza erytreae*, is heat-sensitive and symptoms do not develop in climates where temperatures above 30°C are recorded for several hours a day. In addition to Southern Africa, this greening occurs also in North Yemen (Garnier et al. 1988).

Natural enemies

Identified natural enemies are listed in Table 4.7.3. There are also reports of a number of unidentified predators (coccinellids, chrysopids, mantids, spiders). It is noteworthy that only 2 primary parasitoids—both attacking *D. citri* nymphs—have so far been recorded, the widespread endoparasitic encyrtid *Diaphorencyrtus aligarhensis* and the more restricted ectoparasitic eulophid *Tamarixia radiata*, which has been introduced to several countries for biological control. Both feed on the haemolymph of some hosts, resulting in their death, as well as using other hosts for oviposition.

Where they occur naturally, both *D. aligarhensis* and *T. radiata* are heavily attacked by a wide range of hyperparasitoids (Table 4.7.4). Of these, *Tetrastichus* sp. is the most important for *T. radiata*, causing an average of 21.8% parasitisation in 1988 (rising to a maximum of 87.9%) and 28.7% in 1989 in Fujian Province, China. *Chartocerus walkeri* (9.3% in 1988 and 13.2% in 1989) is the most important for *D. aligarhensis* (Table 4.7.5).

A valuable illustrated guide to the hyperparasitoids associated with *D. citri* is provided by Qing and Aubert (1990).

Table 4.7.3 Natural enemies of *Diaphorina citri* (* indicates introduced to this country)

Species	**Region**	**Reference**
HYMENOPTERA		
ENCYRTIDAE		
Diaphorencyrtus aligarhensis (= *Aphidencyrtus diaphorinae* = *Diaphorencyrtus diaphorinae* = *Psyllaephagus diaphorinae* = *Aphidencyrtus aligarhensis*)	India	Shafee et al. 1975; Hayat 1981
	Vietnam	Myartseva & Tryapitzyn 1978; van Lam 1996 Prinsloo 1985
	Taiwan	Lin & Tao 1979
	Comores Is	Aubert 1984b
	Réunion	Aubert & Quilici 1984, Quilici 1989
	Philippines	Prinsloo 1985; Gavarra & Mercado 1989; Gavarra et al. 1990
	China	Tang 1989
	Indonesia	Nurhadi 1989; Nurhadi & Crih 1987
	Malaysia	Lim et al. 1990
EULOPHIDAE		
Tamarixia radiata (= *Tetrastichus radiatus*)	India	Waterston 1922; Husain & Nath 1924; Quilici 1989,
	Réunion*	Etienne and Aubert 1980
	Saudi Arabia	Aubert 1984a
	Mauritius*	Aubert 1984c
	Nepal	Lama et al. 1988; Otake 1990
	Taiwan*	Chiu et al. 1988
	China	Liu 1989; Tang 1989; Qing & Aubert 1990
	Indonesia	Nurhadi & Crih 1987; Nurhadi 1989
	Malaysia	Lim et al. 1990
	Thailand	Qing & Aubert 1990
	Vietnam	Myartseva & Trijapitzyin 1978; van Lam 1996

Table 4.7.3 (cont'd) Natural enemies of *Diaphorina citri* (* indicates introduced to this country)

Species	Region	Reference
COLEOPTERA		
COCCINELLIDAE		
Cheilomenes sexmaculata	China	Xia et al. 1987
NEUROPTERA		
CHRYSOPIDAE		
Chrysopa boninensis	China	Liu 1989
ARACHNIDA		
SALTICIDAE		
Marpissa tigrina	India	Sanda 1991
FUNGI		
Beauveria bassiana	China	Chen et al. 1990
Cephalosporium (= *Verticillium*) *lecanii*	China	Xie et al. 1988
Fusarium lateritium	China	Xie et al. 1988
Paecilomyces sp.	China	Xie et al. 1988

Table 4.7.4 Hyperparasitoids of *Diaphorina citri* (mostly after Tang 1989)

Hyperparasitoid	Attacks	Region	Reference
EULOPHIDAE			
Tetrastichus sp.	*T.r.* & *D.a.*	China	Tang 1989
	D.a.	Taiwan	Hayat & Lin 1988; Chien et al. 1989
		Philippines	Balthazar 1966, unpublished
ENCYRTIDAE			
Syrphophagus taiwanus	*T.r.* & *D.a.*	Taiwan	Hayat & Lin 1988; Chien et al. 1989
	T.r. & *D.a.*	China	Tang 1989
Ageniaspis sp.	*D.a.*	Taiwan	Hayat & Lin 1988; Chien et al. 1989
Cheiloneurus sp.	*D.a.*	Taiwan	Hayat & Lin 1988; Chien et al. 1989,
	?	Philippines	Baltazar 1966, unpublished
?*Psyllaephagus* sp.	*T.r.* & *D.a.*	China	Tang 1989
		Philippines	Balthazar 1966, unpublished
			Tang 1989
Several unidentified	*D.a.*	China	Tang 1989
SIGNIPHORIDAE			
Chartocerus walkeri	*T.r.* & *D.a.*	Taiwan	Hayat & Lin 1988; Chien et al. 1989
	T.r. & *D.a.*	China	Tang 1989
Signiphora sp.	*D.a.*		Gavarra et al. 1990
PTEROMALIDAE			
Pachyneuron concolor	*T.r.* & *D.a.*	Taiwan	Hayat & Lin 1988; Chien et al. 1989
APHELINIDAE			
Coccophagus ceroplastae	*D.a.*	Taiwan	Hayat & Lin 1988; Chien et al. 1989
Coccophagus sp.	*D.a.*	Taiwan	Hayat & Lin 1988; Chien et al. 1989

Table 4.7.4 (cont'd) Hyperparasitoids of *Diaphorina citri* (mostly after Tang 1989)

Hyperparasitoid	Attacks	Region	Reference
APHELINIDAE (cont'd)			
Marietta leopardina	*T.r.* & *D.a.*	Taiwan	Hayat & Lin 1988; Chien et al. 1989
(= *Marietta javensis*)	*D.a.*	Philippines	Balthazar 1966, unpublished
Encarsia spp.	*T.r.* & *D.a.*	Taiwan	Hayat & Lin 1988; Chien et al. 1989
		China	Tang 1989
Unidentified sp.	*T.r.* & *D.a.*	Taiwan	Chien et al. 1989

T.r. = *Tamarixia radiata* *D.a.* = *Diaphorencyrtus aligarhensis*

Table 4.7.5 Hyperparsitoids of *Tamarixia radiata* and *Diaphorencyrtus aligarhensis* in Fujian and Taiwan (after Qing 1990)

	Percentage of hyperparasitisation					
		T. radiata			***D. aligarhensis***	
Hyperparasitoid	**Fujian**	**Fujian**	**Taiwan**	**Fujian**	**Fujian**	**Taiwan**
EULOPHIDAE						
Tetrastichus sp.	21.82	28.65	0.01	2.90	3.68	
PTEROMALIDAE						
Pachyneuron concolor			0.45			18.50
SIGNIPHORIDAE						
Chartocerus walkeri	0.08	1.09	0.03	9.26	13.16	13.50
ENCYRTIDAE						
Syrphophagus taiwanus			0.05	1.09	4.21	6.80
?*Psyllaephagus* sp.	0.04	0.10		10.35	6.58	
Cheiloneurus sp.						0.01
Ageniaspis sp.						
unidentified sp.A				3.45	0.26	
Sp.B				0.91		
Sp.C				0.18		
Sp.D				0.18		
APHELINIDAE						
Encarsia sp. near *transvena* (= *E. shafeei)*			0.11			0.80
Encarsia sp. A	0.08	0.10		0.91	1.05	
Encarsia sp. B	0.22	0.20		0.91		

Table 4.7.5 (cont'd) Hyperparsitoids of *Tamarixia radiata* and *Diaphorencyrtus aligarhensis* in Fujian and Taiwan (after Qing 1990)

	Percentage of hyperparasitisation					
	T. radiata			***D. aligarhensis***		
Hyperparasitoid	**Fujian**	**Fujian**	**Taiwan**	**Fujian**	**Fujian**	**Taiwan**
APHELINIDAE (cont'd)						
Marietta leopardina			0.25			2.50
Coccophagus ceroplastae						0.01
Coccophagus sp.						0.10
Unidentified sp.			0.05			0.01
Totals	22.24	30.14	0.90	30.14	28.94	39.72

It is noteworthy that *T. radiata*, which has fairly recently (1984–1988) been introduced into Taiwan, was hyperparasitised to the extent only of 0.95% in 1989, whereas 42.2% of the native *D. aligarhensis* was attacked (Qing 1990).

The levels of hyperparasitisation of both primary parasitoids seriously affects their capacity to develop high populations and hence to produce maximum reduction of host populations. Nevertheless, each primary parasitoid killed is also a *D. citri* killed, so the overall mortality of *D. citri* is the sum of the mortalities produced by both primary parasitoids and their hyperparasitoids. It is abundantly clear that all hyperparasitoids must be rigorously excluded when transferring primary parasitoids from one region to another.

Attempts at biological control

The parasitoid *Tamarixia radiata*, obtained originally from India, has been used in successful biological control projects in Réunion, Mauritius and Taiwan and in an attempt in the Philippines (Table 4.7.6). These projects and comments on the situation in several other countries follow.

Table 4.7.6 Introductions for the biological control of *Diaphorina citri*

Species	From	To	Year	Result	Reference
EULOPHIDAE					
Tamarixia radiata	India	Réunion	1978	+	Aubert & Quilici 1984; Quilici 1989
	Réunion	Mauritius	after 1978	+	Quilici 1989
	Réunion	Taiwan	1983–86	+	Chiu et al. 1988; Chien et al. 1988
	Réunion	Philippines	1989	+ ?	Gavarra et al. 1990 Mercado et al. 1991

CHINA

In Guangdong, predators (lacewings, ladybird beetles, thrips, spiders) caused about 80% mortality of *D. citri*. Duration of daylight (short days reducing oviposition), quality of the flushes, and pesticide usage were other important factors influencing *D. citri* populations (Chen 1988). It appears that some Chinese farmers may spray citrus up to 50 times a year.

In Fujian there are 8 generations a year of *D. citri* on jasmin orange, *Murraya paniculata* and populations reach their peak in summer and early autumn during hot, dry weather when fresh shoots appear regularly. Populations are lowest in cold, wet weather with average temperatures of

9.1° to 12.2°C. Rainfall affects populations since eggs are laid on very young twigs and are easily washed off. A *Tamarixia* sp. was recorded in September 1987 and caused 83.3% parasitisation of nymphs in late autumn. In spring 1988 its population was low, but *D. citri* mainly overwinters as the adult and *Tamarixia* only attacks nymphs. Predators included coccinellids (especially *Cheilomenes sexmaculata* and *Harmonia axyridis*), lacewings, spiders and praying mantids (Xia et al. 1987; Ke 1991).

In Guangdong a maximum of 75% mortality of *D. citri* was recorded as being due to the hyperparasitoid *Tetrastichus* sp. (Liu 1989).

Beauveria bassiana (Chen et al. 1990a), *Cephalosporium* (*Verticillium*) *lecanii* and two other fungi (*Fusarium lateritium* and *Paecilomyces* sp.) were found attacking *D. citri*. Suspensions of *C. lecanii* sprayed on to *D. citri* displayed a very high pathogenicity (Xie et al. 1988, 1989b).

INDONESIA

Citrus greening is also known as citrus vein phloem degeneration. In East Java, both *T. radiata* (the commoner) and *D. aligarhensis* (the more widespread) were found in 1987 attacking *D. citri* on *Murraya paniculata* (Nurhadi and Crih 1987). *D. citri* is known to occur in Irian Jaya and may have been introduced in recent times, but it is not known if it is parasitised there.

MALAYSIA

Both *Tamarixia radiata* and *Diaphorencyrtus aligarhensis* are present with parasitisation rates ranging up to 28% in 4th and 5th instar nymphs (Osman and Quilici 1991) or up to 36% parasitisation (Lim et al. 1990). *T. radiata* is also present in Sarawak (S. Leong, pers. comm. 1995).

NEPAL AND BHUTAN

Both *T. radiata* and *D. aligarhensis* are present in some parts of both counties and may cause parasitisation of *D. citri* in excess of 90% (Lama and Amtya 1991; Lama et al. 1987).

PHILIPPINES

Citrus greening, also known as citrus leaf mottle, was already causing serious damage in the early 1960s. However, as late as 1988, the windward side of Mindoro island with an average rainfall of 3000 mm was virtually free of *D. citri* and citrus greening, presumably due to the adverse effects of high rainfall (Aubert 1989a). *D. aligarhensis* was reared from *D. citri* (25.7% parasitisation) and also 4 hyperparasitoids (*Marietta* sp. and 3 unidentified species), resulting in an overall mortality of *D. citri* of 48.3%. A *Beauveria* sp. attacked many psyllids and in turn was parasitised by another ascomycete, probably a *Melanospora* sp. (Gavarra and Mercado 1989). Later (Mercado et al. 1991), up to 62.2% parasitisation by *D. aligarhensis* was reported in Mindoro. In another study, Gavarra et al. (1990) recorded that, in addition to the primary parasitoid *D. aligarhensis* (17.6 to 36.1% parasitisation), 5 hyperparasitoids were reared from *D. citri*: *Marietta leopardina* (= *M. javensis*), *Tetrastichus* sp., *Psyllaephagus* sp., *Chiloneurus* sp. and *Signiphora* sp.

Because it was apparently absent from the Philippines (Baltazar 1966), *Tamarixia radiata* was introduced from Réunion in 1988, but attempts to rear it failed. A second consignment late that year was soon followed by the discovery of it nearby in the field in April 1989, with recoveries continuing in 1990 (Gavarra et al. 1990). However, Mercado et al. (1991) expressed some doubts that it had become established. It is thus not clear whether *T. radiata* ever occurred naturally in the Philippines.

RÉUNION

The rainy, windward, east side of Réunion has much lower *D. citri* populations and citrus trees there are much less exposed to transmission of greening (Aubert 1989a). Quilici (1989) has provided a valuable overview of the biological control of citrus psyllids in Réunion. In the early 1970s, Réunion and Mauritius were the only places known where *Diaphorina citri* and *Trioza erytreae*, the two psyllid vectors of citrus greening disease, occurred (Aubert 1987c). (Both are now known also from Saudi Arabia and Yemen: Bové 1986). Both psyllids were abundant in Réunion and Mauritius and citrus greening was seriously affecting citrus production in both islands. The Asian citrus psyllid *D. citri* was most abundant below 500 m in the hotter and drier leeward side of Réunion, where the average rainfall is below 1000 m. On the other hand, the drought-sensitive African psyllid *T. erytreae* was particularly abundant in the cooler, moister regions above 600 m. The only nymphal parasitoid of both species was the relatively ineffective *D. aligarhensis*. Several predators exerted little control.

Tamarixia dryi was introduced in 1974 from South Africa and, after elimination of hyperparasitoids, was mass produced and released in neglected, unsprayed citrus orchards colonised by *D. citri*. Populations of *Trioza erytreae* diminished progressively from 1979 to 1982, since when *T. erytreae* has not been recorded, although *Tamarixia dryi* is still abundant on another psyllid, *Trioza litseae* (= *T. eastopi*).

In 1978 *Tamarixia radiata* was introduced from India and released on the leeward (west) side of Réunion. From 1982 onwards *D. citri* has virtually disappeared from commercial citrus orchards, although on *Murraya paniculata* hedges there persist low populations of *D. citri* which are parasitised by *T. radiata* and occasionally, especially at higher altitudes, by *D. aligarhensis*.

The excellent success of these two biological control projects is ascribed to 3 factors:

(i) the absence of hyperparasitoids of the primary parasitoids of *Tamarixia dryi* and *T. radiata*.

(ii) the presence of an alternative host for *Tamarixia dryi*, which enabled it to maintain itself as *Trioza erytreae* populations diminished.

(iii) the maintenance on *Murraya paniculata* hedges of low populations of *D. citri*, heavily parasitised by both *T. radiata* and *D. aligarhensis* (Aubert 1987c; Etienne and Aubert 1980; Quilici 1989).

SAUDI ARABIA AND YEMEN

In Saudi Arabia, both *D. citri* and *Trioza erytreae* are present; the former is the main vector of citrus greening. Both vectors are also present in Yemen where citrus greening at high elevations is probably the African form transmitted by *T. erytreae* (Bové 1986). In Saudi Arabia lime and lemon trees are favoured hosts of *D. citri* (Wooler et al. 1974).

TAIWAN

The nymphal ectoparasitoid *Tamarixia radiata* was introduced from Réunion and, after mass rearing, released widely in citrus orchards and on *Murraya paniculata* hedges from 1984 to 1988. It became established, attaining parasitisation rates of up to 100%. Hyperparasitisation was initially, in 1988, below 1% (Chien 1989; Chien et al. 1988; Su and Chen 1991), but by 1991 had risen gradually to 5.6% (Chien et al. 1991a). This is in contrast with levels of 72% by some 10 species attacking the native *Diaphorencyrtus aligarhensis*. High levels of attack on *D. aligarhensis* is one reason why this species is far less effective against the citrus psyllid than the introduced *T. radiata* (Chien et al. 1988). *T. radiata* was capable of maintaining *D. citri* at low densities in relatively stable habitats where *Murraya paniculata* was occasionally present, whereas *D. aligarhensis* has adapted to unstable habitats. However, it only provides partial control due to 25.5 to 51.1% hyperparasitisation throughout the island. In the Taichung area, *T. radiata* was more abundant than *D. aligarhensis*, but the peak abundance of the two did not overlap and the total parasitisation varied from 80 to 100% from February to April and 32 to 80% for the remainder of the year. Application of methomyl gave good control of *D. citri*, but it reduced parasitisation to a level of 0 to 4%. In an untreated citrus orchard with only 0.1 to 0.4 *D. citri* adults per 10 cm length branch, the parasitoids caused 15.5 to 46.7% parasitisation (Chien et al. 1991a). Citrus greening in Taiwan is known as likubin or leaf mottle disease.

VIETNAM

Tamarixia radiata was found parasitising 3 to 10% of 4th and 5th instar nymphs of *D. citri* and *Diaphorencyrtus aligarhensis* was also present (Myartzeva and Trijapitzyin 1978; Trung 1991; van Lam 1996).

Major natural enemies

HYMENOPTERA

Diaphorencyrtus aligarhensis Hym.: Encyrtidae

This primary endoparasitoid was described by Shafee et al. (1975), from India as *Aphidencyrtus aligarhensis*. Its hosts include *Diaphorina citri*, *D. auberti*, *D. cardiae* and *Psylla* sp. (Qing and Aubert 1990).

The *D. citri* mummy parasitised by *D. aligarhensis* is brownish and hemi-spherical and encloses the parasitoid pupa. The parasitoid emerges from the side of the abdomen. Development from egg to adult takes 18 to 23 days at 25 ± 1°C and 80 to 85% relative humidity (Tang and Huang 1991). No males occur and unmated females produce females. On average, 4.5 eggs are laid per day with an average production of 144 per female. Third and 4th instar *D. citri* nymphs are preferred over 2nd instar, and 1st and 5th instars are not parasitised. Usually only one egg is inserted into each host, but the haemolymph of many young nymphs is consumed leading to their death (Tang and Huang 1991).

Tamarixia radiata Hym.: Eulophidae

This ectoparasitoid was described from India (Waterston 1922) where it is an important species (Husain and Nath 1924). It has been recorded in China (in 1982: Tang 1989), Indonesia (Nurhadi 1989), Malaysia (Lim et al. 1990), Nepal (Lama et al. 1988), Saudi Arabia (Aubert 1984a), Thailand (Qing and Aubert 1990) and Vietnam (Myartzeva and Trijapitzyin 1978). *T. radiata* has been introduced to, and established in, Réunion (Aubert and Quilici 1984), Mauritius (Quilici 1989) and Taiwan (Chiu et al. 1988).

T. radiata was found to be the dominant parasitoid of *D. citri* on *Murraya paniculata* in Fujian, comprising 62.6% of all parasitoids and hyperparasitoids emerging. The second in abundance was the hyperparasitoid *Tetrastichus* sp., most of which were bred from *T. radiata*, an average of 21.8% hyperparasitisation, rising to a maximum of 87.9%, whereas the other primary parasitoid *D. aligarhensis* was hyperparasitised to an average of 34.1% (Tang 1989).

The *T. radiata* female oviposits ventrally between the thorax and abdomen of the nymph, preferably of the 5th instar, and its fully grown larva spins silk to attach itself and its host to the plant substrate. The *D. citri* mummy parasitised by *T. radiata* has a dark brown, flattened body and the parasitoid pupa remains external to, and on the ventral surface of, the host. The adult wasp emerges via a hole cut through the thorax of the host (Qing 1990; Tang and Huang 1991). Under favourable conditions, parasitisation can exceed 90%, as in India (Husain and Nath 1927) and also in Réunion, Nepal and Taiwan (Quilici and Fauvergue 1990).

Male *T. radiata* are capable of multiple matings, but females usually mate only once. The egg to adult period was 11.4 days (egg 1.9, larva 4.0, prepupa 0.6, pupa 4.9 days), females lived 23.6 days and males lived 14.8 days (Chien et al. 1991a,b; Chu and Chien 1991). Fauvergue and Quilici (1991) report reduction of the duration of immature stages with increasing temperature from 17 days at 20°C to 8 days at 30°C. Adult females lived 37 days at 20°C and 8 days at 35°C. Females kill some 80% of *D. citri* hosts by parasitisation and 20% by host feeding. When 40 psyllids were presented per day a female killed 513 psyllids in a lifetime. At an optimum temperature of 25°C, 24, 5th instar nymphs were killed per day (Chien et al. 1993). Adult parasitoids can be cold stored at 8°C for between 46 and 60 days (Chien et al. 1993). Oosorption occurred when hosts were unavailable. This extended the reproductive period, but diminished the total number of eggs laid (Chien et al. 1994b). Feeding by females on the honeydew produced by the host and on host haemolymph provides nutrients for egg production. The parasitoid fed on the exudate of 28% of host eggs parasitised (Chien et al. 1994a). The optimal host density over the entire *T. radiata* lifetime was found to be 2 to 8 per day, of which 90 to 94% were utilised. For the peak oviposition period, optimal density was 2 to 20, of which 87 to 90% were utilised (Chien et al. 1995).

The sex ratio of *T. radiata* is 1:3 in favour of females. Unmated females give rise only to male offspring. Oviposition occurs on 3rd, 4th and 5th instar nymphs and there is discrimination against ovipositing in nymphs containing older *D. aligarhensis* larvae. The average number of offspring is reported as 134 with 6.5 eggs laid per day (Tang and Huang 1991). Observations in China indicate that *T. radiata* is more affected by low temperatures than *D. citri*. Thus *T. radiata* breeds more effectively in Xiamen, where the lowest winter temperature is 3.9°C, than in Fuzhou, where overwintering is jeopardised by lowest minimum temperatures of –2.5°C (Aubert 1990).

Tetrastichus sp. Hym.: Eulophidae

This undescribed species is an important hyperparasitoid of *Tamarixia radiata* in China. Average hyperparasitisation amounted to nearly 25%, with a maximum of 87.9%. The genus *Tetrastichus* contains more than 150 species attacking a wide variety of hosts.

ARACHNIDA

Marpissa tigrina: Salticidae

The number of *D. citri* consumed daily by an individual spider increased with an increase in available prey up to 40. Further increases in prey numbers reduced predation. The results suggest that *M. tigrina* is a highly efficient predator of *D. citri* (Sanda 1991).

Comments

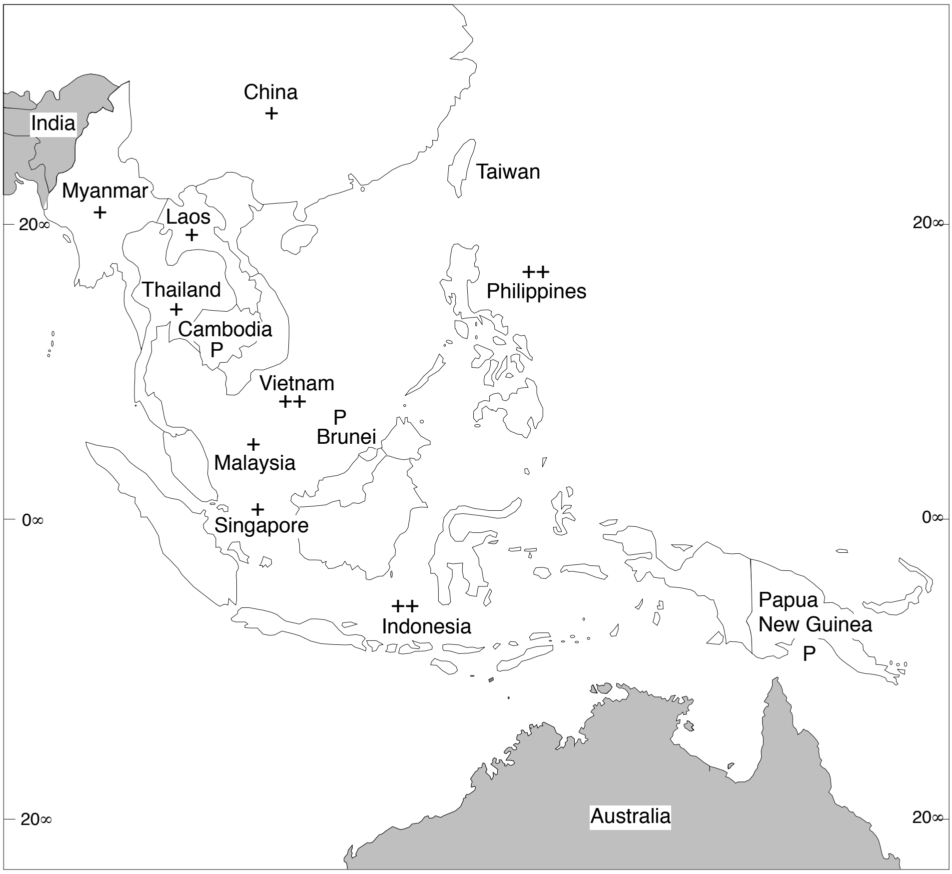
Diaphorina citri and its two primary parasitoids, *Diaphorencyrtus aligarhensis* and *Tamarixia radiata*, are (especially the first two species) very widespread in Southeast Asia. In these countries the prospects for biological control are unpromising, although the careful timing of least harmful, but still effective, insecticides (or, preferably, special petroleum oils) would favour a build up of the parasitoids. The role played by hedges and other plantings of the common, favoured host, jasmin orange, *Murraya paniculata* in encouraging either *D. citri* or its parasitoids is worthy of careful investigation, for this may differ widely according to the insecticidal treatments in the nearby citrus plantings. Overhead irrigation to reduce numbers of eggs and young nymphs during periods of growth flushes is probably uneconomical in most situations, but is possibly a factor to consider in a pest management approach.

Although *D. aligarhensis* appears to be a less effective parasitoid than *T. radiata*, it still may contribute useful suppression of *D. citri* where it can be introduced without encountering hyperparasitoids.

In contrast to much of Southeast Asia, the prospects for successful biological control of *D. citri* appear to be promising for countries that have been recently invaded, particularly if there are few or no hyperparasitoids already present that are capable of attacking *T. radiata* and/or *D. aligarhensis*. In this context it may be valuable to explore the situation in Irian Jaya and Timor where *D. citri* has been recorded only recently. Successful biological control there may slow the spread of *D. citri* into Papua New Guinea, Australia and the oceanic Pacific. Brazil has a range of native psyllids that are attacked by *Tamarixia* spp. so it is possible that there are already hyperparasitoids present that would attack *T. radiata* were it to be introduced.

Since *Tamarixia leucaenae* attacks both *Heteropsylla cubana* and *H. spinulosa*, it would be valuble to know whether *Tamarixia radiata* will also attack *Heteropsylla spinulosa*. This is the psyllid that has been successfully introduced to Papua New Guinea, Australia and some oceanic Pacific countries for the biological control of creeping, sensitive plant, *Mimosa invisa*. If it does attack *H. spinulosa*, there would clearly be a conflict of interest between biological control of *D. citri* and of *M. invisa*, were *Heteropsylla spinulosa* to be considered for the latter. However, at least some species of *Tamarixia* are satisfactorily host restricted and it is quite possible that *T. radiata* is one of them.

4.8 *Dysdercus cingulatus*



Dysdercus cingulatus is native to the Southeast Asian region.

No parasitoids of the cotton stainer are known and surprisingly few predators are reported. No effective parasitoids of the many *Dysdercus* species that occur in other parts of the world are known. On present knowledge, therefore, the prospects for classical biological control of this bug would appear to be very remote.

Dysdercus cingulatus (Fabricius)

Hemiptera, Pyrrhocoridae
cotton stainer, red cotton bug, red seed bug

Rating

Southeast Asia			**China**	**Southern and Western Pacific**	
	++	Viet, Indo, Phil			
11	+	Myan, Thai, Laos, Msia, Sing	+		
	P	Brun		P	PNG, Sol Is, Van, Marianas, Carolines, N Cal.

Origin

Southeast Asia.

Distribution

Waterhouse (1993a) was in error in accepting Kalshoven (1981), who listed the distribution of *D. cingulatus* as ‘widespread from the Mediterranean to Australia’. In fact, it occurs from north eastern India through Bangladesh to all Southeast Asian countries, southern China, southern Japan, Irian Jaya, Papua New Guinea, eastern Australia, Saipan, Palau, Pohnpei, Yap, Solomon Is., Vanuatu and New Caledonia (CIE 1985). There are some 50 species of *Dysdercus*, some of which appear to be native to the African, Ethiopian, Southern Asian and American regions respectively (Freeman 1947). *D. cingulatus* is not recorded from Africa, Europe, Western Asia or the Americas.

Biology

Eggs are usually laid singly in batches of about 100 (range 25 to 112) in small depressions in the soil under the host plant. They are camouflaged with soil particles or other debris. Some 80% of the eggs hatch in about 6 days if there is the essential high humidity. The optimum hatch occurs at 30°C and 80% RH. There are 5 nymphal instars which take 25 to 27 days to complete and the oviposition to adult period is thus 31 to 33 days. The first instar nymphs do not feed. Later instars suck sap with a preference for pods and seeds. All stages are gregarious. The male:female ratio is 3:2 and mating takes place readily and repeatedly, pairs often remaining *in copula* for 2 to 4 days, during which they move and feed (Srivastava and Bahadur 1958; Thomas 1966; Ahmad and Aziz 1982, 1983, Farine and Lobreau 1984, Siddiqi 1985, 1987; Khoo et al. 1991).

D. cingulatus is one of the commonest insects in cultivated land in Indonesia. Adults range from 11 to 17 mm in length and are orange and black in colour, with a characteristic white band on the pronotum and single large black spots on each orange forewing.

Both adults and nymphs produce a complex mixture of compounds as a defensive secretion (Farine et al. 1992, 1993) and females produce a sex pheromone from glands in the thorax (Siddiqi 1988; Siddiqi and Khan 1982).

Host plants

The principal host plants of *D. cingulatus* are in the families Malvaceae and Bombacaceae and include cotton, kapok, okra and rosella. It was the most important pest of cotton in the coastal districts of Malaysia in the early days and also fed on the seeds of kapok, rosella, hibiscus, hemp, okra and other malvaceous plants (Jack and Sands 1922; Dresner 1955). In a host preference test in Malaysia, the following order was recorded kapok > okra > urena > maize > sorghum (Chong 1975). It has also been recorded on wheat (Srivastava and Gupta 1971), pearl millet, *Pennisetum glaucum* (= *P. americanum*) (Ahmad 1979) and a range of weeds.

Damage

Like other species of *Dysdercus* throughout the world *D. cingulatus* is most important as a pest of cotton. The sap removed and the fungus introduced into the punctures caused when feeding on the developing cotton bolls causes staining of the lint, giving rise to one of its common names.

Natural enemies

Very little has been published on the natural enemies of *D. cingulatus* and no parasitoids are known. In view of the large number of parasitoids of *Nezara viridula* eggs (Table 4.12.1), it seems strange that none are recorded from eggs of the cotton stainer. There appear to be no statements in the literature that they have been looked for unsuccessfully.

The few records retrieved of natural enemies of *D. cingulatus* are shown in Table 4.8.1. The pyrrhocorid predator *Antilochus coquebertii* has been reported attacking the cotton stainer in India and Malaysia (Yunus & Ho 1980; Zaidi 1985). It is believed to inject saliva containing proteolytic enzymes into eggs, nymphs or adults before sucking out the liquified contents. In the Philippines an ectoparasitic mite, *Hemipterotarseius* sp. was found on the pronotum of adult bugs, two species of spiders were observed attacking bugs and a nematode was found in the abdomen of a female. No egg parasitoids were found (Encarnacion 1970). Singh and Bardhan (1974) showed that *D. cingulatus* was moderately susceptible to the DD 136 strain of the nematode *Steinernema carcocapsae*.

A superficial review of the literature on the natural enemies of other species of *Dysdercus* revealed two tachinid parasitoids, one of each in South America and Africa and three asassin bug predators in Africa but no egg parasitoids (Table 4.8.2).

Comment

Too little is known about the natural enemies of *D. cingulatus* to indicate whether there are any prospects for classical biological control or for manipulating them where they already occur. Since *D. cingulatus* now appears to have evolved in the Southeast Asian region and since effective natural enemies of related species elsewhere are not known, the prospects for its classical biological control would appear to be remote.

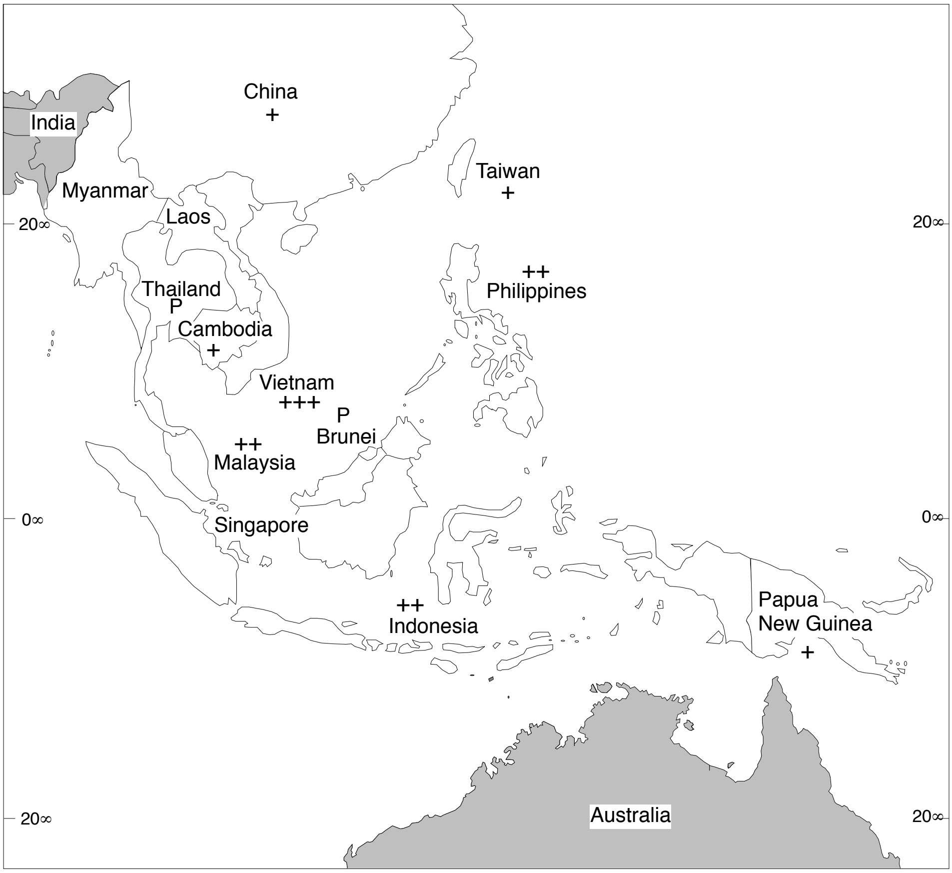
Table 4.8.1 Natural enemies of *Dysdercus cingulatus*

Enemy	Country	Reference
INSECTA		
HEMIPTERA		
PYRRHOCORIDAE		
Antilochus coquebertii	India	Zaidi 1985
	Malaysia	Thomas 1966; Yunus & Ho 1980
ACARINA		
Hemipterotarseius sp.	Philippines	Encarnacion 1970
ARACHNIDA		
Spider 1	Philippines	Encarnacion 1970
Spider 2	Philippines	Encarnacion 1970
NEMATODA		
Species 1	Philippines	Encarnacion 1970
FUNGI		
Aspergillus flavus	India	Kshemkalyani et al. 1989

Table 4.8.2 Natural enemies of *Dysdercus* spp.

Enemy	Country	Reference
HEMIPTERA		
REDUVIIDAE		
Phonoctonus nigrofasciatus	Zimbabwe	Sweeney 1960
Phonoctonus subimpictus	Ivory Coast	Galichet 1956
Phonoctonus sp.	Mozambique	Barbosa 1950
DIPTERA		
TACHINIDAE		
Acaulona brasiliana	Argentina	Blanchard 1966
Bogosia helva	Ivory Coast	Galichet 1956

4.9 *Dysmicoccus brevipes*



The pineapple mealybug, *Dysmicoccus brevipes*, is of Central or South American origin. It occurs in both parthenogenetic and bisexual forms, the females of which are morphologically indistinguishable, although they may possibly prove to be distinct species. The closely-related, bisexual, *D. neobrevipes* also occurs on pineapple.

Attempts have been made by several countries to establish natural enemies for biological control, but none has had any great success without the control of attendant ants. When ants were controlled the mealybug was no longer a problem. Ant control is less likely to be an answer to the problem in the absence of suitable natural enemies. It is desirable, therefore, to establish appropriate natural enemies in anticipation of effective ant control, an aspect which is now being actively investigated in Hawaii.

Dysmicoccus brevipes (Cockerell)

Hemiptera, Pseudococcidae
pineapple mealybug

Rating

Southeast Asia			China	Southern and Western Pacific		
	+++	Viet			+++	Cook Is, Guam
10	++	Msia, Indo, Phil		17	++	FSM, Niue, Van
	+	Camb	+		+	Kiri, N Cal, PNG, Sam, Sol Is
	P	Brun, Thai			P	Fiji, Fr P, A Sam. Tok, Tong, Tuv

Origin

Carter (1935) considered *D. brevipes* to be native to South America, although Ferris (1950) believed it to be of North American origin. The pineapple plant (*Ananas comosus*) is thought to be native to South America and has been known in Central America since pre-Columbian times. Although the pineapple mealybug is widely polyphagous, if it evolved in association with pineapple plants, it would appear to be logical to assign its origin to Central and/or South America.

Distribution

D. brevipes is one of the most widespread mealybugs, occurring throughout the tropics and in many temperate areas, especially those where pineapples are grown (Williams and Watson 1988). These include tropical Africa, Mauritius, tropical Asia, Southeast Asia, Taiwan, Australia, Pacific islands (including Hawaii), southern USA (Florida, Louisiana) West Indies and Central and South America (Bartlett in Clausen 1978).

Taxonomy

Dysmicoccus brevipes was earlier known as *Pseudococcus brevipes*, but its genus was changed by Ferris (1950). Before 1959 it was confused with a similar mealybug (often on the same host plants), which was described by Beardsley (1959) as *Dysmicoccus neobrevipes*. Both species occur in Hawaii, where *D. brevipes* is parthenogenetic and the females are pink, whereas *D. neobrevipes* is bisexual and females are grey in colour. Parthenogenetic *D. brevipes* is known also from Jamaica and West Africa (Beardsley 1965).

In some countries (Ivory Coast, Madagascar, Dominican Republic, Martinique, Malaysia) both sexes of *D. brevipes* occur (Beardsley 1965; Lim 1973). *D. neobrevipes* is known from many countries in Central and South America and probably also originated there (Williams and Watson 1988). It is known from Mexico, Jamaica, American Samoa and Samoa, Cook Is, Kiribati and Guam. In Southeast Asia it occurs in Malaysia, the Philippines and Thailand (where there have been recent serious outbreaks (Beardsley 1965; Rohrback et al. 1988; Williams and Watson 1988).

Biology

D. brevipes females are broadly oval to rotund in shape, pinkish in colour, and have a thick waxy covering with short conical waxy projections (Kalshoven 1981). In Hawaii, *D. brevipes* is parthenogenetic and ovoviviparous (i.e. it produces its young alive). About 250 crawlers are produced per female over a 3 to 4 week period and take some 34 days to mature. Females start producing young about 25 days after the third moult (Ito 1938).

In peninsular Malaysia the bisexual form is widespread but the parthenogenetic form was not found (Lim 1973). In the male, there are two nymphal, one prepupal and one pupal instar of 10, 6, 3 and 4 days duration respectively. Adult males live for 1 to 3 days, whereas adult females live 17 to 49 days. The female has 3 nymphal instars, lasting 10, 7 and 7 days respectively. A female produces 19 to 137 offspring with a sex ratio of 1:1 (Lim 1973). The bisexual form in Malaysia has a 10 day shorter life cycle than the parthenogenetic form in Hawaii and might have as many as 9 generations a year (Lim 1973). The bisexual form of *D. brevipes* is capable of producing green spotting on pineapple leaves, whereas the parthenogenetic form is not (Beardsley 1965).

In India, Ghose (1983) studied the parthenogenetic form of *D. brevipes* at 30°C and 60–66% R.H. The nymphs completed their development in 19 days and, after a pre-oviposition period of 16 days, produced an average of 240 young over a period of 40 days.

D. brevipes occurs mainly on the underground parts of the pineapple stem (where the stem is covered by leaf bases) and on the roots. Leaves or fruit are less heavily infested, except on weak plants. However the bisexual form also infests the crown of the pineapple plant (Rohrbach et al. 1988).

By comparison, *D. neobrevipes*, which is always bisexual, is found only on the aerial parts of the pineapple plant — leaves, stems, aerial roots, flowers and fruit clusters. Unlike *D. brevipes*, it does not infest grasses . In Hawaii, only *D. neobrevipes* causes green spotting of pineapple leaves (Beardsley 1959).

The pineapple mealybug is generally attended by ants seeking honeydew. They not only protect it against natural enemies but also assist in dispersal by transporting it to new plants. Where appropriate natural enemies are present, but attendant ants are not, the mealybug is no longer a problem (Beardsley et al. 1982). The identity of the ants varies from place to place, although 3 very widespread species are often involved, the bigheaded ant, *Pheidole megacephala*, the Argentine ant, *Iridomyrmex humilis*, and the fire ant *Solenopsis geminata*. The gradual invasion of new pineapple plantings by ants is accompanied by progressive outbreaks of mealybugs, so ant control is essential. It is interesting that mated queens of *P. megacephala* must, following the nuptial flight, rejoin established colonies to survive. Thus, invasion into new territory is accomplished by extension of existing nests, a feature that is of importance in controlling the big-headed ant (Beardsley et al. 1982).

Hosts

D. brevipes occurs widely on its preferred host, pineapple, wherever this is grown in moist tropical or subtropical areas, but it can be found on almost any kind of plant and is sometimes a pest of sugarcane and bananas. It also occurs on areca palm, coffee, groundnut, oil palm, rice, sisal, soybean, *Pandanus* palm and a range of grasses and weeds (Clausen 1978; Kalshoven 1981; Khoo et al. 1991).

Damage

In Hawaii, through their feeding, both *D. brevipes* and *D. neobrevipes* produce symptoms of toxicosis on pineapple, including stunting, reddening and wilting of young plants, due to what is now held to be a virus, and termed pineapple mealybug wilt. *D. neobrevipes*, but not the parthenogenetic form of *D. brevipes,* also produces a green spotting on the leaves. Where the bisexual form of *D. brevipes* occurs elsewhere it is capable of producing green spotting.

Unless collected by ants, honeydew produced by the mealybugs, leads to the massive growth of sooty moulds which reduces photosynthesis, affects sales of fruit and attracts *Carpophilus* spp. beetles, which contaminate canned fruit. Large colonies of *D. brevipes* in leaf sheaths near the roots of sugarcane result in poor growth and, when on groundnuts, cause the seed pods to become discoloured.

Natural enemies

A number of coccinellid predators are recorded attacking *D. brevipes* (Table 4.9.1) and it is possible that some of these have a sufficiently narrow host range to be considered for introduction. However, it is more likely that the dipterous and lepidopterous predators will be more specific. The encyrtid parasitoids would appear to be even more promising and it seems that the full range of species attacking *D. brevipes* in Central and South America has not yet been identified.

Attempts at biological control

A number of natural enemies, mainly encyrtid parasitoids and coccinellid and dipterous predators have been successfully introduced, in particular into Hawaii, Puerto Rico and the Philippines (Table 4.9.2). Details are provided in the country accounts that follow. It will become clear that a substantial degree of control of *D. brevipes* can be achieved in the absence of ants, which clearly protect the mealybugs against parasitoids and predators.

HAWAII

The pineapple mealybug has, for many years, constituted the most serious insect problem of the pineapple industry (Carter 1932; Beardsley 1959) and it is also a minor pest of sugarcane and bananas. An encyrtid wasp *Euryrophalus schwarzi* (= *E. pretiosa*) was reared from *D. brevipes* collected from sugarcane (Beardsley 1959).

In the early 1920s several natural enemies were introduced from Mexico and Panama, but none became established (Rohrbach et al. 1988). *Anagyrus ananatis* and *Hambletonia pseudococcina* from Central America and Brazil were established in 1935–36 and were effective in Maui where the dominant ant was the crazy ant *Paratrechina longicornis*. Parasitisation was high and pineapple wilt quite severe (Carter 1945). Other introductions known to have become established are an encyrtid parasitoid (*Euryrhopalus propinquus*), a cecidomyiid predator (*Vincentodiplosus pseudococci*), and two less effective coccinellid predators (*Scymnus* (= *Nephus*) *bilucenarius* and *Scymnus uncinatus*) (Lai and Funasaki 1986).

Overall, although the biological control of the pineapple mealybug has not been completely successful, a considerable reduction in abundance has resulted from the combined action of the cecidomyiid predator *Vincentodiplosis* and the encyrtid parasitoids *Anagyrus ananatis* and *Hambletonia pseudococcina*. They are highly effective only where ants are adequately controlled (Clausen 1978). Coccinellids are important for short periods, particularly in the middle of large plantings, where the absence of ants renders *D. brevipes* exposed to attack (Carter 1935, 1944).

Table 4.9.1 Natural enemies of *Dysmicoccus brevipes*

	Country	References
HEMIPTERA		
DIASPIDIDAE		
Diaspis bromeliae	Mauritius	Jepson 1939a
ORTHOPTERA		
Conocephalus saltator	Hawaii	Carter 1935
NEUROPTERA		
CHRYSOPIDAE		
Chrysopa irregularis	Fiji	Lever 1940
Chrysopa ramburi	Fiji	Lever 1940
Chrysopa sp.	Fiji	Lever 1940
COLEOPTERA		
COCCINELLIDAE		
Brachycantha sp.	Guatemala	Carter 1935
Cryptolaemus montrouzieri	Hawaii	Kalshoven 1981
	Fiji, New Caledonia	Williams & Watson 1988
Cryptolaemus sp.	Fiji, New Caledonia	Williams & Watson 1988
Rhizobius ventralis	Hawaii, New Caledonia	Williams & Watson 1988
Scymnus apiciflavus	Malaysia	Yunus & Ho 1980
Scymnus bilucenarius	Guatemala	Carter 1935
Scymnus mauritiusi	Mauritius	Jepson 1939a
Scymnus sp.	Fiji, New Caledonia	Cohic 1958
Sticholotis quatrosignata	Malaysia	Yunus & Ho 1980
Coccinellids	Taiwan	Takahashi 1939
Other species in introductions listed in table 4.9.2		

Table 4.9.1 (cont'd) Natural enemies of *Dysmicoccus brevipes*

	Country	**References**
DIPTERA		
CECIDOMYIIDAE		
Schizobremia formosana	Taiwan	Takahashi 1939
Cecidomyiid sp. 1	Guatemala	Carter 1935
Cecidomyiid sp. 2	Mauritius	Jepson 1939a
Cecidomyiid sp. 3	Puerto Rico	Plank & Smith 1940
DROSOPHILIDAE		
Gitonides perspicax	Mauritius	Jepson 1939a
Pseudiastata nebulosa	Guatemala	Carter 1935
LEPIDOPTERA		
PYRALIDAE		
Species 1	Puerto Rico	Plank & Smith 1940
TINEIDAE		
Drosica abjectella	South Africa	Büttiker 1957
Species 1	Puerto Rico	Plank & Smith 1940
HYMENOPTERA		
ENCYRTIDAE		
Aenasius acuminatus	Trinidad	Kerrich 1967
Aenasius theobromae	Trinidad	Kerrich 1953
Anagyrus ananatis	Brazil	Carter 1937; Gabriel et al. 1982
Anagyrus sp.	Brazil	Compere 1936
Encyrtid sp. 1	Brazil	Compere 1936
Euryrhopalus propinquus	Brazil, Guyana, Hawaii	Kerrich 1967

Table 4.9.1 (cont'd) Natural enemies of *Dysmicoccus brevipes*

	Country	**References**
HYMENOPTERA		
ENCYRTIDAE (cont'd)		
Euryrhopalus schwarzi (= *E. pretiosa*)	Guatemala Hawaii	Clausen 1978 Beardsley 1959
Hambletonia pseudococcina	Brazil, Colombia, Venezuela	Carter 1937
Leptomastix dactylopii	California	Clausen 1978
Pseudaphycus angustifrons	Cuba	Gahan 1946
Pseudaphycus dysmicocci	Trinidad	Clausen 1978
Pseusaphycus sp.	Brazil	Clausen 1978
Thysanus niger	Puerto Rico	Bartlett 1945
CHALCIDIDAE		
Species 1	Guatemala	Carter 1935
Species 2	Guatemala	Carter 1935
UNIDENTIFIED FAMILY		
7 species	Malaysia	Yunus & Ho 1980
ARACHNIDA		
spiders	Hawaii	Carter 1944

Table 4.9.2 Introductions for the biological control of *Dysmicoccus brevipes*

	Country	From	Year	Result	Reference
HYMENOPTERA					
ENCYRTIDAE					
Aenasius colombiensis	Colombia		1935	–	Lai & Funasaki 1986
Aenasius sp.	Panama		1931	–	Lai & Funasaki 1986
Anagyrus ananatis	Hawaii	Brazil	1934–35	+	Carter 1937
(= *Anagyrus coccidivorus*)	Peurto Rico	Brazil via Hawaii	1937–38	–	Bartlett 1939, 1943 Clausen 1978
Anagyrus kivuensis	California		1946	–	Lai & Funasaki 1986
Euryrhopalus propinquus	Hawaii	British Guiana	1935	+	Lai & Funasaki 1986
Euryrhopalus schwarzi	Hawaii	Guatemala	1935	+	Clausen 1978
Hambletonia pseudococcina	Hawaii	Brazil	1935–36	–	Carter 1937; Clausen 1978
		Colombia	1935–36	+	Carter 1937; Clausen 1978
		Venezuela	1935–36	+	Carter 1937
	Jamaica	Hawaii	1936	–	Clausen 1978
	Puerto Rico	Brazil via Hawaii	1937–38	+	Bartlett 1939
	Florida	Puerto Rico	1944	+	Annand 1945; Clausen 1956
Leptomastix dactylopii	Hawaii	California		?	Clausen 1978
Pseudaphycus dysmicocci	Hawaii	Trinidad	1958	?	Clausen 1978
Pseudaphycus sp.	Hawaii	Brazil	1946	?	Clausen 1978
Zaplatycerus fullawayi	Mexico		1930	–	Lai & Funasaki 1986
PLATYGASTERIDAE					
Allotropa sp.	Panama		1931	–	Lai & Funasaki 1986

Table 4.9.2 (cont'd) Introductions for the biological control of *Dysmicoccus brevipes*

	Country	From	Year	Result	Reference
COLEOPTERA					
COCCINELLIDAE					
Cleothera sp.	Panama		1931	–	Lai & Funasaki 1986
Cryptolaemus montrouzieri	Mauritius	S. Africa	1938–39	–	Jepson 1939b, Moutia & Mamet 1946
	Easter Is (Chile)			+	Ripa et al. 1995
Cryptolaemus sp.	Taiwan			?	Sakimura 1935
Diomus sp.	Jamaica	Hawaii	1939	–	Lai & Funasaki 1986
	Panama		1931	–	Lai & Funasaki 1986
Hyperaspis albicollis	Panama		1924	–	Lai & Funasaki 1986
Hyperaspis c-nigrum	Brazil		1935	–	Lai & Funasaki 1986
Hyperaspis silvestri	Philippines	Hawaii	1931	+	Clausen 1978
Hyperaspis 12 × spp.	Hawaii	various		?	Clausen 1978
Hyperaspis sp.	Jamaica	Hawaii	1939	–	Clausen 1978
Scymnus (=Diomus) margipallens	Philippines	Hawaii	1931	+	Clausen 1978
Scymnus (=*Nephus*) *bilucernarius*	Hawaii				Lai & Funasaki 1986
	Mexico		1930	+	Lai & Funasaki 1986
Scymnus pictus	Panama		1924	–	Lai & Funasaki 1986
Scymnus quadrivittatus	California		1948	–	Lai & Funasaki 1986
Scymnus uncinatus	Hawaii	Mexico, Panama	1922	+	Lai & Funasaki 1986
Scymnus 6 × spp.	Hawaii	various		?	Clausen 1978
Scymnus sp.	Taiwan	Saipan		?	Sakimura 1935

Table 4.9.2 (cont'd) Introductions for the biological control of *Dysmicoccus brevipes*

	Country	From	Year	Result	Reference
DIPTERA					
CECIDOMYIIDAE					
Cecidomyiid sp.	Panama		1931	–	Lai & Funasaki 1986
Cleodiplosis koebelei	Philippines	Hawaii	1931	+	Clausen 1978
Dicrodiplosis guatemalensis	Hawaii	Guatemala	1935	+	Clausen 1978
Vincentodiplosis (= *Lobodiplosis*) *pseudococci*	Hawaii	Mexico	1930	+	Clausen 1978
DROSOPHILIDAE					
Pseudiastata nebulosa	Hawaii	Guatemala	1924	–	Carter 1935
			1932	–	Carter 1935
Pseudiastata pseudococcivora	Panama		1931, 1951	–	Lai & Funasaki 1986

BRAZIL

Bisexual *D. brevipes* is present wherever pineapples are grown, but it is not recorded whether the parthenogenetic strain also occurs. Mealybug wilt was rare in 1946 and large mealybug colonies uncommon and always covered with soil mounds built by *Solenopsis* sp. ants. Sparse green spotting was general on the leaves of these plants. Natural enemies were numerous and included *Anagyrus* sp., *Hambletonia pseudococcina* and *Pseudaphycus* sp. The latter parasitised mealybugs on the aerial parts of the pineapple plant, so that large colonies were rare. It was never found on colonies under the soil surface. Its life cycle lasts 14 to 20 days and up to 6 individuals may emerge from a single host. Predators, mainly coccinellids, were generally present and attacked the underground mealybug colonies (Carter 1949).

COOK IS

Carter (1973) reported that mealybug wilt of pineapple was a serious threat to the newly-developing pineapple industry on Atui and Mangaia. *D. brevipes* was present, but not *D. neobrevipes*, and the mealybug was attended by *Pheidole megacephala*.

FIJI

D. brevipes is the main pest on pineapple and causes pineapple wilt—the only record in the Pacific outside Hawaii of this condition. It is also a minor pest of sugarcane. It is controlled to some degree by the coccinellids *Cryptolaemus* sp., *C. montrouzieri* and *Scymnus* sp. (Lever 1945). Three chrysopids were predators, including *Chrysopa ramburi* and *C. irregularis* (Lever 1940).

GUATEMALA

Two coccinellid predators of *D. brevipes* were reported by Carter (1935), *Scymnus bilucenarius* was widespread except in highest elevations, but it apparently exerted little control; and *Brachycantha* sp. which was uncommon. A drosophilid fly, *Pseudiastata nebulosa*, which was heavily parasitised by two chalcidid wasps, was found and frequently in large numbers. It was regarded as a promising species for biological control by Carter (1935), who introduced it to Hawaii in 1932, but the colony died out. Cecidomyiid predators were very common in the lowlands and occurred occasionally in the highlands. They attacked large mealybug colonies on fruit, but were apparently a minor control factor. No hymenopterous parasitoids were discovered.

GOLD COAST

The parasitoid *Pseudaphycus angelicus* was reared on *D. brevipes* in the laboratory (Anon. 1953) as also was *Anagyrus ananatis* from California (Anon. 1957). Both were released in 1953–54 and the former became established. *Scymnus sordidus* was also introduced from California, reared on *D. brevipes* and released, but establishment is not reported (Anon. 1957).

INDONESIA

Kalshoven (1981) reported that *D. brevipes* is attended by the ant, *Monomorium* sp.

IVORY COAST

D. brevipes is bisexual with a sex ratio usually of 2 males to 1 female. Ants attending the pineapple mealybug were species of *Camponotus*, *Crematogaster* and *Pheidole* (Reál 1959).

JAMAICA

Here and throughout Central America *D. brevipes* colonies of any size were invariably attended by *Solenopsis* ants. Where *Solenopsis* was not present mealybug colonies were rare and small (Carter 1935).

MALAYSIA

The pineapple mealybug *D. brevipes* is the most serious insect pest of pineapple in peninsular Malaysia. Infected plants become stunted and reddish and eventually wilt. Fruit are small and unsuitable for canning. In addition to wilting, the mealybug causes green spotting of the leaves, which is not of economic importance (Khoo et al. 1991).

The bisexual form of *D. brevipes* has been studied in some detail by Lim (1972). It was the only form found in 14 pineapple areas visited in Johore and Selangor. The bisexual form had a life cycle 10 day shorter than the parthenogenetic form in Hawaii, although it was less prolific.

MAURITIUS

D. brevipes was first reported as a major pest of pineapples in 1933, probably having been introduced on pineapple suckers from Hawaii about 1931. It was attacked by three native predators, the coccinellid *Scymnus mauritiusi*, the drosophilid fly *Gitonides perspicax*, and the pineapple scale, *Diaspis bromeliae* (Jepson 1939b) but they produced little impact. The coccinellid *Cryptolaemus montrouzieri* was introduced from South Africa and liberated, but did not become established (Moutia and Mamet 1946). The mealybug is attended by *Pheidole megacepahala*, *Solenopsis geminata* and *Technomyrmex detorquens* (Jepson and Wieke 1939).

PAPUA NEW GUINEA

D. brevipes is recorded attacking taro where it is subject to predation by the coccinellids *Cryptolaemus affinis*, *C. montrouzieri* and *C. wallacii* (Shaw et al. 1979).

PHILIPPINES

Two strains (grey and pink) of the pineapple mealybug are present and it is suggested that they may have been introduced with planting material from Hawaii, in which case they would represent *D. neobrevipes* and *D. brevipes* respectively. The grey strain produces green spotting of the leaves, whereas the pink strain produces only chlorotic spots. Some pineapple cultivars can be seriously damaged by pineapple wilt which is caused by both strains. Two species of ants are almost invariably in attendance on the mealybugs, namely *Solenopsis geminata* and *Pheidole megacephala* (Serrano 1934). Three predators from Hawaii were established in 1931 (*Cleodiplosis koebelei*: Cecidomyiidae, *Scymnus margipallens* and *Hyperaspis silvestri*: both Coccinellidae), but there is no information on their effectiveness (Clausen 1978).

PUERTO RICO

D. brevipes is the most serious pest of pineapples, attacking the roots, leaves and fruits of all varieties grown. *Anagyrus ananatis* was imported in 1936 from Brazil and both *A. ananatis* and *Hambletonia pseudococcina* in 1937 from Hawaii where they had been introduced from Brazil and Venezuela respectively. Both were released in 1937 and 1938. Only half grown or older hosts were attacked by *H. pseudococcina*, the life cycle from oviposition to adult emergence taking 24 to 30 days. In one instance, 3 parasitoids emerged from the same host. Frequent recoveries were made from the field. Development from egg to adult took 19 to 21 days for *A. ananatis* and the sex ratio was 1:1 (Bartlett 1939). Recoveries of this species were reported later (Bartlett 1943). The larvae of a tineid moth, a pyralid moth and of a cecidomyiid fly were found living in the waxy secretions around large groups of mealybugs and were thought to be predators. Three species of ants, including *Solenopsis geminata* were frequently observed carrying young mealybugs around. There do not appear to be any recent reports of the effectiveness of the introduced parasitoids (Plank and Smith 1940).

SOUTH AFRICA

Larvae of the moth *Drosica abjectella* were observed preying on *D. brevipes* on pineapple in the Transvaal. The number of moth larvae and pupae per pineapple plant varied from 1 to 15 and these occurred in the leaf axils. Large nymphs and fully-fed mealybug females were preferred and moth larvae each consumed an average of 6.5 hosts in the laboratory. In winter, development of fourth instar *D. abjectella* took 15 to 26 days, the prepupal period 1 to 3 days and the pupal stage 35 to 45 days. The adults lived for 3 to 6 days (Büttiker 1957).

SRI LANKA

Both a bisexual and a parthenogenetic strain of *D. brevipes* are present. The former, which causes green spotting of pineapple leaves, occurs in the west and the latter in the Bibile area (Carter 1956).

TAIWAN

D. brevipes is widely distributed on pineapple up to about 750 m and also occurs on banana (Chiu and Cheng 1957). It appears that *D. neobrevipes* is also present. Natural enemies include the cecidomyiid predator *Schizobremia formosana* and also coccinellids, but these are less effective

(Takahashi 1939). *Cryptolaemus*, imported for control of *D. brevipes* and other mealybugs, was only partially effective. A *Scymnus* sp., said to be effective against *D. brevipes* in Saipan, was introduced, but no further information is available (Sakimura 1935). The most abundant attendant ants were *Pheidologeton diversus*, *Anoplolepis longipes* and *Camponotus friedae* (Lee 1974).

TRINIDAD

The encyrtid *Pseudaphycus dysmicocci* was reared as a solitary parasitoid of second instar female nymphs of *D. brevipes* on pineapple (Bennett 1955).

USA

D. brevipes was a common pest in southern Florida and *Hambletonia pseudococcina* was introduced from Puerto Rico and liberated in 1954. Although it became established, information on its abundance and effectiveness is not available. It was postulated that the widespread use of organic pesticides had probably reduced the parasitoid to very low levels (Clausen 1956).

Major natural enemies

Anagyrus ananatis Hym.: Encyrtidae

This moderately polyphagous wasp is widespread in Brazil, where it is known as a parasitoid of *D. brevipes*, but also parasitises, *inter alia*, rhodes grass scale (*Antonina graminis*) and citrus mealybug (*Planococcus citri*) (Gabriel et al. 1982). It was established in Hawaii (Carter 1937), where it completes a generation in about 20 days.

Hambletonia pseudococcina Hym.: Encyrtidae

This parasitoid occurs as a bisexual form on *D. brevipes* in Brazil and as a parthenogenetic one in Colombia and Venezuela. The bisexual form failed to reproduce on *D. brevipes* in Hawaii, but the parthenogenetic form did so successfully (Carter 1937). About 24 to 30 days is required for the life cycle under tropical outdoor conditions and up to 4 individuals may emerge from a single host (Compere 1936). In laboratory trials, *H. pseudococcina* showed a high degree of specificity for *D. brevipes* and did not oviposit in 8 closely related mealybug species. Of 3 additional mealybugs tested, it attempted oviposition only in an unidentified species from a grass (Clancy and Pollard 1947).

Pseudiastata nebulosa Dipt.: Drosophilidae

This predator is native to Guatemala. It was introduced to Hawaii in 1924 but did not become established. Except in the highlands of Guatemala, it is frequently found in large numbers on a single plant, both above and below the soil line. It was again introduced in 1932, but the colony died out. This was possibly due to its requirement for large numbers of hosts, since 7 larvae consumed over 100 medium to large sized hosts during the last half of their larval lives. In Guatemala it is highly parasitised by two species of chalcidid wasps. Carter (1935) regarded it as a promising species for biological control.

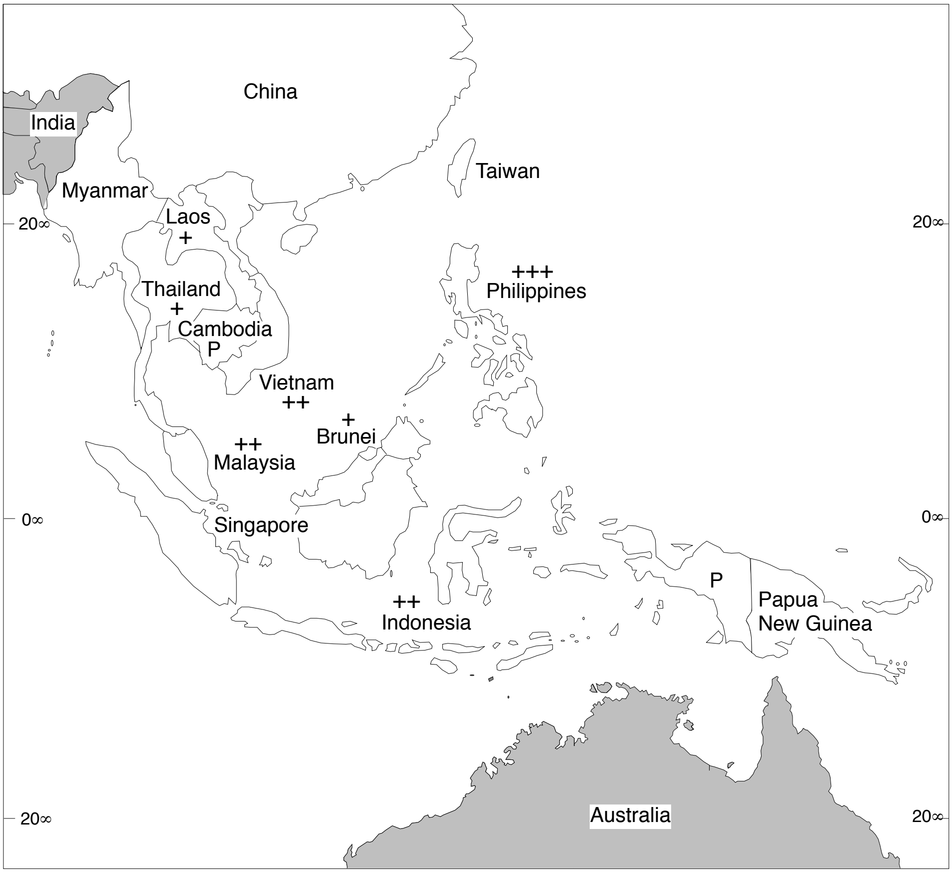
Vincentodiplosis pseudococci Dipt.: Cecidomyiidae

This midge is native to Mexico and was established in Hawaii in 1950. In neglected, weedy pineapple plantations in Hawaii, where the ant *Pheidole* sp. was less reliant on mealybug honeydew, the midge was sufficiently effective in controlling *D. brevipes* as to almost completely eliminate the mealybug from the fruit. Many fruit were covered with the old webs produced by midge larvae, but there were no live mealybugs. The midge is rarely found on leaves, but its larvae are commonly found attacking large mealybugs at the base of the fruit (Carter 1935, 1944).

Comments

It is very likely that *D. brevipes* evolved in South and/or Central America and there is, therefore, a *prima facie* case to consider it as a candidate for classical biological control in Southeast Asia and the Pacific. Indeed, there are 2 parasitoid species (*Anagyrus ananatis* and *Hambletonia pseudococcina*: both Eulophidae) and 2 predator species (*Vicentodiplosis pseudococci*: Cecidomyiidae and *Pseudiasta nebulosa*: Diastadidae) that are capable of reducing the mealybug to subeconomic levels. However, when any one or more of a number of ant species attends the mealybug it is largely protected from natural enemies and is able to build up to damaging numbers. In the absence of both ants and natural enemies the unharvested honeydew it produces leads to heavy growth of sooty moulds and there is transmission of pineapple mealybug wilt. Since apparently suitable natural enemies are available for introduction, the key to *D. brevipes* control is to deal with the attendant ants. There are several ant baits that have been used successfully for this purpose, but these are no longer registered for use in USA and, hence, cannot be recommended. No doubt suitable replacements will soon emerge. When extensive plantings of pineapples are made on areas where the soil has been worked to kill weeds, very few ant colonies survive. Recolonisation of the planted area occurs as colonies move along the rows towards the centre of the crop. One cultural method recommended to delay this spread is to plant several peripheral rows parallel to each boundary. Ants will then move along these, rather than into the crop and control measures can be concentrated on these rows (Rohrback et al. 1988). Promising results obtained with the integrated management of *D. brevipes* in Hawaii suggest that it would be well worth exploring similar methods elsewhere.

4.10 *Hypothenemus hampei*



Hypothenemus hampei is native to Central Africa but has spread to most coffee producing countries in Central and South America, to Southeast Asia and to several Pacific countries. Significant coffee-growing areas not yet infested are Hawaii, Papua New Guinea, Vanuatu and Solomon Islands.

It is a pest exclusively of coffee berries and does not damage the vegetative parts. It is difficult to control with chemicals and, although plantation management methods can reduce damage, the coffee berry borer remains an important pest.

The most important natural enemies appear to be 3 parasitic wasps native to Africa, *Cephalonomia stephanoderis*, *Phymastichus coffea* and *Prorops nasuta*. The last of these has been established in Brazil and Colombia without its own natural enemies, but has not so far produced spectacular results. *C. stephanoderis* has been established recently in Colombia, Ecuador, Mexico and New Caledonia, but it is too early to evaluate its impact. *Phymastichus coffea* has not yet been established anywhere, but this is foreshadowed in Colombia. The fungus *Beauveria bassiana* shows early promise. A thorough study is in progress of the interactions of the parasites and other natural enemies of *H. hampei* and the influence on them of various components of the environment. Optimism has been expressed about the outcome of this program.

Hypothenemus hampei (Ferrari)

Coleoptera: Scolytidae

coffee berry borer

Rating

Southeast Asia			Southern and Western Pacific		
	+++	Phil		+++	N Cal
12	++	Viet, Msia, Indo	7	++	Fiji, Fr P
	+	Thai, Laos, Brun			
	P	Camb		P	Pohnpei, Saipan

This account updates the chapter on *H. hampei* in Waterhouse and Norris (1989) and the valuable review of Murphy and Moore (1990) in relation to prospects for biological control.

Origin

Ferrari's specimens, described in 1867 under the generic name *Stephanoderes*, were obtained from trade coffee beans in France. There appears to be no record of the country of origin of the material, but in 1867 infested beans could only have come from Africa or Saudi Arabia, because *Hypothenemus hampei* did not obtain a footing on other continents until later. The seed used to establish *Coffea arabica* in Saudi Arabia was probably obtained from the Ethiopian highlands centuries ago. There the coffee berry borer is native, though scarce (Davidson 1967), but if it did not accompany the original seed it could easily have reached Saudi Arabia through Arabian-African commerce over the centuries.

The wider range of parasitoids (3) in West Africa than in East Africa (2, with one shared with the West) suggests that *H. hampei* has been in the West for a very long time and may indeed have evolved there (L.O. Brun pers. comm.).

Distribution

This was given by CIE (1981) as: **Africa** (Angola, Benin, Burundi, Cameroon, Canary Is, Central African Republic, Chad, Congo, Ethiopia, Fernando Poo, Gabon, Ghana, Guinea, Ivory Coast, Kenya, Liberia, Malawi, Mozambique, Nigeria, Principe, Rio Muni, Rwanda, São Tomé, Senegal, Sierra Leone, Sudan, Tanzania, Togo, Uganda and Zimbabwe); **Middle East** (Saudi Arabia), **Asia** (Indonesia, Cambodia, Laos, Malaysia, Philippines, Sri Lanka, Thailand, Vietnam); **Central America** (Guatemala, Honduras, Greater West Indies); **South America** (Brazil, Peru, Surinam); **Pacific** (Caroline Is, Irian Jaya, Marianas Is, New Caledonia, Society Is).

To these must be added: **South America** (Colombia in 1988 (D. Moore pers. comm. 1989), Ecuador (CIBC 1988a, b)); **Central America** (El Salvador, Mexico (Baker 1984)); **Asia** (India (Kumar et al. 1990)) and the **Pacific** (Fiji (Anon. 1979a), Tahiti (Johnston 1963)). In the **West Indies**, Reid (1983) reported the beetle from Jamaica and Puerto Rico, but it has not been reported from the lesser West Indies (Guadeloupe).

Significant coffee-growing or potential coffee-growing areas not yet infested are Solomon Is, Vanuatu, Hawaii and Papua New Guinea, although the latter is at serious risk because it shares a common land frontier with Irian Jaya (Indonesia), where *H. hampei* has been present for many years (Thomas 1961). *H. hampei* is not present in Australia.

Biology

The following description of the life cycle refers exclusively to the relationship of the beetle with *Coffea* spp., and principally with Arabian coffee *C. arabica* and robusta coffee *C. canephora*, the most important cultivated species. Infestations of *H. hampei* occur in coffee seeds while they are enclosed in berries on the trees and in berries that fall to the ground. They will also continue vigorously in processed beans in storage, but not if the moisture content has been reduced below 12.5% (robusta beans) or 13.5% (arabica beans) (Hargreaves 1935). Apart from dispersive flight by adult females and the walking by males from one berry to another on the same branch (P. Cochereau pers. comm. 1995), no part of the life cycle of the coffee berry borer is passed through outside of the coffee bean.

The length of adult females of *H. hampei* of American origin is given as 1.4 to 1.7 mm (Wood 1982) and of Ugandan females and males as about 1.9 mm and 1.3 mm respectively (Hargreaves 1926). Malaysian females averaged 1.58 mm and males 0.99 mm (Corbett 1933). Females outnumber males by at least 10 to 1 and the ratio is frequently much higher. The beetle is brown when it first emerges from the pupa but in the course of 4 or 5 days it becomes generally black, although the prothorax has a slightly reddish tinge. The prothorax is markedly humped, so that the down-turned head is not visible from above. The tibiae have strong spines which doubtless assist in such activities as tunneling through the pulp of coffee berries, ejecting the resulting frass, and forcing a way to the soil surface should the berry become interred.

Beetle attack tends to be aggregated on some trees or on particular branches within trees, rather than evenly distributed (Baker 1984). The fertilised female flies to coffee berries that have begun to ripen and bores an entrance hole at the apex, either in the terminal pore or in the calyx ridge or annulus of differentiated tissue that surrounds the pore. Sometimes this annulus is perforated by several holes, but boring into the fruit elsewhere is unusual. The colour of berries appears not to influence choice by females seeking oviposition sites (Morallo-Rejesus and Baldos 1980). Young berries, containing seeds with a watery endosperm, usually do not come under attack if more advanced berries are plentiful. If they do they are soon abandoned, after the female has fed on some of the pulp, and they then tend to fall prematurely, being particularly vulnerable to infection by disease organisms. The falling of such immature berries after being attacked often contributes significantly to the amount of crop lost. After the endosperm has passed from the watery to the milky stage in the course of maturation, beetles invading the berry will wait in the pulp until the seed tissue is firm enough to excavate (Penatos and Ochoa 1979). Rhodes and Mansingh (1981) cite opinions to the effect that females that become static in this fashion for several weeks (May to mid-July in the Jamaican lowlands) are in a state of reproductive diapause. When available, berries are selected that are already suitable for colonisation. The green berry is favoured for feeding and the ripe (i.e. red) berry for breeding purposes, but the ripe berries are also very suitable for feeding (Corbett 1933). In a ripe berry the female bores in one operation through skin, pulp and the endocarp and pellicle surrounding one of the two seeds (beans) present in each berry. Ejected frass may surround the entrance hole during boring (Hutson 1936). Several days may be occupied in this boring process, and the female then tunnels into the endosperm, the substance of the seed, which is the basis of the world's US$8 billion annual coffee crop (Bardner 1978). Berries that fall to the ground may generate considerable numbers of beetles, but these are from their on-tree infestation, since the female berry borers do not appear to visit fallen fruit (Baker 1984).

The eggs are laid at the rate of two or three a day in batches of 8 to 12 in chambers chewed out of the maturing bean tissue. Oviposition extends over a period of three to seven weeks, each female producing from about 30 to over 70 eggs. According to some authors, laying is not necessarily confined to one bean because the female that has initiated an infestation may fly to other berries during the oviposition period. According to others (e.g. Bergamin 1943) the female that has initiated an infestation only quits the bean when the first of her progeny emerge as adults. Others again (e.g. Hargreaves 1935) state that she remains until all the bean tissue is consumed or has deteriorated in some way. Most likely the pattern is quite flexible. Eggs hatch in three to nine days and young larvae bore into intact bean tissue, making pockets opening off the main tunnel made by the parent female. Male larvae pass through their two instars in the course of about 15 days, and the females pass through three instars in about 19 days (Bergamin 1943). Morallo-Rejesus and Baldos (1980) state that the female, like the male, passes through only two instars, indicating the need for further biological study. The long period over which oviposition is spread results in larvae in all stages of development being present in one bean. At the end of the larval stage there is a non-feeding or prepupal stage lasting about two days. The insect then pupates, without any cocoon formation, in the galleries excavated by the larvae. The pupal stage is passed through in four to nine days. The period from egg-laying to the emergence of the adult is 25 to 35 days. The temperatures at which the preceding records were made are generally not specified, but chiefly they relate to warm lowland coffee plantations. Bergamin (1943) recorded that at 24.5°C in Brazil the period from egg-laying to emergence of adult averaged 27.5 days. De Oliveira Filho (1927) found that in Brazil shade temperatures of 20 to 30°C suited the females best. Below 15°C they became inactive, endeavouring to hide, preferably in coffee berries, but sometimes by boring into beans, maize, peanuts or cotton seed of suitably low moisture content. They can survive temperatures just below 0°C, which however are rarely experienced in Brazilian coffee growing areas. At higher elevations development is somewhat prolonged (Le Pelley 1968) and *H. hampei* has a low pest status in highland coffee growing areas in East Africa and Java (Haarer 1962). Baker et al. (1989) conclude that the optimum mean annual temperature for the beetle is 23° to 25°C and that parasitoids for biological control should be sought from a similar climate.

The adult males emerge from the pupa earlier than the females. Their hindwings are short and they do not fly, but remain in the bean, fertilising their female siblings as they emerge. Each male can fertilise two females a day and up to 30 in his lifetime which may extend to 103 days, although averaging less. Corbett (1933) states that the males seldom leave the berries, and then only when they are near death. The vast majority of observers confirm that males never leave the berries. Quite likely they may move from bean to bean within a fruit, thereby gaining access to females other than their sisters. Parthenogenesis does not occur and, although unfertilised females may produce some eggs, these do not hatch. One insemination is sufficient to allow a female to lay fertile eggs throughout her reproductive period. Corbett (1933) stated that, if there are no males in the seed when the females emerge from the pupal skin after their hardening period of a few days, they leave via the entrance hole and seek males in other infested berries. Morallo-Rejesus and Baldos (1980) suggest that sex pheromones secreted by the males guide such females to appropriate berries.

Females that have been fertilised remain in the ‘parental’ bean for three or four days, by which time they have become sexually mature. They then leave the berries via the entrance holes and enter others and, after a preoviposition period of 4 to 20 days, commence egg laying. Females have been known to live up to 282 days, and longevity was stated by Bergamin (1943) to average 156 days. According to Corbett (1933), in Malaysia females survived 81 days without food. There is time for a succession of seven or eight generations a year in lowland coffee growing areas but, on account of the long reproductive period, there are few clearcut population peaks to indicate generations.

Life history studies have been carried out with artificial infestations of coffee trees in southern Mexico (Baker et al. 1992). Morallo-Rejesus and Baldos (1980) observed in the Philippines that beetles are to be observed in flight from 3.00 pm, considerable numbers being visible in the air between 4.00 and 5.00 pm. Corbett (1933) observed in Malaysia that females fly at any time during the day, but in greatest numbers between 2.00 and 5.00 pm, reaching a peak between 3.30 and 4.30 pm. De Oliveira Filho (1927) states that, in Brazil, females ‘are active’ on warm nights, but it is unclear whether this implies flight activity. Kalshoven (1981) states that, in Java, females start flying during the midday period, and that they assemble under leaves and in other places where they dance up and down like gnats. Such activity can have no sexual significance, seeing that the males do not leave the seeds, and its function is obscure. In Java flights up to 345 m have been measured (Leefmans 1920). In Mexico, Baker (1984) carried out experimental studies on flight. Females flew freely in the laboratory for up to 22 minutes, tending to hover or move forward only slowly. In tethered flight, and thus relieved of supporting their own weight, they could fly non-stop for 100 minutes, with a combined aggregate of three hours. Such enduring activity, combined with its afternoon peak of activity, suggests that, in their habits, the beetles resemble aphids and thrips in being adapted to exploiting periods of maximum convection in the atmosphere, so achieving long-distance travel with their own contribution serving chiefly to keep them aloft. De Oliveira Filho (1927) states that local flight occurs when the fertilised female is seeking a place to lay, when (oviposition having commenced) she emerges to seek moister berries after having been driven out by the heat of the sun. It also occurs when unfertilised females seek males (as they do if there are none in the berry when they emerge), when seeds are waterlogged, are overcrowded with adults and larvae, or when the beetles are disturbed.

Rhodes and Mansingh (1981) state that, in the Jamaican lowlands, beetles in dry berries remain in diapause for five months, from mid-December to mid-May. Baker (1984) found that in mid-spring in Mexico females tended to remain in fallen coffee berries at a time when temperatures in berries in the trees ranged up to an inimical 37°C. Soaking the fallen berries in water induced many to emerge, but they did so in a specific pattern, some seven to eight hours after dawn. Possibly the soaking simulated rain that would have made the environment generally more favourable. Baker reminds us that coffee is naturally an understorey plant in tropical forest and, by sheltering in fallen berries, beetles may avoid the harmful effects of strong, direct sunlight. Infestations are carried over between peaks of fruiting by the breeding that occurs in late-maturing berries, or else in those that have fallen to the ground. Females can survive for up to two months in buried beans (Clausen 1978).

It is probable that intercontinental travel is brought about by the agency of man, rather than by travel in moving air masses. Infested beans are an obvious vehicle for dispersal, but there are other avenues to which quarantine measures should be applied. In Jamaica, Reid (1983) observed females among banana trash used in packing boxes on their way to the boxing plant. Commonly, beetles disperse in sacks, empty or otherwise, and on the clothing and equipment of plantation workers. Under some conditions beetles bore for protection into wood or other materials to the extent that Baker (1984) suggested that authorities in beetle-free areas should think very carefully before allowing entry of untreated plant material from an infested area.

Host plants

An important aspect of the biology of any insect pest is its host range. In Africa, in addition to its regular hosts in the genus *Coffea*, *Hypothenemus hampei* has been reported from fruit, pods or seeds of species of *Centrosema*, *Crotalaria*, *Phaseolus* and *Tephrosia* (Fabaceae), *Leucaena* (Mimosaceae), *Caesalpinia* (Caesalpiniaceae), *Hibiscus* (Malvaceae), *Rubus* and *Oxyanthus* (Rubiaceae), *Vitis* (Vitaceae) and *Ligustrum* (Oleaceae), but these associations are all considered to reflect only casual feeding by adults. In Africa, the only species outside of the genus *Coffea* in which immature stages have been found is *Dialium lacourtianum* (Caesalpiniaceae) (Le Pelley 1968).

A review of hosts of the genus *Hypothenemus* was made by Johanneson and Mansingh (1984) who concluded that *H. hampei* was monophagous according to their criteria, as it attacked only six species of the genus *Coffea*. However, they listed 23 other species of plants in 11 families from which *H. hampei* has been recorded, but only as adult females. In contrast, in the Philippines, Morallo-Rejesus and Baldos (1980), whose paper was overlooked by Johanneson and Mansingh, reported finding eggs, larvae and pupae of *H. hampei* in *Leucaena leucocephala* (Mimosaceae), *Gliricidia sepium* (Fabaceae), two species of *Psychotria* (Rubiaceae) and one of *Dioscorea* (Dioscoreaceae). In laboratory tests they found that adults of *H. hampei* fed on pods of four of those species and also on the pods of 19 other species in 9 orders.

Such feeding tests may be of little significance, however, since the survival times recorded are greatly exceeded by the periods for which the beetles are capable of withstanding starvation (Corbett 1933). If the insects were correctly identified, the host plants recorded in the Philippines may help to support a population of *H. hampei* when no coffee berries are available. Reexamination of the host range is necessary. For example Cohic (1958) found *H. hampei* attacking loquat in New Caledonia, and this relationship, though abortive in the end, has not been reported anywhere else in the world. In connection with host records, Johanneson and Mansingh (1984) drew attention to the problem of misidentification of species of *Hypothenemus*, a notoriously difficult genus, and also to misinterpretation of the relative roles of various host plants. Hargreaves (1935) found adults of four species of *Hypothenemus* other than *H. hampei* in seed of *Phaseolus lunatus* (Fabaceae) in Uganda, and Gonzalez (1978) alludes to species of *Hypothenemus*, known as false coffee borers, which occur from Mexico to northern Argentina and greatly complicate quarantine procedures. Such insects would, of course, also raise difficulties in host plant studies. A thorough review of true hosts of *H. hampei* would be relevant to a number of aspects of the control of this pest.

Damage

Hypothenemus hampei is a pest exclusively of the immature and mature coffee berries and does no damage whatsoever to the vegetative parts of the plant. Prates (1969) showed that adults of *H. hampei* were strongly attracted to extracts of green or ripe coffee berries, but not to extracts of coffee leaves or flowers. Significant losses are caused by the female beetles feeding on young berries which are too immature to colonise but which, after the beetle has gone, are invaded by decay organisms, and so fall prematurely. In Java Leefmans (1920) found that 80% of green berries that had fallen through being bored by the beetle contained decayed beans as against 46.5% in unbored beans that had fallen through other causes. In the Congo, Schmitz and Crisinel (1957) found that 64 to 82% of shed berries had fallen on account of *H. hampei* attack. Such losses caused by attack on immature fruits are serious enough, but the bulk of the damage done by this beetle is to the endosperm of the mature beans, which may be extensively damaged or even completely destroyed. Even lightly bored beans acquire a distinctive blue-green staining which significantly reduces their market value (McNutt 1975), but the further tunnelling by the beetles and their larvae brings about progressive degradation, so that the coffee bean is reduced to a mass of frass. Market requirements demand the removal of damaged berries from the harvested crop, which is done by various mechanical processes (fortunately bored beans float), supplemented even by handpicking. The beans removed by such processing are not necessarily a total loss, but can go into only low grade fractions at a much reduced market rate.

In New Caledonia, where no control measures had been implemented, *H. hampei* was found to have attacked 80% of berries (Cohic 1958). Other examples of losses due to *Hypothenemus hampei* are given by Le Pelley (1968). Severe infestations in Uganda may result in 80% of berries being attacked. In the Ivory Coast, damage of 5% to 20% of berries is common, rising to 50% to 80% in some cases. In the Congo, boring of up to 84% of green berries and up to 96% of hard berries has been recorded and, in Tanzania, records indicate up to 96% boring of hard berries. In Malaysia there have been records of up to 90% of beans damaged. In Java crop loss of 40% was recorded in 1929, and in Brazil 60% to 80% losses have been experienced. The above figures apply for the most part to poorly managed situations, and crop losses can be reduced by appropriate management, but the beetle is a constant latent threat if vigilance is relaxed. In Jamaica, Reid (1983) estimated that 27% of the berries harvested were damaged. The studies of Reid and Mansingh (1985) showed that *H. hampei* was responsible for 20.9% reduction of exportable beans in the Jamaican crop of 1980–81. Baker (1984) reported that, in southern Mexico, the attack of *H. hampei* on coffee plantations was so severe that, in spite of application of insecticides in some places in 1982, no berries were harvested because it would not have been economical to do so.

Proper processing results in beans of moisture content too low to permit the borer to multiply. This is below 13.5% for arabica coffee and below 12.5% for robusta coffee. If coffee beans are stored with significantly higher moisture content, beetle reproduction continues. Thus Morallo-Rejesus and Baldos (1980) found that, in the Philippines, infestation in coffee beans stored before drying rose from 20% to 100% in six weeks.

Natural enemies

The cryptic nature of the immature stages and the male of *H. hampei* makes them relatively inaccessible victims for predators, and the only one recorded is the non-specific Javanese bug *Dindymus rubiginosus*. This bug draws the borers from the berries with its beak and sucks them dry. Le Pelley (1968) states that it is of little importance.

The most important parasitic wasps, *Cephalonomia stephanoderis*, *Prorops nasuta*, *Phymastichus coffea* and *Heterospilus coffeicola* are, of course, African in origin and are dealt with in some detail by Klein Koch et al. (1988) and Feldhege (1992). *C. stephanoderis* which is restricted to West Africa is the most important species in Ivory Coast, parasitising up to 50% of *H. hampei* in black berries (Ticheler 1961). The potential of *H. coffeicola* in biological control requires further study because its larvae are not very specific, but the other three species appear to have a narrow enough host range to make them acceptable from this point of view. A fifth parasite, *Goniozus* sp. is recorded, but without further data, from Ivory Coast (Cochereau and Potiaroa 1994).

In addition to the identified arthropod natural enemies (Table 4.10.1), Leefmans (1924a) recorded a non-specific parasite that attacks beetles in newly infested berries and Hargreaves (1926) found an unidentified hymenopterous parasitoid in Uganda, now known also from Togo as *Aphanogmus dictynna* and considered to be a hyperparasitoid of *C. stephanoderis* or *P. nasuta* (Feldhege 1992). Morallo-Rejesus and Baldos (1980) reported the presence in the Philippines of a braconid and an encyrtid parasitoid of *H. hampei*, both unidentified, and presumably non-specific members of the local fauna.

Some ants attack the borer. Swallows and other small birds that feed on the wing consume flying adults of *H. hampei*.

The parasitic fungus *Beauveria bassiana* has been observed attacking *H. hampei* in Brazil (Averna-Saccá 1930; Villacorta 1984), Jamaica (Rhodes and Mansingh 1981), Cameroon (Pascalet 1939), Congo (Sladden 1934; Steyaert 1935), Ivory Coast (Ticheler 1961), India (Balakrishnan et al. 1994), Java (Friederichs and Bally 1922) and in New Caledonia (Cochereau and Potiaroa 1994). Steyaert (1935) and Averna-Saccá (1930) studied the seasonal cycle and the former also made studies of the infectivity and epidemiology of the fungus of which there are many strains. In an analysis of 16 isolates from *H. hampei* adults from 10 countries in Latin America, Africa, Asia and the Pacific, 13 formed a homogenous group with very similar electrophoretic and physiological characteristics, suggesting a distinct strain associated widely with the coffee berry borer. Of the remaining 3 strains, one from Sri Lanka is suspected as having degenerated during some 63 years in storage, but the others (from New Caledonia and Kenya) are probably distinct entities (Bridge et al. 1990). The New Caledonian strain presumably attacked some other host until *H. hampei* arrived there in 1948. It is a particularly virulent strain and can cause death of *H. hampei* in 5 days (Cochereau et al. 1994). Moist, warm conditions favour the incidence of this pathogen, and heavy rain is thought to enhance the rate of infection. If spraying with fungal preparations is avoided on the day of release of parasitoids, adverse effects on the latter are not observed (Reyes et al. 1995). Friederichs (1922) recommended the encouragement of heavy shade to increase the incidence of fungal pathogens, but this runs counter to the fact that intensity of shade must often be reduced to encourage hymenopterous parasitoids which, however, may still prove to be of minor significance in population regulation. Certainly, Klein Koch (1989a) considered *Beauveria* to be the most important natural enemy of *H. hampei* in Ecuador. In Colombia, preparations of selected strains of *Beauveria* in oil have produced 20 to 95% adult mortality, slightly higher than the 20 to 90% produced by selected strains of *Metarhizium* (P. Cochereau, pers. comm. 1995). Varela and Morales (1996) have characterised a number of *Beauveria* isolates and their virulence against *H. hampei*.

Pascalet (1939) advocated the spraying of suspensions of spores, before sunrise, but no results are available. As with so many parasitic fungi, its application would be limited by intolerance of dry conditions. Another fungus that attacks *H. hampei*, *Paecilomyces javanicus*, is Afro-Asian in distribution and wide spectrum in its host range (Samson 1974), attacking also Lepidoptera. Its use against *H. hampei* appears not to have been attempted.

There appears to be only one record of nematodes attacking *H. hampei* in the field (Varaprasad et al. 1994), but in addition, Allard and Moore (1989) showed that a *Heterorhabditis* sp. could cause high mortality of both adult and larval *H. hampei* under laboratory conditions and that infective juveniles were produced from adults and larger larvae. Spraying of nematodes on fallen berries might remove the need to collect them (which involves much labor), leaving them to provide mulch. Dispersal of infected adults may also spread the nematodes into the pest population. Further work with nematodes is clearly desirable.

Table 4.10.1 Natural enemies of *Hypothenemus hampei*

Species and type	Country	Reference	Comment
HEMIPTERA			
PYRRHOCORIDAE (Predator) *Dindymus rubiginosus*	Java	Wurth 1922	Not specific
HYMENOPTERA			
BETHYLIDAE (ectoparasites of immature stages)			
Cephalonomia stephanoderis	Ivory Coast	Betrem 1961; Ticheler 1961; Cochereau & Potiaroa 1994;	A promising parasite
	Togo	Klein Koch et al. 1988	
Goniozus sp.	Ivory Coast	Cochereau & Potiaroa 1994	
Prorops nasuta	Cameroon	Klein Koch et al. 1988	
	Congo	Klein Koch et al. 1988	
	Ivory Coast	Klein Koch et al. 1988	
	Kenya	Klein Koch et al. 1988	
	Tanzania	Rangi et al. 1988	
	Togo	Klein Koch et al. 1988	
	Uganda	Klein Koch et al. 1988; Klein Koch et al. 1988; Waterston 1923	
Scleroderma cadaverica	Uganda	Benoit 1957	Causes severe dermatitis in man
CERAPHRONIDAE			
Aphanogmus (= *Calliceras*) dictynna	Uganda	Waterston 1923	Possibly hyperparasitic
EULOPHIDAE			
Phymastichus coffea (attacks adult beetles)	Ivory Coast	Cochereau & Potiaroa 1994	
	Kenya	La Salle 1990	
	Togo	Klein Koch et al. 1988	

Table 4.10.1 (cont'd) Natural enemies of *Hypothenemus hampei*

Species and type	Country	Reference	Comment
HYMENOPTERA			
BRACONIDAE			
(ectoparasitoid and predator)	Uganda	Schmiedeknecht 1924	Kills larvae with sting
Heterospilus coffeicola	Tanzania	CIBC 1988b	Attacks larvae of other parasites of *H. hampei* — also may be cannibalistic
	Cameroon	Klein Koch et al. 1988	
	Congo	Klein Koch et al. 1988	
FORMICIDAE			
(predator)			
Crematogaster curvispinosa	Brazil	Pinto da Fonseca & Araujo 1939	Can cause high mortality of immature stages in coffee berries
ACARI			
Pyemotid mite	New Caledonia	P. Cochereau pers. comm.	
NEMATODA			
Heterorhabditis sp.		Moore & Prior 1988	
Panagrolaimus sp.	India	Varaprasad et al. 1994	
FUNGI			
HYPHOMYCETES			
Beauveria bassiana	Java	Friederichs & Bally 1922	Cosmopolitan, in a variety of strains
(= *Botrytis stephanoderis*)	Cameroon	Pascalet 1939	
Metarhizium anisopliae		Moore & Prior 1988	
Nomuraea rileyi		Moore & Prior 1988	Usually recorded from Lepidoptera
Paecilomyces (= *Spicaria*) *javanicus*	Java	Friederichs and Bally 1922; Samson 1974	Indonesia, Asia, Africa
P. tenuipes		Moore & Prior 1988	

Attempts at biological control

Published information is summarised in Table 4.10.2, but there were probably a number of transfers of parasites within Africa and perhaps South America that have gone unrecorded. In the past decade the International Institute for Biological Control had adopted the policy of breeding African parasitoids in England on *H. hampei* in coffee beans from the country of destination. This is because of the possibility that the wasps might carry spores of fungal diseases of coffee, especially new strains of coffee leaf rust (*Hemileia vastatrix*) and coffee berry disease (*Colletotrichium coffeanum*) (Moore and Prior 1988; Rangi et al. 1988; Nemeye et al. 1990; Murphy and Rangi 1991). The danger of fungal transmission could also be reduced by breeding *H. hampei* on an artificial diet (Brun et al. 1993; Perez et al. 1995; Villacorta 1985).

Africa

CAMEROON

Pascalet (1939) recommended the introduction of *Heterospilus coffeicola*, *Prorops nasuta* and *Beauveria bassiana* to any plantations lacking them. There is no record that this was implemented anywhere, nor whether any or all of the organisms were not already generally present.

CONGO

Sladden (1934) and Leroy (1936) suggested that, by breeding and liberating them, it would be possible to increase the efficiency of *P. nasuta* and *H. coffeicola*, which he knew to be already present in the Congo and he made a similar suggestion for fungus diseases. However, there is no indication of the extent to which this was done.

KENYA

Prorops nasuta was sent from Uganda to Kenya in 1930 (Greathead 1971), but according to Evans (1965) that wasp and *H. coffeicola* were probably native there. Abasa (1975) considered that parasites were of doubtful value in controlling *H. hampei* in Kenya.

UGANDA

Prorops nasuta and *Heterospilus coffeicola* are both native to Uganda. Hargreaves (1935) considered that some areas lacked these parasites, and so he introduced cultures from Kampala County, north of Lake Victoria, to Bwamba County on the western border. He stated that this introduction resulted in a great reduction in the previously intense infestation of coffee berry borer but, in view of the natural occurrence of *P. nasuta* over a wide area to the west of the Ugandan border (Le Pelley 1968), it seems unlikely that the distribution was discontinuous and that it was lacking in Bwamba

County. Hargreaves' claims that the introduction brought about a great reduction in the impact of the coffee berry borer in Bwamba County must be treated with reserve, the more so since De Toledo Piza and Pinto da Fonseca (1935) state that neither *P. nasuta* nor *H. coffeicola* appeared to control the borer in nearby Kampala. More recently, *P. nasuta* was reported to achieve 20% parasitisation in western Kenya in the dry season (Barrera et al. 1990b).

Asia

SRI LANKA

Stock of *P. nasuta* and *H. coffeicola* from Uganda were liberated in Sri Lanka in 1938, but neither species became established (Hutson 1939).

INDONESIA

The introduction of *Prorops nasuta* to Java from Uganda in 1923 was the earliest attempt to bring about the biological control of *H. hampei* which had first been reported in Java in 1909 (Kalshoven 1981). *P. nasuta* was found to be easily propagated (Leefmans 1924a), was distributed widely in considerable numbers (Begemann 1926) and became established (Le Pelley 1968). However, it apparently could not maintain itself and was still being bred for distribution in 1928 (Ultée 1928) and in 1932 (Betrem 1932; Schweizer 1932; Ultée 1932).

Leefmans (1924a) drew attention to the fact that the *P. nasuta* did not thrive in shade, and that it flourished best in black berries which tend to be most abundant after harvest, when the parasite is least needed. The former problem was solved by appropriate pruning but, despite improvements in management to favour it and the long period spent in breeding and disseminating it, the parasite seems not to have become established in Java (Clausen 1978; Kalshoven 1981).

Cultures of *Heterospilus coffeicola* were taken to Java from Uganda along with those of *P. nasuta* in 1923, but the wasp appears not to have been released. Leefmans (1924a) seems to have concluded that it was likely to be incompatible with *P. nasuta*.

Table 4.10.2 Introductions for the biological control of *Hypothenemus hampei*

Country and species liberated	Year	From	Result	Reference
BRAZIL				
Cephalonomia stephanoderis	?	?	+	Benassi & Berti-Filho 1989
Prorops nasuta	1929	Uganda	+	Hempel 1933; Yokoyama et al. 1978
COLOMBIA				
Cephalonomia stephanoderis	1988	Kenya via U.K.	+	C. Klein Koch pers. comm. 1995; Sponagel 1993
Prorops nasuta	1995		+	Bustillo et al. 1995; Portilla & Bustillo 1995
ECUADOR				
Cephalonomia stephanoderis	1988	Togo via U.K.	+	CIBC 1988b; Klein Koch 1989a,b,c; Klein Koch et al. 1988; Delgado et al. 1990; Sponagel 1993
Prorops nasuta	1987–1990	Kenya via U.K.	–	CIBC 1988a; Klein Koch et al. 1988; Rangi et al. 1988; Murphy & Rangi 1991; Sponagel 1993
	1988	West Africa	–	
EL SALVADOR				
Cephalonomia stephanoderis	1988	Kenya via U.K.	+	Sponagel 1993; C. Klein Koch pers. comm. 1995
GUATEMALA				
Cephalonomia stephanoderis	1988	Kenya via U.K.	?	Sponagel 1993
	1993-1995			Garcia & Barrios 1996
HONDURAS				
Cephalonomia stephanoderis	1988	Kenya via U.K.	?	Sponagel 1993

Table 4.10.2 (cont'd) Introductions for the biological control of *Hypothenemus hampei*

Country and species liberated	Year	From	Result	Reference
INDONESIA				
Cephalonomia stephanoderis	1988		?	Sponagel 1993
Heterospilus coffeicola	1923	Uganda	not liberated	Kalshoven 1981
	1931	Uganda	?	Le Pelley 1968
Prorops nasuta	1923–1925	Uganda	–	Begemann 1926 Kalshoven 1981
KENYA				
Prorops nasuta	1930	Uganda	already present	Evans 1965
MEXICO				
Cephalonomia stephanoderis	1988–1989	Togo via U.K.	+	Barrera et al. 1990 a, b; CIBC 1988b
Prorops nasuta	1988–1989	Kenya and Togo via U.K.	?	Barrera et al. 1990a, b; Murphy & Rangi 1991
NEW CALEDONIA				
Cephalonomia stephanoderis	1993	Ivory Coast	+	Cochereau & Potiaroa 1994
UGANDA (BWAMBA COUNTY)				
Prorops nasuta	1932	Uganda (Kampala county)	+ ?already present	Hargreaves 1935
PERU				
Prorops nasuta	1962			Clausen 1978
	1964?	Brazil	–	De Ingunza 1964
SRI LANKA				
Heterospilus coffeicola	1938	Uganda	–	Hutson 1939
Prorops nasuta	1938	Uganda	–	Hutson 1939

Pacific

NEW CALEDONIA

Infestation of coffee berries with *H. hampei* ranges from 0% to 100%, with an overall average of 33%. *C. stephanoderis* from West Africa was released in 1993 and recovered almost a year later. However, wherever the aggressive, little red fire ant (*Wasmannia auropunctata,* introduced around 1970) is present this parasitoid is unable to survive. When the fire ant is eliminated from a plantation by banding the trees with insecticide the wasp is established. Ant control is, thus, a prerequisite for biological control (Cochereau and Potiara 1994; P. Cochereau pers. comm. 1995). *Phymastichus coffea* is currently under consideration for liberation (P. Cochereau pers. comm.). Cochereau et al. (1994) have examined in some detail the effectiveness against *H. hampei* of a virulent New Caledonian strain of *Beauveria bassiana*, which shows considerable promise in the field.

Central America

GUATEMALA

Cephalonomia stephanoderis was mass produced and released during 1993 to 1995. Infestation by *H. hampei* was reduced 75%, to 2.7 to 5.3% in 1993 and to 0.4 to 0.9% in 1994, but an increase was observed in 1995 (1.6 to 2.4%, compared with the control of 3.8% infestation), resulting in 48% control (Garcia and Barrios 1996). The cost of mass liberations of *C. stephanoderis* was comparable with that of chemical control (Decazy et al. 1995).

MEXICO

Cephalonomia stephanoderis from Togo and *Prorops nasuta* from both Togo and Kenya were raised in U.K. in coffee beans from Mexico before being sent there for mass production and liberation during 1988 and 1989. *C. stephanoderis* has become established, but the situation with *P. nasuta* is unclear (Barrera et al. 1990a, b). The impact of these parasitoids remains to be reported.

South America

BRAZIL

Prorops nasuta was imported into Brazil from Uganda in 1929, and by 1933 it was established in several coffee plantations (Hempel 1933, 1934). As in Java, breeding and distribution continued and in 1937 (Anon. 1937) it was stated to be of considerable value in controlling the coffee berry borer in São Paulo, but only if its numbers were boosted by rearing between coffee production seasons. Puzzi (1939) studied the reproduction of the parasite in relation to that of its host in Brazil and concluded that, in theory, it was more prolific, but that the efficiency of the parasite was limited by the tendency of the female to remain in one berry. De Toledo (1942) examined rates of parasitisation, but his figures do not suggest that the wasp could have been having any significant impact. De Toledo et al. (1947) were only mildly enthusiastic about the value of the wasp, mentioning a continuing need for repeated liberations and the requirement for boosting the effect of the parasite by cultural practices. Le Pelley (1968) stated that, at that time, Brazilian entomologists appeared satisfied that *P. nasuta* was of value in their country, but he could find no conclusive evidence that the amount of routine work required for the control of *H. hampei* had decreased. Yokayama et al. (1978), considered that the climate of the São Paulo district in Brazil was unfavourable for this wasp, in which the growers lost interest when BHC was found to give satisfactory control. Nevertheless, they reported that it had recently been recovered in coffee plantations in São Paulo, having survived pesticide usage, severe droughts and winter frosts. The fact that *P. nasuta* has been transferred more recently to areas in Brazil where it is not established indicates that the wasp is considered to be of some value (Ferreira and Batistela Sobrinho 1987).

Although there is no record of its release, a species of *Cephalonomia*, presumably *C. stephanoderis* was recovered in the field in Brazil between 1986 and 1988 (Benassi and Berti-Filho 1989).

A survey of natural enemies of *H. hampei* in northern Espirito Santo from 1986 to 1994 revealed 3 parasitoids (*Prorops nasuta*, *Cephalonomia* sp., and a species of Proctotrupoidea), an ant predator (*Crematogaster curvispinosa*) and a fungus (*Beauveria bassiana*) (Benassi 1995).

COLOMBIA

The rate of population increase of *H. hampei* in the field has been studied by Gaviria et al. (1995). A major program of integrated management commenced in 1992, involving local strains of the fungi *Beauveria bassiana* and *Metarhizium anisopliae* and parasitoids, in particular *Cephalonomia stephanoderis* and *Prorops nasuta* (CABI: IIBC 1993; C. Klein Koch pers. comm. 1994; Bustillo et al. 1995). Methods for mass production of *C. stephanoderis* and *Prorops nasuta* are provided by Portilla and Bustillo (1995). Sixty million parasitoids were released and 100 tons of *B. bassiana* and *M. anisopliae* were applied (Bustillo et al. 1995).

ECUADOR

Klein Koch (1986) proposed the introduction of 3 parasitoids from Africa, *Prorops nasuta*, *Heterospilus coffeicola* and *Cephalonomia stephanoderis*. *C. stephanoderis* was first introduced from Togo in 1988 and *P. nasuta* from Tanzania and Kenya in 1987–88 and Togo in 1988 (Klein Koch 1989c).

Liberations continued in subsequent years with some 920000 of the former species and 30,000 of the latter being released in 1992. Both species are now well established and having a significant effect. In field experiments with caged coffee trees 86% of berries on the bush and 87% on the ground contained *C. stephanoderis* and up to 52% and 31% parasitisation respectively was recorded from tree and ground berries in the open (Klein Koch 1989b,c, 1990). However the results are poor in the Amazon region of the country where the rainfall is very high. Elsewhere, as part of an integrated approach, infestation levels on *Coffea arabica* are as low as 0.4 to 1.4%. Recently introduced *catimor* varieties are resistant to coffee rust, so sprays are no longer required (Klein Koch pers. comm. 1994). In addition, the fungus *Beauveria bassiana* and the ant *Azteca* sp. cause considerable mortality of *H. hampei* when humid weather conditions prevail (Klein Koch et al. 1987).

PERU

According to De Ingunza (1964) *Prorops nasuta* was introduced from Brazil to Peru in 1962, but failed to become established.

Major parasite species

Cephalonomia stephanoderis Hym.: Bethylidae

Cephalonomia stephanoderis is a small black bethylid wasp which is native to West Africa (Ivory Coast, Togo). The females, which are 1.6 to 2.0 mm in length, enter bored coffee berries and deposit eggs on the ventral surface of final stage larvae and prepupae of *H. hampei*. Its larvae feed as ectoparasites, exhausting the tissues of the host in 4 to 6 days, then spinning a silken cocoon in which to pupate. The pupal stage lasts about 15 days. Fertilisation takes place in the berry where the wasps emerge, and seemingly, the males, although fully winged, remain there after the females have left. Females must feed for two days at 27°C or 6 to 11 days at 24°C before they can mature eggs. Adult females feed by preference on *H. hampei* eggs and young larvae but also on prepupae and they chew holes in the intersegmental membrane of adult beetles, between the prothoracic and mesothoracic tergites, and feed on the haemolymph. Females cannot produce eggs on a diet of borer eggs or adults alone, but need to feed first on the larvae and/or prepupae of the borer. They can lay up to 70 eggs (Barrera et al. 1989, 1993; Abraham et al. 1990; Wegbe 1990; Infante et al. 1994a) and can distinguish between parasitised and unparasitised hosts (Barrera et al. 1994). In the Ivory Coast, Koch (1973) found that adult *C. stephanoderis* each required two eggs, two larvae or two adults per day for survival. At the end of the coffee season *H. hampei* populations were reduced by parasitisation by 20%

to 30%, but by not more than 5% between seasons. Ticheler (1961) recorded up to 50% parasitisation by this, the most important parasitoid in the Ivory Coast. In West Africa *C. stephanoderis* is commoner than *P. nasuta* (Abraham et al. 1990). A major mass production and release program commenced in Colombia in 1993, with a production of 10 million wasps per month. When 400 000 wasps were released in a 2 million ha area of coffee trees 85% parasitisation was attained when there was 80% infestation of coffee berries and 20% parasitisation when there was 5% infestation. The target for the releases was 12.5 wasps per berry and 300 berries containing wasps for each 15 trees, giving 20 000 to 30 000 wasps per ha (P. Cochereau pers. comm. 1995). Life tables were developed for *C. stephanoderis* in Mexico (Infante and Luis 1993; Infante et al. 1994b).

Studies of mass releases of *C. stephanoderis* suggest that they can control low density populations of *H. hampei* in commercial coffee plantations, adult predation by the wasp probably being the most important mortality factor. However, mass production costs are too high for releases to be economically viable and cheap artificial diets for mass rearing are being investigated, with successful rearing already achieved for four generations (CABI:IIBC 1996).

Heterospilus coffeicola Hym.: Braconidae

Heterospilus coffeicola is a braconid wasp about 2.5 mm long. It does not enter the borehole of the beetle, but travels from berry to berry inserting its ovipositor into the boreholes in the course of seeking *Hypothenemus* larvae. Only one small egg is laid in each berry, and the larva that emerges after about six days feeds on beetle eggs and larvae over a period of 18 to 20 days, consuming 10 to 15 eggs and larvae per day. In this regard it is more of a predator than a parasite. According to De Toledo Piza and Pinto da Fonseca (1935) the larva kills the adult *H. hampei* before pupating inside a white silken cocoon. The wasp emerges after a comparatively brief pupal period (Hargreaves 1926; De Toledo Piza and Pinto da Fonseca 1935, Le Pelley 1968). In Uganda it is attacked by a chalcidid of the genus *Closterocerus* (Schmiedeknecht 1924).

Hargreaves (1926, 1935) stated that *Heterospilus coffeicola* contributed substantially to the control of *H. hampei* in Uganda. The Brazilian entomologists De Toledo Piza and Pinto da Fonseca (1935) studied the wasp in Uganda with a view to assessing its potential value as a biological control agent in Brazil. They concluded that *H. coffeicola* can thrive only in areas with a continuous production of coffee berries throughout the year, and as such conditions prevail nowhere in Brazil they recommended against its importation. One possible disadvantage of this wasp is that its larvae feed on the larvae of other wasps as well as those of *H. hampei*, and it may even be cannibalistic (Hargreaves 1924). If these statements are verified then there may be reservations about the employment of *H. coffeicola* in biological control. A further difficulty associated with this species as a biological control agent is that a number of workers have been unable to breed it in the laboratory, a problem also experienced by CIBC (1987) during its current program, although Rangi et al. (1988) have reported limited success. The free-living existence of the adults may involve special nutritional or mating requirements that have not yet been met experimentally.

Phymastichus coffea Hym.: Eulophidae

This parasitoid was first recorded in Togo as recently as 1989 (Borbon-Martinez 1989), causing up to 30% parasitisation, but is now known also from Ivory Coast and Kenya. It is an endoparasite of the adult female *H. hampei*, which is usually attacked as she is commencing to tunnel in to a coffee berry. *P. coffea* also enters the berry to parasitise male *H. hampei*. Oviposition occurs in both the thorax and the abdomen of the host, the former producing a male and the latter a female. Although several eggs may be laid in each host, only two wasps are produced. Males range in length from 0.45 to 0.55 mm and females from 0.8 to 1.0 mm. Females do not require to be fertilised before they commence oviposition shortly after emergence. At 27°C, larval development takes about 21 days, the pupal stage about 8 days and adult longevity appears to be a few days only. In the field 20 females were produced for each male and it was estimated that between 4 and 7 hosts could be parasitised in a 4-hour period.

P. coffea was the most important parasitoid of *H. hampei* in the majority of coffee holdings on the Togolese Plateau at about 800m above sea level and is fairly common around Man (West Ivory Coast) near the Liberian border (La Salle 1990; Feldhege 1992; P. Cochereau pers. comm. 1994; Infante et al. 1994a,).

Mass production methods have been developed in Colombia for *P. coffea* and a decision to release is expected shortly (CABI:IIBC 1996).

Prorops nasuta Hym.: Bethylidae

Prorops nasuta is native to Uganda, Kenya, Tanzania and Cameroon, Ivory Coast and Togo. It is a dark brown bethylid wasp about 2.3mm in length, the name *nasuta* referring to the characteristic bilobed ‘nose’ protruding forwards above the antennal bases. This wasp parasitises and preys upon several species of *Hypothenemus* (Clausen 1978). Males that emerge first from pupae always stay on the remaining cocoons within the coffee berry and mate with the females as they emerge. Because *P. nasuta* populations are, thus, highly inbred it is probable that there are different strains of

P. nasuta in West Africa and East Africa, (Abraham et al. 1990; Griffiths and Godfray 1988; Murphy and Rangi 1991) and testing these may be highly relevant to biological control. On coffee the fertilised female enters an infested berry via the borehole of the adult *H. hampei*, choosing berries on the trees rather than those on the ground. If the parent borer beetle is still present she may kill it and use the cadaver to plug the entrance hole, over which she stands guard. According to CIBC (1987) the female wasp does not feed upon borer beetles she may kill, but other authors state that she will do so if no other life history stages are available, but that she cannot mature eggs on a diet of adults alone. Several larvae and pupae may be injured with the ovipositor before any oviposition occurs, and these victims succumb in a few days. *P. nasuta* feeds by preference on the eggs and young larvae of *H. hampei* and oviposit on the late third stage larvae and pupae. The hosts chosen for oviposition are stung, sometimes several times, and thus paralysed before one, or sometimes two, eggs are laid upon them. Eggs are placed ventrally on larvae and on the abdominal dorsum of pupae. The eggs (0.55 × 0.18mm) are large for a wasp of this size. They hatch in an average of about three days and the larval stages last three to eight days. The ectoparasitic larva may consume more than one host. There is a prepupal (non-feeding) period of about three days, passed inside a silken cocoon spun by the fully fed larva. It is common to find 20 cocoons in a coffee bean, and up to 62 have been recorded. The pupal stage lasts on an average about 21 days, varying from 9 to 27 days according to temperature.

The life cycle from egg to adult lasts 17 to 33 days (average 29) at 25°C and may be as long as 66 days at 18°C. There are considerable discrepancies between figures given by various authors for the duration of the life history stages, but there is general agreement that the female is quite long-lived — up to 135 days being cited in Brazil, given an abundant supply of larvae and prepupae as food. By contrast it appears that the males do not feed and they do not survive longer than 13 days. Females outnumber the males, a figure of three to one being recorded. Statements as to duration of the preoviposition period give rather diverse figures. Usually a few days are indicated but one record is of 17 days. Parthenogenesis may occur, when only male progeny are produced. Females may lay up to 66 eggs at a rate of one or two a day, utilising several berries in the process.

In feeding, females consume several eggs and unparasitised larvae per day and they will also eat pupae. Normally all stages of the beetle in a berry are killed either by parasitisation, predation or merely by stabbing before the female leaves (Leefmans 1924a; Begemann 1926; Hempel 1933; De Toledo Piza and da Fonseca 1935; Hargreaves 1935; Hutson 1936; Puzzi 1939; De Toledo 1942; Le Pelley 1968; Abraham et al. 1990;). The low abundance of

P. nasuta in Western Kenya suggests that it may not be suited to high altitudes (Murphy and Rangi 1991). In one locality in São Paulo (Brazil) the percentage of infested berries that contained parasitoids rose to a maximum of 2.4 in autumn (De Toledo 1942).

Scleroderma cadaverica Hym.: Bethylidae

Scleroderma cadaverica is listed by Herting and Simmonds (1973) as a natural enemy of *H. hampei*, but only some of the specimens before Benoit (1957) when he prepared the taxonomic description had been reared from that species, others being stated to come from small beetles boring in cane furniture. The North American species of *Scleroderma* are stated by Krombein et al. (1979) to be parasitic on the larvae of small wood-boring beetles, the female wasps frequently stinging people inhabiting infested houses. The African specimens of *S. cadaverica* were submitted to European specialists for identification and description because stinging by females (which may be either winged or apterous) had caused severe dermatitis to African and European people. No responsible person would consider using this insect in biological control projects.

Comments

Hypothenemus hampei has established itself in most of the coffee growing areas of the world, but there are still uninfested countries, such as Australia, Hawaii, Papua New Guinea, Vanuatu and the Solomon Islands. Quarantine is of critical importance to these countries and it is important to ensure that coffee imported into clean areas has been completely disinfested. Thorough drying of the seed coffee is an indispensable supplement to disinfestation techniques.

Although great advances have been made in recent years in the chemical control of *H. hampei*, it would be a great advantage to have the support of additional measures. Rhodes and Mansingh (1981) found chemical control inadequate on its own in Jamaica and advocated its integration with cultural practices and Bardner (1978) emphasised the need to harmonise cultural, biological and chemical control of coffee pests. Hernandez Paz and Penagos Dardon (1974) found, in Guatemala, that low-volume sprays of endosulfan could completely destroy *H. hampei* in berries on the bushes and, according to Mansingh and Rhodes (1983), this chemical is in extensive use in Central and South America. However, a very high level of resistance to endosulfan in *H. hampei* is reported in New Caledonia (Brun et al. 1989, 1990), raising concern that this valuable insecticide may not remain an effective material for long.

Plantation sanitation is an old-established tradition in pest control, and the coffee berry borer has long been attacked from this angle. The life cycle of the borer, indeed, lends itself to this approach, as it is narrowly specific to the coffee berries. In Java, Roepke (1912) and Leefmans (1924b) recommended the total destruction of infested or susceptible berries over a period long enough to break the life cycle of the coffee berry borer. A period of three months was aimed at, although some records of the longevity of beetles exceed this. Measures taken involve the collection of all fallen berries and the picking of any that may have escaped the harvest, plus the continuous removal of all young berries on which adult female beetles might feed. Friederichs (1922) and Rutgers (1922) reported successful application of the method in Java. The latter reported that, on estates which had applied the measures, the percentage of infested berries fell from 40% to 90% to between 0.5% and 3.0%. In New Caledonia application of the method reduced infestation from 80% to 10% (Cohic 1958). In Malaysia, Corbett (1933) recommended picking at weekly intervals (or the shortest period practicable, according to size of holding) of all bored green, ripe and blackened berries on the bush and from the ground. A host-free period of six months was recommended for the eradication of the beetle from isolated plantations. In Mexico, Baker (1984) concluded that berries are not infested while lying on the ground surface. Nevertheless any infested berries allowed to lie where they fell ultimately generated large numbers of beetles.

Turning to biological control, it is generally possible to gain some idea of the likely effectiveness of natural enemies in a new country from their impact in their country of origin. In a new country the enemies may be more effective if freed from hyperparasites before transfer or less effective if they are poorly adapted to their new environment. Based on their evaluation of the population dynamics of *H. hampei* and its parasitoids, Moore and Prior (1988) and Murphy and Moore (1990) were optimistic about the value of biological control as a key component of successful integrated management of *H. hampei*. Although this indeed seems probable, the reports from Africa are far from uniform and the coffee berry borer is a problem in some areas. This may be due to whether arabica or robusta coffee is involved and to the widely different conditions under which coffee is grown and harvested since, for example, parasitoids may be less effective when coffee is shaded (Hargreaves 1935).

Hargreaves (1926, 1935) considered that both *Prorops nasuta* and *Heterospilus coffeicola* were important in regulating populations of *H. hampei* in commercial coffee at about 1200m in Uganda and Pascalet (1939) arrived at a similar view concerning these parasitoids in Cameroon. On the other hand, Abasa (1975) in Kenya, De Toledo Piza and Fonseca

(1935) and Ingram (quoted by Le Pelley 1968, p 125) in Uganda and Sladden (1934) and Schmitz and Crisinel (1957) in Zaire concluded that parasitoids had little influence on the number of bored berries. Murphy and Moore (1990) considered that *P. nasuta* did not have a major impact in Western Kenya where *H. coffeicola* was not encountered. There, coffee berries infested with *H. hampei,* ranged in being attacked by *P. nasuta* from 0% in the wet season to 25% in the dry season and *P. nasuta* populations did not build up until after the annual coffee harvest when populations of *H. hampei* had already crashed from their annual peak.

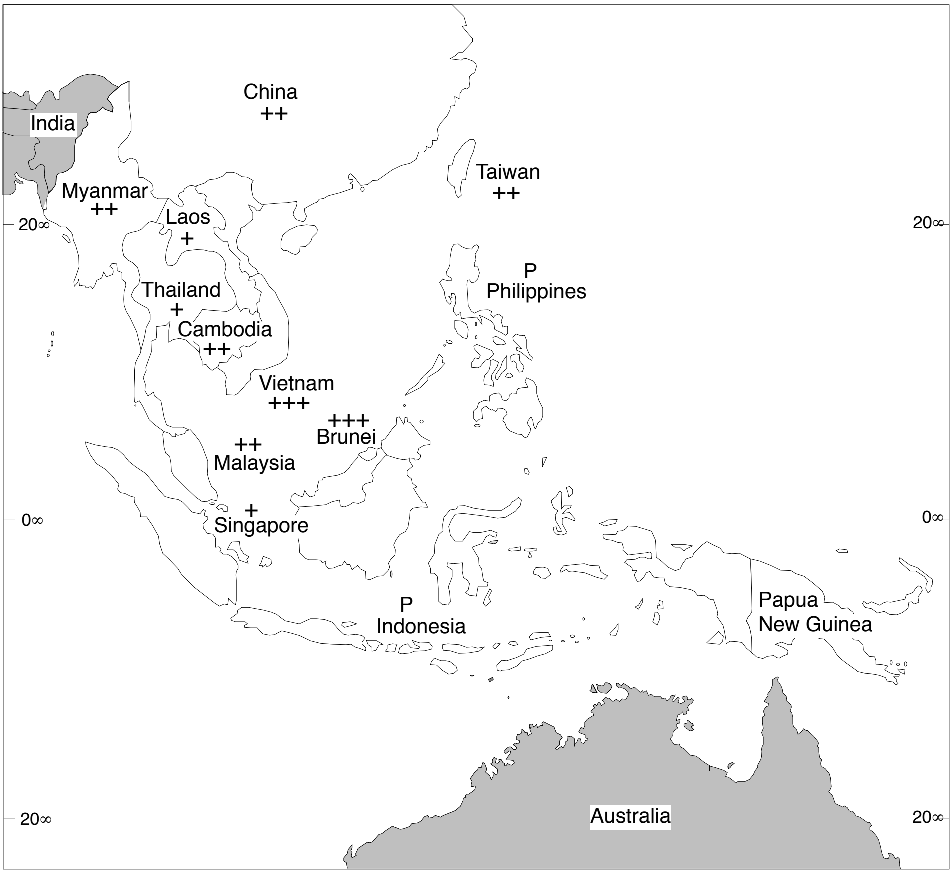
Although *P. nasuta* is present in Ivory Coast (Diro, Man) it is usually rare and *H. coffeicola* apparently absent. However, *Cephalonomia stephanoderis* was common and up to 50% of colonies of *H. hampei* in black berries were parasitised, resulting in important population reduction (Ticheler 1961), a conclusion contested by Koch (1973) on unsubstantiated grounds. It is relevant that, in the presence of *C. stephanoderis*, but without any chemical treatment, Cochereau and Potiaroa (1994) reported that only 2% of the coffee beans (4% of the berries) were attacked in Ivory Coast by *H. hampei*. They contrast this with the situation in New Caledonia where it was common to find 50% of the berries bored, even in plantations treated with endosulfan.

Experience in biological control suggests that the negative assessments of the value of parasites in Africa may reflect the restraining influence of hyperparasites (such as *Aphanogmus* (= *Ceraphron*) *dictynna*), predators, competitors and diseases, but it seems that no such impediments were taken to Brazil with the original stocks of *Prorops nasuta*. Nevertheless, Le Pelley (1968) stated that there was no evidence that, 35 years after the introduction, Brazilian coffee growers had to invest less effort in other control measures and Yokayama et al. (1978), 45 years after its introduction, gave a depressing picture of its impact. Greater success may attend the more recent employment of *Cephalonomia stephanoderis*.

In spite of the conflicting reports, there are, on balance, good reasons for maintaining optimism that natural enemies can play an important role in reducing the losses caused by *H. hampei*. There are the still to be evaluated prospects that *C. stephanoderis* will prove useful and there are various strains (and intraspecific crosses) of *P. nasuta*, in addition to *Phymasticus coffea*, *Heterospilus coffeicola* and *Goniozus* to consider. It is quite possible also that further work, especially in countries such as Ethiopia, which have not been studied, will reveal additional parasitoid species. It is possible that nematodes may prove effective in controlling infestations in fallen berries and likely that applications of a virulent strain of *Beauveria bassiana* may prove to be a valuable alternative to pesticides. It is fortunate for Southeast

Asian countries that active work on both parasitoids and *B. bassiana* is in progress in a number of South American countries and in New Caledonia, from which valuable new information will emerge. However, this is not a justification to delay action if *H. hampei* is high enough on the priority list, since it is likely that parasitoid cultures and relevant expertise will be more readily and economically available now than they will be some years hence.

4.11 *Leucinodes orbonalis*



It appears that *Leucinodes orbonalis* has been introduced from India to Southeast Asia. In India and most other countries, egg plant (brinjal) is protected against insect pests with heavy applications of broad spectrum pesticides, which must also suppress parasitoids and predators. Several parasitoids, and especially the ichneumonid *Trathala flavoorbitalis*, are capable of producing in excess of 50% combined mortality. If levels of this magnitude are combined with the widespread adoption of partially resistant egg plant cultivars, there are good reasons for believing that substantial pest control would be achieved.

Leucinodes orbonalis Guenée

Lepidoptera: Pyralidae
brinjal fruit borer, eggplant fruit and shoot borer

Rating

Southeast Asia			China	Southern and Western Pacific
18	+++	Viet, Brun, Phil	++	absent
	++	Myan, Camb, Msia		
	+	Thai, Laos, Sing		
	P	Indo		

Origin

According to Purseglove (1968), eggplant (*Solanum melongena*) is native to India and there are certainly many varieties in cultivation there. It is probably safe to conclude that *L. orbonalis* is also native to India, although it is not confined to eggplant and also occurs widely in Africa (see below). *Leucinodes orbonalis* is closely related to Central American *Neoleucinodes* species such as *N. elegantalis*, which is a widespread pest there of eggplant, and other Solanaceae. This suggests that parasitoids of *Neoleucinodes* may be of interest for *Leucinodes* and vice versa.

Distribution

L. orbonalis occurs in the **Indian subcontinent** (Andaman Is, India, Pakistan, Nepal, Bangladesh, Sri Lanka), **Southern Asia** all 10 Southeast Asian nations, also Hong Kong, China, Taiwan, Japan, **Africa** (Burundi, Cameroon, Congo, Ethiopia, Ghana, Kenya, Lesotho, Malawi, Mozambique, Nigeria, Rwanda, Sierra Leone, Somalia, South Africa, Tanzania, Uganda, Zimbabwe) (CIE 1976; Tamaki and Miyara 1982; Whittle and Ferguson 1987; Veenakumari et al. 1995) and is also reported from Congo (Dhankar 1988) and Saudi Arabia (FAO 1982). It is not recorded from Australasia, Oceania, the Americas or Europe and was apparently absent until recently from the Philippines (CIE 1976), although Navasero (1983) has now reported it there. Between 1977 and 1987 there were 1291 interceptions of *L. orbonalis* at U.S. ports of entry, most on eggplant fruit in passenger baggage (Whittle and Ferguson 1987), and there must be significant risks also of its entry to Australia and the Pacific.

Biology

The flat, oval eggs are mostly laid at night, either singly or in groups of 2 to 4 (and up to 200 per female), on the lower surface of young shoots, flower buds and calyces of developing fruits. They hatch in 4 days at an optimum temperature of 30°C and relative humidity of 70% to 90%. Larval development occupies 14 days and pupal development 19 days. With a preoviposition period of 2 days, this results in a generation time of about one month. Details from three authors are shown in Table 4.11.1. Up to 9 larvae have been found in a single fruit and, when mature, pupate within a tough silken cocoon on the fruit, stem or among ground litter (Tamaki and Miyara 1982; Khoo et al. 1991; Yin 1993). In the absence of fruit, larvae feed on the growing points of the plant. In the plains of India it occurs throughout the year but, at higher altitudes, cold weather interrupts its development and it overwinters as a larva in a silken cocoon, usually 1 to 3 cm below the soil surface. It is capable of surviving temperatures as low as –6.5°C (Lal 1975). It thrives best under warm, moist monsoonal conditions. *L. orbonalis* can be reared in the laboratory on dried eggplant fruit or on a semi-synthetic diet (Islam et al. 1978, Patil 1990). Virgin females produce a pheromone that attracts males (Gunawardena 1992; Yasuda and Kawasaki 1994).

Host plants

In addition to eggplant, which is its main host, *L. orbonalis* is reported to feed on several other *Solanum* species, e.g. *S. tuberosum* (potato: shoots only) (Fletcher 1916; Mehto et al. 1980; Isahaque and Chaudhuri 1983), *S. nigrum* (black berry nightshade) (Nair 1967; Das and Patnaik 1970; Isahaque and Chaudhuri 1983), *S. indicum*, *S. myriacanthum* (shoots only) (Menon 1962; Isahaque and Chaudhuri 1983) and *S. xanthocarpum* (Menon 1962). It has also been reported from tomato (*Lycopersicon esculentum*) (Hargreaves 1937; Das and Patnaik 1970), potato (*Solanum tuberosum*) and several unexpected plants, including cape gooseberry (Pillai 1922), green pea pods (Hussain 1925), mango shoots (Hutson 1930), cucumber, sweet potato and capsicum (Whittle and Ferguson 1987). Screening egg plant varieties for resistance to *L. orbonalis* has revealed several that are relatively resistant. Thick-skinned varieties appear to be more resistant (Patil and Ajri 1993; Patel et al. 1995).

Table 4.11.1 Development times, and other life history data (rounded) of *Leucinodes orbonalis*

Reference	**Atwal and Verma 1972**				**Baang and Corey 1991**	**Mehto et al. 1983**
Temperature	**20°C**	**25°C**	**30°C**	**35°C**		
egg development(days)	9	6	4	3	5	6
egg survival (%)	63	69	78	55		
larval development(days)	29	20	14	12	18	15
larval survival (%)	53	72	69	48		
pupal development(days)	17	13	9	7	10	12
pupal survival (%)	57	65	71	55		
longevity females(days)	11	7	6	3	3	8
males(days)	9	7	4	2	2	4
eggs/female	188	225	248	86	85–254	122

Damage

All stages of eggplant are attacked by *L. orbonalis*, which is regarded as one of its major insect pests. Larvae bore into the tender shoots of both seedlings and after transplantation older plants, causing wilting and death of the growing tips. Later, they bore into flower buds and fruits. The damaged buds are shed and the fruits carry circular holes, sometimes plugged with frass. Such fruits are unmarketable. The yield loss varies with location and season and is greatest when temperature and humidity is high. Losses range from 20 to 60% (Krishnaiah 1980; Dhankar 1988, Roy and Pande 1994) or even higher (Akhtar and Khawaja 1973; Lal 1991). It is reported that Vitamin C in bored fruit can be reduced by 60% (Hami 1955).

There is an extensive literature dealing with the screening, mainly in India, for resistance of eggplant cultivars to *L. orbonalis*. Some cultivars are far less damaged than others, although no information is available on the genes involved. The less susceptible cultivars generally have one or more morphological characteristics, including compact vascular bundles in a thick layer, lignified cells and less area of pith in the shoots, tougher fruit skin and a tight calyx to hinder larval entry. Biochemical factors involved include a low protein and sugar content in resistant genotypes and a higher silica and crude fibre content in the shoots, which adversely affects growth rate, pupal period, survival, sex ratio and fecundity. The wild relatives of *Solanum melongena* that are not attacked by *L. orbonalis* often have a high alkaloid content, which may be responsible, but this attribute would not be desirable in an edible product (Dhankar 1988).

Natural enemies

Table 4.11.2 lists the natural enemies of *L. orbonalis*. It is striking that most are from India and Sri Lanka, that the records from Malaysia and the Philippines are the only ones from Southeast Asia and that the species there have not been reported elsewhere. Although it is possible that some of the Indian and Sri Lankan species have a restricted distribution, the lack of records from elsewhere probably means that the necessary investigations have not been carried out.

Table 4.11.2 Natural enemies of *Leucinodes orbonalis*

Species	Stage attacked	% parasitisation	Country	Reference
NEUROPTERA				
CHRYSOPIDAE				
Chrysopa kulingensis	egg	12.5	China	Yang 1982
	larva	2-4		
DERMAPTERA				
UNIDENTIFIED		(15)	Philippines	Navasero 1983
DIPTERA				
SARCOPHAGIDAE				
Amobia sp.			Malaysia	Thompson 1946
TACHINIDAE				
Pachyophthalmus sp.			Malaysia	Corbett 1929; Yunus & Ho 1980
Pseudoperichaeta sp.		5.7	India	Patel et al. 1971
Sturmia parachrysops			India	Thompson 1946
UNIDENTIFIED	pupa	5–8	China	Yang 1982
HYMENOPTERA				
BRACONIDAE				
Apanteles sp.		3.1-11.1	Philippines	Navasero 1983
Bracon greeni	larva; ecto	lab only	India	Venkatraman et al. 1948
Bracon sp.	larva; ecto	9.2–28.1	India	Tewari & Sardana 1987a
Campyloneura sp.	larva	1–2	India	Tewari & Moorthy 1984
Chelonus sp.			Philippines	Navasero 1983
		15.5	Sri Lanka	Sandanayake & Edirisinghe 1992
Phanerotoma sp.		4.6	India	Patel et al. 1971
		7.4	Sri Lanka	Sandanayake & Edirisinghe 1992
Phanerotoma sp. nr. *hindecasisella*	larva	1–2	India	Patel et al. 1971; Tewari & Moorthy 1984

Table 4.11.2 (cont'd) Natural enemies of *Leucinodes orbonalis*

Species	Stage attacked	% parasitisation	Country	Reference
HYMENOPTERA				
CHALCIDIDAE				
Brachymeria lasus			Philippines	Navasero 1983
Brachymeria sp.			Philippines	Navasero 1983
EULOPHIDAE				
Dermatopelte (= *Dermatopolle*) sp.	pupa	16	China	Yang 1982
ICHNEUMONIDAE				
Cremastus hapaliae			Malaysia	Yunus & Ho 1980
Eriborus argenteopilosus	larva	0.5–2	India	Tewari & Sardana 1987b
Itamoplex sp.	pupa	9–15	India	Verma & Lal 1985
Pristomerus testaceus	larva; ecto		India	Ayyar 1927
Trathala flavoorbitalis	larva	36.2	Sri Lanka	Sandanayake & Edirisinghe 1992
		3.6–9.1	India	Mallik et al. 1989
		12.9–18.2	India	Naresh et al. 1986a, b,
			India	Patel et al. 1967
			Malaysia	Yunus & Ho 1980
Trathala striata			Malaysia	C.L. Tan pers. comm. 1994
Xanthopimpla punctata			Philippines	Navasero 1983
BACTERIUM	larva	2–3	China	Yang 1982
BACULOVIRUS	larva	1.1–6.4	India	Tewari & Singh 1987

CHINA

The life history of *L. orbonalis* was studied by Yin (1993), in Hunan where up to 6 generations were completed annually and overwintering occurred in the pupal stage. Yang (1982) recorded two pupal parasitoids, the polyembryonic wasp *Dermatopelte* sp., causing 16% parasitisation (and producing 12 to 21 individuals per host pupa) and an unidentified dipteran causing 5% to 8% mortality. A predator, *Chrysopa kulingensis* consumed 12.5% of eggs and 2% to 4% of larvae. A disease, presumably of bacterial origin, killed 2% to 3% of larvae.

INDIA, SRI LANKA

The ichneumonid *Trathala flavoorbitalis* appears to be the most effective parasitoid so far recorded, with an average parasitisation rate in Sri Lanka of 36.2% (Sandanayake and Edirisinghe 1992). In Hanyana, India, Naresh et al. (1986a) recorded rates from 12.9% to 18.2% and in Bihar, Mallik et al. (1989) 3.6% to 9.1%. These were higher than the combined rates of 1% to 2% by *Phanerotoma* sp. and *Campyloneura* sp.. *T. flavoorbitalis* is a very widespread species and attacks the larvae of many species of Lepidoptera. *Bracon* sp. from near Bangalore, India, with a parasitisation rate ranging up to 28.1% (Tewari and Sardana 1987a), *Chelonus* sp. ranging up to 5.5% (Sandanayake and Edirisinghe 1992) and *Itamoplex* sp. up to 15% (Verma and Lal 1985) are all capable of producing significant mortality.

PHILIPPINES

A dermapteran larval predator and 5 parasitoids (the braconids *Apanteles* sp. (on larvae) and *Chelonus* sp. (on pupae), the chalcidids *Brachymeria lasus* (= *B. obscurata*) and *Brachymeria* sp. (larvae and pupae), and the ichneumonid *Xanthopimpla punctata*) were found attacking *L. orbonalis* in the field. *Apanteles* sp. and the dermapteran were the most abundant (Navasero 1983). It appears that *L. orbonalis* has only been recognised in the Philippines since the early 1970s.

Attempts at biological control

There have been none.

Major natural enemies

Bracon sp. Hym.: Braconidae

This larval ectoparasitoid was found near Bangalore, India attached to the thorax of the host larva. It pupated in a silk cocoon inside the tunnel made by its host and caused parasitisation ranging from 9.2% to 28.1%. It was regarded as a promising parasitoid (Tewari and Sardana 1987a).

Itamoplex sp. Hym.: Ichneumonidae

Adult *Itamoplex* sp., 8 to 10 mm in length, were reported from Kulu Valley, Himachal Pradesh, India where the winter temperature drops as low as –8°C. *L. orbonalis* overwinters in the larval (?prepupal) stage in an earthen cocoon attached to the host plant, usually 1 to 3 cm below the soil surface. The parasitoid emerged from 9% to 15% of these cocoons. *Itamoplex* (= *Cryptus*) sp. is recorded attacking a range of host Lepidoptera in cocoons (Verma and Lal 1985).

Trathala (= Cremastus) flavoorbitalis Hym.: Ichneumonidae

This is a widespread, non-specific parasitoid of lepidopterous larvae. It occurs naturally in India, Japan, Myanmar, Sri Lanka, the Philippines and Singapore and has been established in Canada, Hawaii and continental USA for biological control of several important lepidopterous pests. It is recorded from at least 5 families of Lepidoptera, involving over 40 different hosts, most of them pest species (Bradley and Burgess 1934). It is not known whether there are strains that prefer to attack particular hosts.

T. flavoorbitalis is recorded from *L. orbonalis* in India and also in Sri Lanka where *L. orbonalis* is its major host and where an average parasitisation level of 36.2% is reported (Sandanayake and Edirisinghe 1992, 1993). In Hissar, India, *Trathala* was the only parasitoid of *L. orbonalis*, with levels of attack on larvae ranging from 13.2% to 18.2% in winter to 12.9% in summer at a time when 95.2% of fruit was infested (Naresh et al. 1986a, b).

T. flavoorbitalis females commence ovipositing 4 days after emergence, with a preference for 3rd, 4th and 5th instar host larvae. In the laboratory, only a fraction of 1st instar larvae are stung and all soon die from the encounter, a fate shared by about half the 2nd instar larvae that are stung. In later instars 68–91% were stung, but without early mortality. Not all of these received eggs, although some received up to 5, with only one parasitoid larva developing beyond the first instar. Parasitoid development time from egg to adult was about 23 days at 28°C. Successful development occurred in 53% of the 3rd, 57% of the 4th and 41% of 5th instar host larvae, adult wasps emerging after pupation of the host. In the field, the parasitoid attacks the host larva by inserting its ovipositor into the hole bored into the fruit and through which the larva pushes out frass (Bradley and Burgess 1934; Naresh et al. 1986a; Sandanayake and Edirisinghe 1992, 1993).

Comments

It is not clear how many of the natural enemies are sufficiently host specific to be confidently transferred as biological control agents although, where alternative hosts are known, these are also pests. Thus, *Eriborus argenteopilosus* has a wide host range, including *Condica* (= *Prospalta*) *capensis*, which attacks safflower and sunflower, *Helicoverpa armigera*, and *Spodoptera exigua* (Tewari and Sardana 1987a,b). The ichneumonid *Pristomerus testaceus* has been bred from the brinjal stem-borer *Euzophera ferticella* (Ayyar 1927). It is not known whether the ichneumonid *Phanerotoma* sp. nr *hindecasisella* is a distinct species. True *P. hindecasisella* has been reported from several lepidopterous families in India or Sri Lanka: Gelechiidae (*Dichomeris eridantis*), Noctuidae (*Earias insulana*), Pyralidae (*Eutectona* (= *Pyrausta*) *macheralis*, *Hendecasis duplifascialis*, *Maruca vitrata* (= *M. testulalis*), *Nephopterix rhodobasalis*, *Syllepte derogata*) and Tortricidae (*Leguminivora* (= *Cydia*) *ptychora*) (Thompson 1953; Fellowes and Amarasena 1977; Kumar et al. 1980; Tewari and Moorthy 1984).

Bracon greeni is best known as a primary ectoparasitoid of the lepidopterous lac predator *Eublemma amabilis* (Noctuidae) and has not been reported to parasitise any other host in nature. However, under laboratory conditions, it was successfully reared on *L. orbonalis* (Venkatraman et al. 1948).

Although entomopathogenic nematodes have not been recorded attacking *L. orbonalis* in the field, *Steinernema* (=*Neoaplectana*) *carpocapsae* (DD136 strain) produced 73.3% mortality of larvae in the laboratory in 72 hours (Singh and Bardhan 1974).

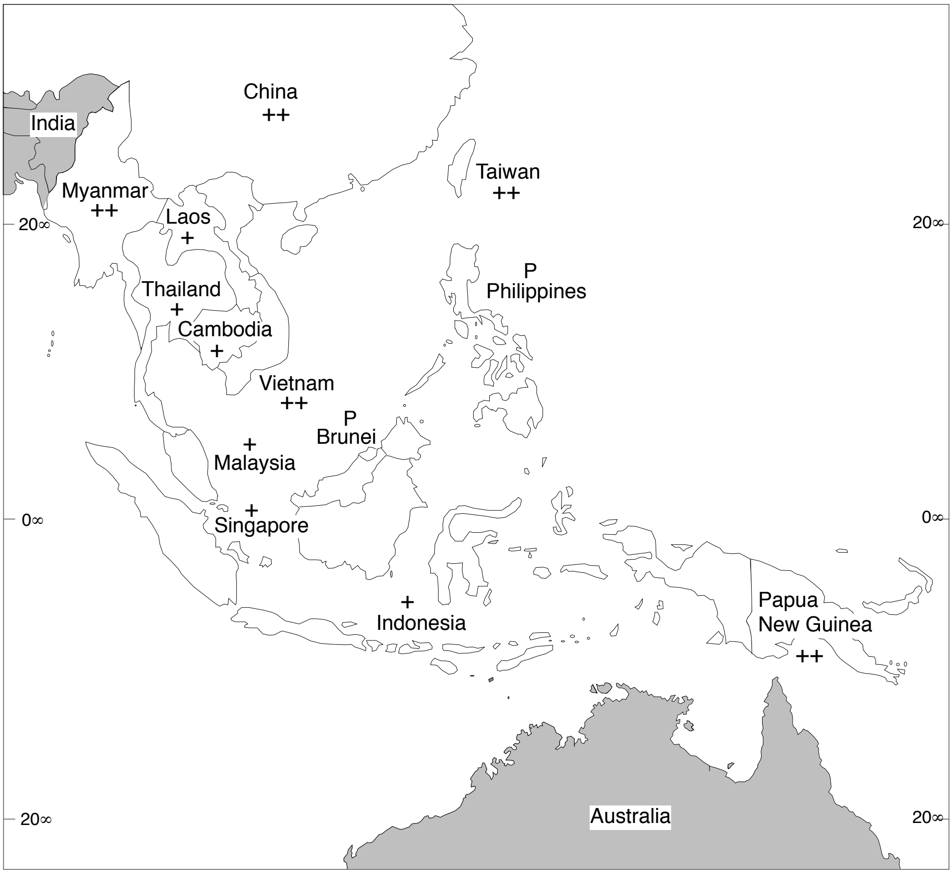
The weight of evidence suggests that *L. orbonalis* originated in India and spread into Southeast Asia. It is most surprising that it has only comparatively recently become a pest — and a serious one — in the Philippines which, in 1990, had 16 000ha under egg plant and produced 113 000 tonnes, second only to Indonesia in production in Southeast Asia (FAO 1991). In view of the steady spread around the world of so many other pests it is also surprising that Australia, the Pacific, the Americas and Europe are still free from *L. orbonalis*.

It might well be assumed that not all of its natural enemies in India have accompanied it during its spread. However, reports of high damage levels to susceptible egg plant cultivars in India do not provide much confidence that the natural enemies there are particularly effective, unless their efficacy is, perhaps, reduced by insecticide applications or so-far-unreported hyperparasitoids.

Nevertheless, parasitisation in Sri Lanka is quite impressive, with *Trathala flavoorbitalis* averaging 36.2%, *Chelonus* sp. 15.5% and *Phanerotoma* sp. 7.4%. The combined average rate of 59.1% would certainly be capable of causing an important lowering of moth populations, particularly if associated with the high levels of host plant resistance that are available. It is probable that the widespread high rates of application of broad spectrum insecticides currently used are preventing natural enemies from exerting much effect. An investigation of what natural enemies of *L. orbonalis* are already present in Southeast Asia is required to enable a decision on the attractiveness of this pest as a biological control target. It is probably safe to conclude that *T. flavoorbitalis*, the most effective parasitoid so far reported, is present in most, if not all, of Southeast Asia, but it would be relevant, in relation to possible host-preferring strains, to determine whether it attacks *L. orbonalis* throughout the region.

It is interesting that the closely related South American *Neoleucinodes elegantalis* has a quite different suite of parasitoids. Of 2500 larvae collected in the field 1.6% were parasitised by the encyrtid *Copidosoma* sp. and 0.08% by the tachinid *Lixophaga* sp. Of 527 pupae, 0.38% were parasitised by the ichneumon *Calliephialtes* sp. The fungus *Beauveria* sp. caused 55% mortality. *Trichogramma* sp. parasitised 89% of eggs laid on egg plant and tomato (Plaza et al. 1992). Of these species, *Beauveria* and the *Trichogramma* sp. might be relevant to the Southeast Asian scene.

4.12 *Nezara viridula*



Nezara viridula is probably native to the Ethiopian region, but is now dispersed widely throughout the warmer regions of the world.

There have been a number of major successes with biological control of the green vegetable bug, particularly with an egg parasitoid, *Trissolcus basalis*. Control has been supplemented in Hawaii by two parasitoids of adults, *Trichopoda pilipes* and *T. pennipes*, which, however, have failed to establish in most other places.

The main areas where biological control using *T. basalis* has been unsuccessful are often associated with extensive plantings of soybean. It has been suggested that the surface hairyness of most soybean cultivars reduces the effectiveness of this parasitoid. If this proves to be correct the way is open for the selection of cultivars with this attribute modified.

Over 80 parasitoids of *N. viridula* are known, amongst which there are several potentially valuable, untried species that are clearly worthy of investigation.

N. viridula is an attractive target for biological control, especially where it is a problem in an area not closely associated with extensive soybean plantings.

Nezara viridula (Linnaeus)

Hemiptera, Pentatomidae
green vegetable bug, southern green stink bug (USA)

Rating

Southeast Asia			**China**	**Southern and Western Pacific**		
10	++	Myan, Viet	++	14	++	Cook Is, Fr P, Niue, PNG, Sam
	+	Thai, Laos, Camb, Msia, Sing, Indo			+	Fiji, Kiri, N Cal, A Sam
	P	Brun, Phil			P	FSM, Guam, Sol Is, Tong, Van

This account updates the chapter on *Nezara viridula* in Waterhouse and Norris (1987), and the valuable account of Jones (1988), in relation to prospects for biological control.

Origin

The locality of the holotype ‘in Indiis’ (Linnaeus 1758) has been interpreted as India or the East Indies. However it may well have been brought there by European travel since an analysis of genetic colour variants and the relative abundance of fairly specific insect parasitoids led Hokkanen (1986) and Jones (1988) to the conclusion that the original home of *N. viridula* was in the Ethiopian (Afrotropical) or Mediterranean region, rather than in Southeast Asia (Yukawa and Kiritani 1965). Furthermore, Africa is considered to be the centre of the genus *Nezara* (Freeman 1940).

Distribution

Azores, Canary Is, Bermuda, the Mediterranean littorale, most of Africa and the Middle East, Madagascar, Mauritius, Reunion, Rodriguez, Seychelles, Asia (exclusive of desert areas and those with very cold winters) Korea and southern Japan, Southeast Asia, Papua New Guinea (including Bismarck Archipelago), most of the oceanic Pacific nations (Butcher 1981), Australia, New Zealand, Hawaii, southern USA, Mexico and other Central American countries, West Indies generally, and much of South America (Anon. 1970). It is not known to occur in Tokelau, Tuvalu or the Marquesas (Waterhouse 1985, 1997).

The entirely green colour form *smaragdula* of *N. viridula* is the one that occurs widely in the Pacific area. In other areas of the world it is accompanied by several other colour forms (Yukawa and Kiritani 1965).

Biology

The barrel-shaped eggs are usually laid at night in neat rafts, commonly of 80 to 120 or more eggs and they are cemented firmly to one another and to the sheltered surface of a leaf. The eggs hatch in 4 to 9 days, and the newly emerged nymphs remain together near the eggshells for a day or two, a degree of gregariousness persisting also in the next instar or two. There are five nymphal stages before the adult emerges, 24 to 60 days after hatching, depending on temperature. At 25–28°C, 55–65% RH and 14 hours daylight the development periods (in days) were: egg, 4.8; 1st instar nymph, 3.8; 2nd instar, 5.2; 3rd instar, 4.5; 4th instar, 6.4; 5th instar, 11.9 (Harris and Todd 1980). The nymphal stages are multicoloured, but the adults are a uniform green in the form *smaragdula*. The adults can fly strongly. There may be four generations in a year in coastal New South Wales, and perhaps more in areas with no perceptible winter.

The adult bugs live up to 3 weeks in hot weather. In regions with a cold winter those of the autumn generation may live much longer, hibernating in debris, under bark, or in buildings, inactive and non-reproductive. Such hibernating bugs change colour from green to brown. In areas with a less severe winter the still-green adults may remain active, although non-reproductive. Waite (1980) showed that the adults and nymphs tend to bask exposed on the surface of the plant canopy in the early daylight hours—behaviour that can be availed of in applying chemical control measures (Kamal 1937; Clausen 1978; Hely et al. 1982; Singh and Rawat 1982; Todd 1989).

Damage

When not controlled by chemicals or natural enemies, this bug can be a serious pest of a very wide range of crops and ornamental plants. In Australia there are recommendations for its chemical control on beans, cucurbits, peas, potatoes, tomatoes, passionfruit, groundnuts, sorghum, soybeans, sunflowers and tobacco (Anon. 1967, 1979b; Miller et al. 1977), but it also attacks maize, crucifers, spinach, lucerne and many other legumes, grapes, oranges and many other fruits and seeds, and macadamia (Ironside 1979; La Croix 1986) and pecan nuts (Seymour and Sands 1992). Undoubtedly there would be recommendations for a much wider range of cultivated plants were it not for the fact that biological control is effective now in many situations

(Anon. 1967; Hely et al. 1982). In other countries it can be a pest of rice, sesame and other grains, lablab, guavas, cowpeas, capsicums, cotton and many other plants. It also infests and breeds on many weeds, which afford it harborage.

The attack of the bugs is concentrated chiefly on fruits and fruiting bodies, which, through the removal of sap and the injection of saliva, show discoloration, malformation, stunting and shrivelling. Heavily attacked tomatoes, for instance, are repulsive and inedible and even lightly attacked ones are unmarketable. Passlow and Waite (1971), Goodyer (1972) and Romano and Kerr (1977) attribute serious losses in Australian soybean crops to the attack of this pest. Miller et al. (1977) measured the yield reduction on soybeans and showed that an important effect of the bugs feeding was a reduction in the germinability of seed. On soybean in Brazil, Corso et al. (1975) showed that green vegetable bug attack affected pod development, increased pod fall, and reduced the number of seeds per pod. Link et al. (1973) demonstrated reductions in germination percentage and oil content and an increase in relative protein content in heavily damaged seeds. A list of references dealing with *N. viridula* and its association with soybeans has been prepared by DeWitt and Godfrey (1972).

Some cultivars of soybeans are less damaged by *N. viridula* than others and a strain of soybean that appears to have a high level of resistance has been selected (Gilman et al. 1982). Mild antibiosis and non-preference were factors contributing to resistance (Kester et al. 1984). The adverse effects of the genotype (PI 171444) on the biology of a parasite *Telenomus chloropus* attacking the eggs of *N. viridula* feeding on it have been studied by Orr et al. (1985b).

The green vegetable bug has been shown to carry spores of fungal diseases from plant to plant (Corso et al. 1975) and to transmit plant pathogens during feeding (Kaiser and Vakili 1978).

Natural enemies

Introduced parasitoids have brought about successful biological control of this pest in a number of countries and there is an extensive literature on the subject. Nine species of parasite attacking *Nezara viridula* were listed by Thompson (1944), 27 by Hokkanen (1986) and 57 by Jones (1988). At least eighty are now included in Table 4.12.1 which is a modification and extension of that in Jones (1988).

The species belong to two families of Diptera and six families of Hymenoptera. It is notable from the entries that relatively little is known of the parasitoids of *N. viridula* in the Ethiopian or Mediterranean regions, which constitute the presumed area of origin of the green vegetable bug. Egg parasitoids are the most numerous and all are Hymenoptera, whereas nymphal and adult parasitoids are, with one exception, all Diptera. Two hyperparasitoids of the major egg parasitoid *Trissolcus basalis* are known from Australia, (both are species of *Acroclissoides*: Clarke and Seymour 1992) and one hyperparasitoid of the fly *Trichopoda pennipes* from Hawaii (*Exoristobia philippinensis*: Davis and Krauss 1965). Predators are not dealt with as all are known to be, or suspected as being, widely polyphagous and hence unlikely to be approved for introduction to new areas. Nevertheless, they play a significant role in maintaining *N. viridula* populations at low levels. For example, in one study in soybeans in Louisiana, Stam et al. (1987) found 18 insect and 6 spider species to be predators and that they were responsible for 33.6% of the total mortality of *N. viridula* that occurred from egg to adult.

The Scelionidae is the most important of the six families of hymenopterous egg parasitoids. In it *Trissolcus basalis* is not only the most important species, but also the most widespread. It attacks the eggs of a number of other pentatomids, but appears to have a preference for *N. viridula*: it is the dominant parasitoid of *N. viridula* eggs wherever it occurs. Many other species are listed, in particular in the genera *Trissolcus*, *Telenomus, Ooencyrtus* and *Gryon*, but a number appear to have no close relationship with *N. viridula* and are unlikely to be of value as potential biological control agents. Some drought-resistant species from the Mediterranean may prove useful. The better known of the more promising species are discussed later.

The tachinid parasitoids of adult *N. viridula* also oviposit on the cuticle of 4th and 5th instar nymphs. Often these eggs are shed before hatching along with the cuticle at moulting but, if hatching and penetration of the bug occurs, the parasitoid larva matures in the adult. More of the species of tachinids are native to South America than elsewhere. They were clearly dependent upon other pentatomids before the arrival of *N. viridula*, but several now appear to have a preference for it. The most promising of the three tachinid parasitoids occuring in the Ethiopian region is the widespread *Bogosia antinorii*, which is known only from *N. viridula* (van Emden 1945; Barraclough 1985).

A picorna-like and a toti-like virus are known from *N. viridula* (Williamson and Wechmar 1992, 1995).

Table 4.12.1 Parasitoids of the green vegetable bug, *Nezara viridula* (modified after Jones 1988)

Parasitoid	Geographic range	Known host relations	Selected references
DIPTERA			
SARCOPHAGIDAE			
Sarcodexia innota	Southern USA	Two records ex *N. viridula*; wide host range as primary parasitoid and scavenger	Drake 1920; Temerak & Whitcomb 1984
Sarcodexia sternodontis			Hokkanen 1986
TACHINIDAE			
Bogosia antinorii	Widespread in Africa	Recorded only ex *N. viridula*	Greathead 1966, 1971; Barraclough 1985
Cylindromyia rufifemur	Australia	One record ex *N. viridula*	Cantrell 1984
Ectophasia crassipennis	Italy	Bred ex *N. viridula*	Colazza & Bin 1995
Ectophasiopsis arcuata	Chile	Well adapted to *N. viridula*	Jones 1988
Euclytia flava	USA	Generalist parasitoid	Aldrich 1995
Gymnosoma clavata	Palaearctic, Israel	One record ex *N. viridula*	Herting 1960
Gymnosoma kuramanum	Japan		Takano 1956
Gymnosoma rotundata	Palaearctic	Wide host range; attacks *Nezara* spp. in Japan	Kiritani et al. 1963; Kiritani & Sasaba 1969
Trichopoda giacomellii (=*Trichopoda nigrifrontalis*, = *T. gustavoi* = *Eutrichopodopsis nitens*)	Argentina, Brazil, Colombia, Paraguay	Well adapted to *N. viridula*	Blanchard 1966; Mallea et al. 1968; Gastal 1977a,b; Liljesthröm 1980, 1981; Ferreira 1984
Trichopoda lanipes	Southern USA	One record ex *N. viridula*; attacks other species	Drake 1920
Trichopoda pennipes	North America, Hawaii	Well adapted to *N. viridula*	Drake 1920; Todd & Lewis 1976; Jones 1979; Buschman & Whitcomb 1980; McPherson et al. 1982

Table 4.12.1 (cont'd) Parasitoids of the green vegetable bug, *Nezara viridula* (modified after Jones 1988)

Parasitoid	Geographic range	Known host relations	Selected references
DIPTERA			
TACHINIDAE (cont'd)			
Trichopoda pilipes	West Indies, Hawaii	Well adapted to *N. viridula*	Myers 1931; Nishida 1966; Davis 1967
Trichopoda sp.	Uruguay	One record ex *N. viridula*	Guido & Ruffinelli 1956
HYMENOPTERA			
EULOPHIDAE			
Pleurotropitiella albipes	Argentina		Esquivel 1950
EURYTOMIDAE			
Neorileya sp.	Brazil	Recorded only ex *N. viridula*	Ferreira 1981, 1984, 1986
EUPELMIDAE			
Anastatus bifasciatus	Italy	Bred ex *N. viridula*	Colazza & Bin 1990
Anastatus dasyni	Malaysia	Pentatomidae, Coreidae; described ex *N. viridula*	van der Vecht 1933
Anastatus japonicus	East Asia	Lepidoptera, Heteroptera; produces only males in *N. viridula*	Hokyo et al. 1966b; Kiritani & Sasaba 1969
Anastatus sp.	Thailand	Emerged ex imported eggs of *N. viridula*	Jones 1988
Anastatus sp.	Southern USA	Two records ex *N. viridula*	Jones 1988
Anastatus sp.	Australia (Queensland)	One record ex *N. viridula*	Seymour & Sands 1993
Unidentified sp.	Hawaii	ex *N. viridula* on macadamia	Jones 1992
ENCYRTIDAE			
Hexacladia hilaris	USA	One record ex *N. viridula*	Buschman & Whitcomb 1980
Ooencyrtus californicus	California	ex *N. viridula* and other pentatomids	Hoffmann et al. 1991

Table 4.12.1 (cont'd) Parasitoids of the green vegetable bug, *Nezara viridula* (modified after Jones 1988)

Parasitoid	**Geographic range**	**Known host relations**	**Selected references**
HYMENOPTERA			
ENCYRTIDAE (cont'd)			
Ooencyrtus fecundus	Morocco		Voegelé 1961
Ooencyrtus johnsoni	California	ex *N. viridula* and other pentatomids	Hoffmann et al. 1991
Ooencyrtus malayensis	Malaysia, Philippines	Pentatomidae, Coreidae, Lepidoptera	van der Vecht 1933; Jones et al. 1983
Ooencyrtus nezarae	East Asia	Coreidae, Pentatomidae, Plataspidae; not uncommon on *N. viridula* in Japan	Hokyo & Kiritani 1966
Ooencyrtus pityocampae	Italy	Breeds in eggs of *N. viridula* and other pentatomids in the laboratory	Tiberi et al. 1991
Ooencyrtus submetallicus	West Indies, Central and South America	Pentatomidae, Coreidae	Gahan 1927; Lee 1979; de Santis 1985; Ferreira 1986
Ooencyrtus trinidadensis	West Indies, Argentina	Pentatomidae, Coreidae	Davis & Krauss 1963; Davis 1967; de Santis 1985
Ooencyrtus sp.	Brazil	One record ex *N. viridula*	Ferreira 1986
Ooencyrtus sp.	Thailand	Emerged ex imported eggs of *N. viridula*	Jones 1988
Ooencyrtus sp.	Philippines	Possibly is *O. malayensis*	Davis 1967; Corpuz 1969
Ooencyrtus sp.	France	One record; recovered ex other pentatomids	Jones 1988
Ooencyrtus sp.	Italy	Bred ex *N. viridula*	Colazza & Bin 1995
Ooencyrtus sp. (spp.?)	Southern USA	Taxonomy and host range not known	Drake 1920; Buschman & Whitcomb 1980; Jones 1988
Xenoencyrtus hemipterus (= *X. niger*)	Australia		Seymour & Sands 1993
Xenoencyrtus rubricatus	Australia	Described ex *N. viridula*	Riek 1962
Xenoencyrtus sp.	Australia	Bred ex *N. viridula*	Forrester 1979

Table 4.12.1 (cont'd) Parasitoids of the green vegetable bug, *Nezara viridula* (modified after Jones 1988)

Parasitoid	Geographic range	Known host relations	Selected references
HYMENOPTERA			
PTEROMALIDAE			
Pteromalus sp.	Egypt	One record ex *N. viridula*	Adair 1918
3 spp.	Brazil		Ferreira & Moscardi 1995
SCELIONIDAE			
Gryon fulviventris	Africa, Asia	Pentatomoidea; attacks *N. viridula* only in Thailand	Anderson 1919; Dry 1921, Jones 1988
Gryon japonicum	Japan, Brazil	native of Japan	Kishino & Teixeira 1994
Gryon obesum	Southern USA, Brazil	Records ex *N. viridula*; attacks other pentatomids	Buschman & Whitcomb 1980; Masner 1983; Hoffmann et al. 1991; Correa & Moscardi 1995
Gryon sp.	Australia	Minor attack on *N. viridula*	Titmarsh 1979
Gryon sp.	Laos	One record ex *N. viridula*; may be *G. fulviventris*	Grist & Lever 1969; Dean 1978a,b
Gryon sp.	India	One record ex *N. viridula,* may be *G. fulviventris*	Yadava et al. 1982
Psix lacunatus	Asia, Australia	Pentatomidae, Scutelleridae; ex *N. viridula* in Pakistan	Johnson & Masner 1985
Psix striaticeps	Africa, India Togo	Pentatomidae; recorded once ex '*Nezara*' Common on *N. viridula* and 2 other pentatomids	Fouts 1934; Johnson & Masner 1985; Poutouli 1995
Telenomus chloropus	Palearctic	Pentatomidae; major parasitoid of *Nezara* spp. in E. Asia; females only in Japan	Kiritani & Hokyo 1962; Hokyo & Kiritani 1963; Johnson 1984a
Telenomus comperei	Philippines		Cadapan & Alba 1987
Telenomus cristatus	Southern USA, West Indies	Known only ex *N. viridula* and *Acrosternum hilare*	Johnson 1984a; Orr et al. 1986

Table 4.12.1 (cont'd) Parasitoids of the green vegetable bug, *Nezara viridula* (modified after Jones 1988)

Parasitoid	Geographic range	Known host relations	Selected references
HYMENOPTERA			
SCELIONIDAE (cont'd)			
Telenomus cyrus	Java, Philippines, Taiwan	Descr. ex *N. viridula*; host relations unknown	Nixon 1936; Taiwan Agricultural Research Institute 1984; Jones 1988
Telenomus gifuensis	East Asia	Pentatomidae, Coreidae; not well adapted to *N. viridula*	Hidaka 1958; Hokyo & Kiritani 1963
Telenomus mormideae	South America	Attacks *N. viridula* and other pentatomids	Ferreira 1986; Liljeström & Bernstein 1990
Telenomus pacificus	Philippines		Cadapan & Alba 1987
Telenomus podisi	North and South America	Pentatomidae; not well adapted to *N. viridula*	Buschman & Whitcomb 1980; Correa & Moscardi 1995; Orr et al. 1985a, 1986
Telenomus seychellensis	East Africa	Attacks other spp.; may be common on *N. viridula*	Nixon 1935; Croix & Thindwa 1986
Telenomus sp.	Argentina Vietnam	Minor attack on *N. viridula* eggs	Liljeström & Bernstein 1990 van Lam 1996
Trissolcus aloysiisabaudiae	East Africa	Reportedly common on *N. viridula* in cotton	Fouts 1930; Chiaromonte 1931; Paoli 1933
Trissolcus basalis	N. & S. America, S. Europe, Africa, Hawaii, Australia, New Zealand, Fiji	Most important parasitoid of *N. viridula* outside central Africa and eastern Asia	Miller 1928; Kamal 1937; Lever 1941; Buschman & Whitcomb 1980; Ferreira 1980; Orr et al. 1986; Colazza & Bin 1995
Trissolcus brochymenae	N. and S. America	Recorded ex *N. viridula;* attacks other pentatomids	Johnson 1984b

Table 4.12.1 (cont'd) Parasitoids of the green vegetable bug, *Nezara viridula* (modified after Jones 1988)

Parasitoid	Geographic range	Known host relations	Selected references
HYMENOPTERA			
SCELIONIDAE (cont'd)			
Trissolcus crypticus	Pakistan	ex *Plautia crossota* and *Acrosternum gramineum*; bred readily in *N. viridula* in lab. in Australia and Hawaii	Clarke 1993a
Trissolcus euschisti	California	ex *N. viridula* and other pentatomids	Hoffmann et al. 1991
Trissolcus hullensis	North America, Venezuela	Recorded ex *N. viridula*; attacks other pentatomids	Johnson 1985
Trissolcus lepelleyi	Central Africa	Descr. ex *N. viridula*, an apparently common host	Nixon 1936; Le Pelley 1979
Trissolcus lodosi	Turkey	Descr. ex *N. viridula*; nothing else known	Szabó 1981
Trissolcus maro	Southern Africa	*N. viridula* is only known host	Nixon 1935; Croix & Thindwa 1986
Trissolcus mitsukurii	Japan	Important parasitoid of *N. viridula* in Japan	Kiritani & Hokyo 1962; Hokyo & Kiritani 1963
Trissolcus oenone	Australia		Johnson 1991
Trissolcus ogyges	Australia	one recent record	Seymour & Sands 1993
Trissolcus rudus	Vietnam		van Lam 1996
Trissolcus scuticarinatus	South America	One record ex *N. viridula*; attacks other pentatomids	Ferreira 1986
Trissolcus sipius	East Africa	Descr. ex *N. viridula* but not reported since	Nixon 1936
Trissolcus solocis	Florida, Mexico	Recorded ex *N. viridula*; attacks other pentatomids	Buschman & Whitcomb 1980; Johnson 1985
Trissolcus thyantae	Eastern N. America	Recorded ex *N. viridula*; attacks other pentatomids	Johnson 1985
Trissolcus urichi	Brazil		Ferreira & Moscardi 1995
Trissolcus utahensis	California	ex *N. viridula* and other pentatomids	Hoffmann et al. 1991
Trissolcus sp.	Taiwan India	Recorded ex *N. viridula*; host relations unknown Recorded ex *N. viridula*	Taiwan Agricultural Research Institute 1984; Nath & Dutta 1994

The role of pheromones and other chemical secretions

Sexually mature male *N. viridula* release a pheromone that is a powerful attractant for mature females and also attracts males and older nymphs, but to a lesser extent. It is produced from the ventral abdominal epidermis (Lucchi 1994). The principal ingredient of the mixture of compounds (obtained from extracts of male cuticle), isolated from bugs collected in southern France, is the sesquiterpene (z)-a-bisabolene *trans* epoxide, whereas the accompanying *cis* isomer is not attractive (Brézot et al. 1993). The pheromone blend differs between some Brazilian (which do not produce the *cis* compound) (Baker et al. 1987) and North American, Hawaiian and Japanese bug populations which do, but in differing ratios. Other related pentatomids (e.g. the North American *Acrosternum hilare*) emit mixtures containing distinctive ratios (but containing more *cis* isomers) of the same sesquiterpenes as in *N. viridula* (Aldrich et al. 1989). Males of the native Japanese *Nezara antennata* and *Acrosternum aseadum* produce species-specific pheromone blends based on the same compounds as *Nezara viridula*. However, whereas the *trans/cis* 1,2 epoxide ratio of *N. antennata* is within the range for most USA. *N. viridula* populations (3 to 4.4:1), the blend from Japanese *N. viridula* males is 0.82:1 to 1:1. The ratio for Italy was 2.16:1, for Brazil 2.28 to 4.67:1, and for Australia 3.90:1. The ratios for *Acrosternum hilare*, *A. marginatum* and *A. pennsylvanicum* are 6:100, 7:100 and 94:100 respectively (Aldrich et al. 1989, 1993). However, the situation is not clearcut. Brezot et al. (1994) studied the proportions of *cis* and *trans* bisabolene epoxides in individuals of a southern France (SF) and a French West Indies (FWI) strain of *N. viridula*. The *trans* isomer composed 42 to 82% of bisabolene epoxides in SF males and 74 to 94% of FWI males. Means differed significantly in spite of this inter-individual variation. Ryan et al. (1995) also found variability in the ratio of isomers within a single *N. viridula* population in Australia.

It is interesting that the pheromone mixture from mature males in southeastern United States is also highly attractive to the tachinid parasitoid *Trichopoda pennipes* (Aldrich et al. 1987), which lays far more eggs on male than on female *N. viridula*. *Trichopoda* spp. and a group of related tachinids are native to the Americas, where they attack a small group of native pentatomid bugs. It is postulated that the chemical similarity of the *Acrosternum* and *Nezara* pheromones facilitated the adoption by the tachinids of *N. viridula* when it reached the Americas (see below). Furthermore, that the immigrant populations of *N. viridula* released both the *trans* and *cis* isomers and that parasitisation by the tachinids preferentially attracted to the *cis* isomer provided the major selection pressure leading to the present *N. viridula* populations having predominantly the *trans* isomer in their pheromone mix. Perhaps in parallel, in the 200 years or so of interaction between *N. viridula* and *T. pennipes* in tropical America, *N. viridula* has evolved a shorter pre-oviposition period and a longer developmental period than an Italian population (Hokkanen and Pimentel 1984; Aldrich et al. 1989). At all events, at least two distinct pheromone strains of *N. viridula* can now be distinguished, based on the presence or absence in the volatile secretions of the cuticle of *cis*-(z)-a-bisobolene epoxide. Mature *N. viridula* males of one population from Brazil produce the *trans*, but not the *cis* isomer (Baker et al. 1987), whereas males from 2 other populations do in ratios of 2.28:1 and 4.67:1 respectively (Aldrich et al. 1993), similar to males from southern USA which produce the *trans* and *cis* isomers in a 3:1 ratio (Aldrich et al. 1987) and those from Southern France in a 2:1 ratio (Baker et al. 1987).

A quite different, but somewhat analogous situation, occurs with the hymenopteran *Trissolcus basalis*. A short chain unsaturated aldehyde, (E)-2-decenal present in the defensive scent produced in the adult *N. viridula* metathoracic gland (Gilby and Waterhouse 1965) is attractive to female *T. basalis*. A different compound, secreted on the eggs by the ovipositing female *N. viridula*, attracts female *T. basalis* to the egg raft (Mattiacci et al. 1991, 1993). This compound is produced in the bug ovary and serves as an adhesive for attaching the eggs to the oviposition substrate. The adhesive and the material(s) responsible for the kairomone activity were partly soluble in water and completely in acetone and elicited recognition behaviour from *T. basalis* females when applied to glass beads. The adhesive appears to be a mucopolysaccharide-protein complex (Bin et al. 1993).

Attempts at biological control

Early attempts at biological control were made chiefly in Australia and the Pacific, countries where the introduction of the bug was comparatively recent, but many other countries have been involved in more recent times.

AUSTRALIA

N. viridula was first reported in Australia in 1916 and soon became a widespread and serious pest. In 1933 the scelionid wasp *Trissolcus basalis* was introduced from Egypt into Western Australia (Table 4.12.2) where it readily became established and produced a great reduction in the pest status of the green vegetable bug. From Western Australia the parasitoid was distributed widely throughout south and southeastern Australia, making a considerable impact on the bug, except in cultivated areas in inland eastern Australia, where the cold winters affected its abundance (Wilson 1960).

Additional strains were later liberated of what, at the time, was believed to be *T. basalis*. These originated from the West Indies (1953), Italy (1956) and Pakistan (1961). However, doubt has been cast on the specific identity of the Italian material, although *T. basalis* is known to occur there. The Pakistan material, originally identified as *T. basalis* (but probably containing two species) has recently been shown (Clarke 1993a) to have consisted mainly of a new species *Trissolcus crypticus*. This bred readily in *N. viridula* eggs in the laboratory and, later, was widely distributed in Australia and Hawaii. However, *T. crypticus* has not been reported since in field collections.

For many years up to the mid 1960s *N. viridula* was a very common and serious pest in the Canberra district, damaging tomatoes and beans in particular. This situation changed dramatically following the liberation of the material from Pakistan (presumably both *T. basalis* and *T. crypticus*) and, since then, *N. viridula* has become a very uncommon insect, appearing only in extremely limited numbers late in the season and only every few years. A great improvement also resulted about the same time in other subcoastal eastern cultivated areas, credited by Ratcliffe (1965) also to the liberation of material from Pakistan.

However, since *T. crypticus* apparently did not become established its role, if any, in the changed situation is unclear. It is not known whether any cross mating with *T. basalis* might have occurred, which might have resulted in greater adaptability of *T. basalis* to the Canberra environment. The continuing very low abundance of *N. viridula* is possibly attributable to a heavy attack on its eggs by a resident population of *T. basalis* which is maintained on native pentatomid hosts, of which there are several (see later).

Table 4.12.2 Introductions for the biological control of *Nezara viridula*

Country and species	Liberated	From	Result	Reference
ANTIGUA				
Anastatus sp.	1961–62	Pakistan	–	Cock 1985
Trichopoda pilipes	1949	Florida	–	Cock 1985
	1955	Montserrat	–	Cock 1985
Xenoencyrtus hemipterus (= *X. niger*)	1963	Australia	–	Cock 1985
ARGENTINA				
Trissolcus basalis	1981	Australia, Hawaii	+	Crouzel & Saini 1983; Porta & Crouzel 1984
AUSTRALIA				
Bogosia antinorii	1958	Kenya	_	Greathead 1971
Telenomus chloropus	1962	Japan	–	Callan 1963
(= *T. nakagawai*)	1980	Japan	–	Field 1984
	1981	Japan	?	Field 1984; J. Turner pers. comm. 1984
Trissolcus basalis	1933	Egypt	+	Kamal 1937; Wilson 1960
	1953	West Indies	+	Wilson 1960
	1956	Italy	+	Wilson 1960
	1961	Pakistan	+	Ratcliffe 1965
	1979–82	USA	+	Field 1984
	1979–82	Brazil	+	J. Turner pers. comm. 1984
	1979–82	South Africa	+	J. Turner pers. comm. 1984
Trissolcus crypticus	1961	Pakistan	–	Clarke 1993a
Trissolcus mitsukurii	1962	Japan	+	Callan 1963
Trichopoda giacomelli		Argentina	?	Liljesthröm 1994

Table 4.12.2 (cont'd) Introductions for the biological control of *Nezara viridula*

Country and species	Liberated	From	Result	Reference
Trichopoda pennipes	1941–43	Florida	–	Wilson 1960
	1949–50	Florida	–	Wilson 1960
	1952–53	Florida	–	Wilson 1960
	1980	Florida	–	Michael 1981
	1980	Florida	–	Michael 1981
	?	Italy	+	Giangiuliani et al. 1994; Colazza & Bin 1995
Trichopoda pilipes	1952–54	West Indies	–	Wilson 1960
	1980	West Indies	–	Michael 1981
	1980	Hawaii	–	Michael 1981
Ooencyrtus submetallicus	1953–57	Trinidad	–	Wilson 1960
	1962	Trinidad	–	CSIRO files
BRAZIL				
Gryon japonicum		Japan	+	Kishino & Teixeira 1994
Gryon obesum		USA	+	Correa & Moscardi 1995
Ooencyrtus nezarae		Japan	–	Kobayashi & Cosenza 1987
Telenomus chloropus		Japan	–	Kobayashi & Cosenza 1987
Telenomus gifuensis		Japan	–	Kobayashi & Cosenza 1987
Trissolcus mitsukurii		Japan	+	Kobayashi & Cosenza 1987; Kishino & Teixeira 1994,
Trissolcus sp.		Japan	–	Kobayashi & Cosenza 1987
CALIFORNIA				
Trissolcus basalis	1987	France	+	Hoffman et al. 1991
	1987	Italy	+	Hoffman et al. 1991
	1987	Spain	+	Hoffman et al. 1991

Table 4.12.2 (cont'd) Introductions for the biological control of *Nezara viridula*

Country and species	Liberated	From	Result	Reference
CHILE (EASTER ISLAND)				
Ectophasiopsis arcuata	1982, 1985/6	Chile	+	Ripa & Rojas 1989; Ripa et al. 1995
Trissolcus basalis	1982	Chile	–	Ripa & Rojas 1989; Ripa et al. 1995
COOK IS				
Trissolcus basalis	1950	New Zealand	?	Cumber 1953, Walker and Deitz 1979; A. Walker pers. comm. 1984
FIJI				
Trissolcus basalis	1941	Australia	+	Lever 1941, 1943
Trichopoda pennipes	1949	Florida	?	O'Connor 1950
HAWAII				
Trissolcus basalis	1962	Australia	+	Davis 1964, 1967
Xenoencyrtus hemipterus (= X. niger)	1962	Australia	–	Davis 1964, 1967
Telenomus chloropus	1967	Japan	–	Davis & Chong 1968
Telenomus sp.	1962	Australia	–	Davis 1964, 1967
Trichopoda pilipes	1962	West Indies	+	Davis 1964, 1967
Trichopoda pennipes	1962	Florida	+	Davis 1964, 1967
Ooencyrtus submetallicus	1962	West Indies	–	Davis 1964, 1967
Ooencyrtus trinidadensis	1962	West Indies	–	Davis 1964, 1967
Trissolcus mitsukurii	1966	Japan	–	Davis & Krauss 1967

Table 4.12.2 (cont'd) Introductions for the biological control of *Nezara viridula*

Country and species	Liberated	From	Result	Reference
ITALY				
Trichopoda pennipes	1984 or earlier	?	+	G.K. Waite pers. comm.
	1989	?	+	Gianguiliani & Farinelli 1995; Colazza et al. 1996a
Trissolcus basalis	1989	?	+	Colazza & Bin 1995
KIRIBATI				
Trissolcus basalis	1979	Fiji	+	Anon. 1979b; Williams 1979; Dhamaraju pers. comm. 1985
MONTSERRAT				
Anastatus sp.	1961–62	Pakistan	–	Cock 1985
Trissolcus mitsukurii	1966	Japan	–	Cock 1985
NEW ZEALAND				
Ooencyrtus submetallicus		West Indies	–	Jones 1988
Trichopoda pennipes	1965–67	Florida	–	Cumber 1967; Clausen 1978
Trissolcus basalis	1949	Australia	+	Cumber 1951
Xenoencyrtus hemipterus	1962	Australia	–	Jones 1988
NEW CALEDONIA				
Trissolcus basalis	1942–43	Fiji	+	Lever 1943
PAPUA NEW GUINEA				
Trissolcus basalis	1978	Australia	+	Anon. 1983
			+	Young 1982
Trichopoda pennipes	1977	Hawaii	–	J.W. Ismay pers. comm. 1985
Trichopoda pilipes	1980–81	Hawaii	–	Young 1982

Table 4.12.2 (cont'd) Introductions for the biological control of *Nezara viridula*

Country and species	Liberated	From	Result	Reference
PITCAIRN IS				
Trissolcus basalis	1952	Fiji	?	Dumbleton 1957
POHNPEI				
Trissolcus basalis	1989	Hawaii	+	Esguerra et al. 1993
AMERICAN SAMOA				
Trissolcus basalis	1953	Fiji	?	Dumbleton 1957
SAMOA				
Trissolcus basalis	1953	?	+	Clausen 1978
SOLOMON IS				
Trissolcus basalis	1940	Australia	+	CSIRO files
Trichopoda pennipes	1940, 1949, 1950	Florida	–	Dumbleton 1957 O'Connor 1950
SOUTH AFRICA				
Trissolcus basalis	1955	Australia	+	Bedford 1964; Greathead 1971; Annecke & Moran 1982; Bennett 1990
Trichopoda pennipes	1986	Florida	?	Bennett 1990
	1994	USA, Italy	?	Farinelli et al. 1994
ST KITTS AND NEVIS				
Anastatus sp.	1961–62	Pakistan	–	Cock 1985
Trissolcus mitsukurii	1966	Japan	–	Cock 1985
ST VINCENT				
Anastatus sp.	1961–62	Pakistan	–	Cock 1985
TAIWAN				
Trissolcus basalis	1983	?	+	Su & Tseng 1984

Table 4.12.2 (cont'd) Introductions for the biological control of *Nezara viridula*

Country and species	Liberated	From	Result	Reference
TONGA				
Trissolcus basalis	1941	Australia	+	Dumbleton 1957 Clausen 1978
USA (CALIFORNIA)				
Trissolcus basalis	1992	eastern USA	+	Pickett et al. 1996
ZIMBABWE				
Trissolcus basalis	1955	Australia	?	Annecke & Moran 1982

Doubt has been cast (Clarke 1990) both on the policy and effectiveness of introducing strains of *T. basalis* from different regions having differing environmental conditions. This practice has either led in Australia to effective biological control of *N. viridula* extending into additional environments or, alternatively, the initial genetic make-up of *T. basalis* has steadily undergone changes to allow progressive adaptation to new environments. It is possible that *T. basalis* consists of a complex of sibling species but, if not, it would be surprising if *T. basalis* has remained a homogenous species worldwide. Johnson (1985) found that American specimens of *T. basalis* showed much less morphological variation than those of Africa suggesting an African origin for the species. Furthermore, Handley (1975) reported that Australian *T. basalis* females would not mate with American males, although Powell and Shepherd (1982) found that reproductive isolation did not occur within any of 3 Australian strains examined; or between them and a strain from Florida. Nevertheless, the latter strain proved least fecund. Ferreira and Zamataro (1989) found no differences in reproductive capacity or longevity between an Australian and a Brazilian strain of *T. basalis* and Awan et al. (1989) concluded that Italian, French and Spanish populations consist of a single biotype, although several significant differences were observed in their biology. On the other hand, differences in courtship behaviour have been observed between different populations of *T. basalis* (Bin et al. 1988; Clarke and Walter 1992). However, it is not known whether any of these differences has any significance for biological control.

Three other wasps have been introduced, *Trissolcus mitsukurii* (Japan 1962), *Telenomus chloropus* (Japan 1962, Japan via USA 1980) and *Ooencyrtus submetallicus* (West Indies 1952–53). Only the former is believed to have become established but its impact has not been reported (Field 1984; J. Turner pers. comm. 1985).

The only parasitoid reported from adult or nymphal *N. viridula* is the native tachinid *Cylindromyia rufifemur* (Cantrell 1984; Coombs and Khan 1997). Three exotic species of parasitic tachinid fly have also been employed in attempts at biological control of *Nezara viridula*, *Trichopoda pennipes* from Florida, *T. pilipes* from the West Indies and *Bogosia antinorii* from Kenya. The *Trichopoda* species were introduced into Australia in the 1940s and 1950s, but failed to become established (Wilson 1960). More recently the *Trichopoda* species were introduced into Western Australia from their native countries and also from Hawaii where they have been successfully established (Michael 1981). They have not become established in Australia. It is tempting to postulate that the pheromone blend secreted by Australian *N. viridula* does not attract *Trichopoda pennipes* and *T. pilipes* females, whereas that of the Hawaiian population does. Whether or not this is true, it is clear that the responses by tachinid females to host pheromones introduces a considerable degree of host specificity to some particular populations of a host.

The Argentinian *Trichopoda giacomellii* has been introduced to Australia for examination in quarantine for host specificity. Tests indicate that it has a limited host range involving only *Nezara* and its very close relations and it has now been approved for release in Australia (D.P.A. Sands pers. comm. 1997).

At least three native wasps parasitise *Nezara* eggs, *Telenomus* sp., *Xenoencyrtus hemipterus* and '*Coruna* sp.' (certainly a misidentification of genus, Z. Boucek pers. comm. 1986), but these are of minor importance.

The successful biological control of *N. viridula* in southern Australia has been repeated more recently in northwestern Australia where the green vegetable bug was first recorded in 1974. By 1976 populations were immense, for example over 33 nymphs and adults being recorded per square metre on a tomato crop and over 20 per head on badly affected sorghum. Since *T. basalis* was not present, it was introduced from southwestern Australia. Although more than 44 000 were released, initial establishment was poor. However, after 4 months, the situation improved dramatically, parasitisation was close to 100% and damage was reduced to sub-economic levels (Strickland 1979), although there are still periods of crop growth when the pest may be a problem (Michael 1981).

T. basalis attacks, sometimes heavily, the egg masses of a range of pentatomid bugs. In southern Australia common pentatomid hosts are the horehound bug *Agonoscelis rutila* (Noble 1937; Clarke and Walter 1994) *Cermatulus nasalis* and *Oechalia schellembergii* (Awan 1989). In northwestern Australia alternative pentatomid hosts include *Piezodorus hybneri* and *Oechalia schellenbergii*, the egg masses of which suffer respectively 68% and 51% parasitisation. The coreid bug *Riptortus serripes* is also attacked, 38% of its egg masses being parasitised (Strickland 1979).

Nezara viridula is under excellent biological control and is generally a very uncommon insect throughout southern Australia. However regular or occasional damage occurs in a subcoastal zone extending from south east Queensland (Titmarsh 1979) to north central New South Wales (e.g. Forrester 1979) and into northern Victoria (Clarke 1992a) and especially on soybeans.

In an attempt to control these damaging populations, nine strains of *T. basalis* were introduced between 1979 and 1981, mass reared and released in southeastern Queensland. One strain came from each of South Carolina, Florida and Mississippi (USA), two from Brazil, two from South

Africa and two from northern Australia (Darwin and Kununurra). Although a slightly higher level of parasitisation has resulted, the problem has not been resolved (J. Turner, pers. comm. 1984; Clarke 1992a). It is notable that *N. viridula* is seldom a pest except in regions where soybean is a major crop. Turner (1983) showed that the rate of movement of *T. basalis* on soybean *Glycine max* was a third of that on cowpea *Vigna unguiculata*, mungbean *V. radiata radiata*, bean *Phaseolus vulgaris*, or sunflower *Helianthus annuus*. The proportion of *N. viridula* eggs parasitised on soybean was down to 25% of that on cowpea, mungbean and sunflower. Observations, since contested by Kelly (1987), suggested that the arrangement and height of the soybean leaf hairs, which are neither evenly spaced nor patterned, were responsible for interfering with the wasps' searching activities and this suggestion needs further investigation. Many soybean varieties have beeen selected for cicadellid resistance, which is directly correlated with the density, length and orientation of the leaf hairs (Broersma et al. 1972). Sesame *Sesamum indicum* leaves were repellent to the wasps, and those that did alight left immediately and engaged in vigorous grooming elsewhere (Turner 1983). Thus the nature of crops in an area can materially affect the success of biological control of the green vegetable bug.

In spite of the foregoing, a claim has been made (Clarke 1990, 1992a,b, 1993a,b, Clarke and Walter 1992), that, in Australia, 'there is little evidence to support claims of successful biological control of *N. viridula*' (Clarke 1993b). It is a mystery how such a view can be maintained in the light of the abundant evidence, available to its authors, from Western Australia, South Australia and coastal and southern New South Wales (Wilson 1960; Callan 1963; Ratcliffe 1965; Strickland 1979; Michael 1981; Field 1984; Waterhouse and Norris 1987). Furthermore, until the 1970s, when increasing plantings of soybean, in particular, have provided highly suitable conditions for *N. viridula* populations to increase greatly in southern Queensland and northern New South Wales, there were even publications by entomologists in the Queensland Department of Primary Industries that, with the exception of the Darling Downs, 'control of the pest has become virtually unnecessary resulting from the introduction and establishment of a tiny parasite … ' (Passlow and Waite 1971) and *Trissolcus basalis* 'has reduced the importance of *Nezara viridula* (L.) in coastal Queensland' (Smith 1977). The highly effective control progressively achieved over a vast area of southern and Western Australia is in no way diminished in validity by the fact that *N. viridula* is, indeed, an important pest in a much smaller area extending from southeast Queensland, through central NSW to northern Victoria (Clarke 1992a). Although it is most commonly associated there with soybean (see later under Italy) it is also found on a range of other crops, including grain legumes, tomatoes and beans.

Clarke and Walter (1992) postulate that, because *N. viridula* oviposits only rarely during summer in southeast Queensland, *T. basalis* is largely without its preferred host for 60–90 days during which daily temperatures average more than 25°C. This exceeds the average survival time of adult females at this temperature. Adult survival of *T. basalis* in summer is thus held to be the most likely factor limiting its populations. This postulate assumes that the egg masses of native pentatomid hosts of *T. basalis* are also in short supply over summer. It also appears not to apply to the far hotter but moister climate of the Ord Irrigation Area in far northern Western Australia, where *N. viridula* continues to be under generally excellent control.

AFRICA

N. viridula does not appear to be regarded as an important pest in northern Africa where its eggs are attacked by a number of Scelionidae, including *Trissolcus aloysiisabaudiae*, *T. basalis*, *T. lepelleyi*, *T. maro*, *T. sipius* and *Telenomus seychellensis*. *Trissolcus basalis* occurs mainly in coastal areas and the others are reported primarily from the eastern and central half of the continent. *T. basalis* was introduced to South Africa from Australia, New Zealand and USA, although there is some evidence that it may have already occurred there prior to these introductions (Giliomee 1958; Greathead 1971). In Malawi eggs laid on macadamia were reported to experience an average of 74% parasitisation by *Trissolcus maro* and *Telenomus seychellensis* (Croix and Thindwa 1986). In Somalia *Trissolcus alloysiisabaudiae* is very abundant and may cause 100% parasitisation of *N. viridula* eggs on cotton (Paoli 1933). *T. lepelleyi* and *T. sipius* attack *N. viridula* eggs in East Africa, the latter being known only from Kenya. *Psix striaticeps,* which occurs in tropical Africa and India, has been bred from *N. viridula* eggs (Jones 1988).

ARGENTINA

N. viridula was first recorded in 1919. Since the native tachinid parasitoid *Trichopoda giacomellii* was unable to maintain populations at sufficiently low levels, three parasitoid wasps were introduced, of which the most effective is *Trissolcus basalis* (Crouzel and Saini 1983; Porta and Crouzel 1984).

In Buenos Aires Province, mortality of *N. viridula* eggs was found to be due mainly to parasitisation by *T. basalis*, that of 1st to 3rd instar nymphs to predation and that of adults (together with reduction in egg production) to parasitisation by *Trichopoda giacomellii*. Adult mortality and reduction in egg production was found to be density dependent. Three egg parasitoids were present, *Trissolcus basalis* (95% of total parasitisation), *Telenomus mormideae* and *Telenomus* sp.. Nymphal mortality was principally due to spiders and predatory bugs (*Podisus* sp.), although there was also some parasitisation by *Trichopoda giacomellii*. Adverse climatic conditions (heavy rain) played a minor role in nymphal mortality (Liljesthröm and Bernstein 1990). Parasitisation of *N. viridula* eggs by *T. basalis* rose to a maximum of 90% in autumn although 33% of the parasitoids died, the majority (60%) in the pupal stage (Liljeström and Camean 1992).

BRAZIL

In Rio Grande do Sul the main causes of mortality of *N. viridula* eggs laid throughout the season on soybean were infertility (2.7%: relatively constant), failure to hatch (14.1%: fluctuating), parasitisation (24%: relatively constant) and predation (17.3%: relatively constant) (Moreira and Becker 1986a). Three scelionid parasitoids were present, *T. basalis*, *Trissolcus* sp. and *Telenomus mormideae*. *T. basalis* killed a greater number of eggs and attacked a larger number of egg rafts than the other species (Moreira and Becker 1986b). A complex of polyphagous predators did not discriminate between parasitised and unparasitised eggs and were responsible for 25.5% mortality. The predators were responsible for 17.3% mortality of *N. viridula* and 34% of *T. basalis* (Moreira and Becker 1986c). Predation on host eggs was the main cause of mortality of *T. basalis* in the pre-emergence period (Moreira and Becker 1987).

The tachinid fly *Trichopoda giacomellii* (= *Eutrichopodopsis nitens*) is the most important parasitoid of *N. viridula* in northern Paraná State. The level of parasitoid attack varies according to the plant on which the host is feeding and is highest when soybean is not available (Panizzi 1989). Although *T. basalis* (introduced) and *Telenomus mormideae* (native) were already present on the Cerrados area, Kobayashi and Cosenza (1987) introduced from Japan 5 additional species. In order of decreasing efficacy in parasitisation and adult emergence these were *Trissolcus mitsukurii*, *Ooencyrtus nezarae*, *Telenomus chloropus*, *Telenomus gifuensis* and *Trissolcus* sp.. Of the introduced species, *T. mitsukurii* parasitised eggs of all major pentatomid species throughout the year and also survived the dry winter season. In addition, it was the dominant competitor on egg masses. However, Bennett (1990) reports, more recently that it is not definite that permanent establishment has been achieved. When compared with *T. basalis*, the latter parasitised about 90% of exposed eggs with 60% adult emergence, whereas *T. mitsukurii* achieved about 70% parasitisation and 40% emergence (Kobayashi and Cosenza (1987). In northern Brazil, Ferreira (1986) reported 40% parasitisation of *N. viridula* eggs by *T. basalis* and that *Telenomus mormideae* was also abundant.

In the Federal District of Brazil the egg parasitoids *Trissolcus mitsukurii* and *Gryon japonicum*, introduced from Japan, gave good levels of parasitisation (Kishino and Teixeira 1994). In Parana State *T. basalis*, *Telenomus podisi* and *Gryon obesum* parasitised up to 60% of *Nezara* eggs on soybean (Correa and Moscardi 1995).

In southern Brazil, *T. basalis* is the main parasitoid, attacking between 97.5% and 100% of *N. viridula* eggs laid on soybean. In 1988, 36.6% of the egg masses were attacked and 10.3% in 1989, with 21.8% and 6.3% of the individual eggs being parasitised respectively (Foerster and Queirōz 1990).

COOK IS

T. basalis was introduced to Mangaia in 1950, but is not known to have become established (Cumber 1953; Walker and Deitz 1979) and this must be assumed not to have occurred.

EASTER IS

Control of *N. viridula* was achieved by the establishment of the tachinid *Ectophasiopsis arcuata* from mainland Chile, so that it is now difficult to find a bug. *T. basalis* was also introduced but was not recovered (Ripa and Rojas 1989; Ripa et al. 1992).

FIJI

N. viridula was first recorded in 1939 and *Trissolcus basalis* was introduced from Australia in 1941 (Lever 1941). Success was immediate and good control resulted (O'Connor 1950). Large populations of *N. viridula* are reported to develop sometimes on cowpeas, but the insect is not troublesome on other legumes (Swaine 1971).

Trichopoda pennipes was introduced from Florida in 1949, but its establishment is not recorded (O'Connor 1950).

HAWAII

N. viridula was first recorded in 1961 and the wasps *Trissolcus basalis*, *Xenoencyrtus hemipterus* (= *X. niger*) and *Telenomus* sp. (all egg parasitoids) from Australia were released in 1962. Other importations in 1962 were the tachinid fly, *Trichopoda pilipes*, which parasities last instar nymphs and adults, and two egg parasitic wasps *Ooencyrtus submetallicus* and *O. trinidadensis* from the West Indies. In 1963 *Trichopoda pennipes* was imported from Florida. Of these parasites, *Trissolcus basalis*, *Trichopoda pennipes* and *T. pilipes* became established (Davis and Krauss 1964; Davis 1964, 1967; Croix and Thindwa 1967; Clausen 1978). *Nezara* populations declined steadily to sub-economic levels, with only sporadic outbreaks, and the species is generally under effective biological control (C.J. Davis, pers. comm. 1985). Average parasitisation by *Trissolcus basalis* ranged up to about 95% and by *Trichopoda pilipes* up to 86%. *Trichopoda* pupae are occasionally parasitised by the encyrtid *Exoristobia philippensis* (Davis 1964).

More recently (1990–91) egg rafts of *N. viridula* placed in weeds at the border of macadamia nut plantations had significantly higher rates of parasitisation (49.9%) than rafts placed in the canopy of macadamia trees (14.7%). Predators were more effective at locating rafts placed in trees than in weeds and were always more efficient than *T. basalis*, regardless of their location. The egg parasitoid, *Anastatus* sp. was equally inefficient in both habitats. In 1990 only 1.2% of the eggs in the trees were parasitised and 8.6% in the weeds. During the same period, predators destroyed 26.0% and 14.5% in trees and weeds respectively.

In 1991 parasitisation of eggs dropped to 0.2% and 1.7% in trees and weeds, whereas predation increased to 47.7% and 36.9% respectively. Doubt was, therefore, cast upon *T. basalis* having a prominent role in biological control of *N. viridula* in Hawaii (Jones 1995). Although this conclusion appears to follow in the macadamia agroecosystem studied, it would be of interest to know whether it applies also to other susceptible crops. Predation was attributed mainly to ants, including *Pheidole megacephala*.

INDIA

Singh (1973) reported no parasitoids in life-table studies of *N. viridula* on soybeans.

INDONESIA

Partial life tables showed on soybeans in Northern Sumatra that mortality of *N. viridula* until the late 1st instar was 50 to 87%, of which 18 to 85% occurred during the egg stage and was caused mainly by predators. Only 2 to 26% of the eggs were parasitised. The main predators were two species of ants (*Solenopsis geminata* and *Dolichoderus* sp. a staphylinid beetle (*Paederus* sp.) and several crickets, although other egg predators belonging to the families Tettigoniidae, Lygaeidae and Anthocoridae were also observed feeding on the eggs. *Trissolcus basalis* parasitised the eggs but no evidence was obtained of the presence of tachinid parasitoids that attack late nymphs and adults (van den Berg et al. 1995).

ITALY

Before production of soybeans began in Italy in 1981 *N. viridula* was only important occasionally. Crops attacked included tomatoes and legumes. The increasing production (over a decade more than a thousand fold increase in area planted to soybeans) filled a temporal and food gap for *N. viridula* and other pentatomids (Colazza and Bin 1990). The second generation of *N. viridula* now migrates each summer into soybeans at the beginning of development of pods, which then provide the main food for reproduction and larval development. Abundance of *N. viridula* increased steadily in the eighties throughout northern and central Italy to a level at which it became a key pest. Three parasitoids were recorded from egg rafts, *Anastatus bifasciatus*, *Ooencyrtus* sp. and *Trissolcus basalis*. However the first 2 species were never bred from egg rafts collected from soybeans. Approximately 20% of egg rafts were parasitised in 1986 and 1987, increasing to 50% in 1988 to 1992. Efficiency of parasitisation (% eggs parasitised divided by the number of egg masses discovered) was 65% in 1986, but rose to 92% in 1988 and 1990.

The early larval instars were generally free from parasitoid attack although two tachinids were occasionally recorded, the native *Ectophasia crassipennis* (5 to 10% parasitisation) and the accidentally introduced *Trichopoda pennipes* (2 to 15% parasitisation).

T. basalis was also recovered from the eggs of 2 other pentatomid bugs present at low levels in soybean fields, *Carpocoris mediterraneus* and *Piezodorus lituratus* (Colazza and Bin 1995).

JAPAN

The widespread *Telenomus chloropus* (= *T. nakagawi*) and also *Trissolcus* (= *Asolcus*) *mitsukurii* which is known only from Japan are the two most important parasitoids of *N. viridula* and have been studied intensively in Fukuoka. The host-finding ability of *T. chloropus* is superior to that of *T. mitsukurii* and it parasitises egg masses more rapidly and more efficiently. Females lay about 100 eggs (which is 1.6 times that of *T. mitsukurii* and live 11 days, or 3 days longer than *T. mitsukurii* (Nakasuji et al. 1966), although the latter may have at least 11 generations a year, whereas the former has some 9 generations (Hokyo et al. 1966b). Hokyo et al. (1966a) have shown experimentally that the two species do not discriminate between each other's parasitised and unparasitised eggs, with *T. mitsukurii* larvae usually being successful in competition with *T.chloropus* larvae (Hokyo et al. 1966a). Furthermore, female *T. mitsukurii* often bite and kill female *T. chloropus* when they meet on the egg mass (Hokyo and Kiritani 1966). It follows that the effectiveness of *T. chloropus* is reduced by the presence of *T. mitsukurii* (Nakasuji et al. 1966), so it would be undesirable, in a biological control program, to introduce the latter along with the former. However, it should be borne in mind that *T. mitsukurii* is more abundant than *T. chloropus* in the southern coastal district of Fukuoka, whereas the reverse is true for the northern mountainous districts. The combined mortality caused by the two species amounted to 60 to 90% of the first spring generation *N. viridula* eggs.

Three minor parasitoids have been bred from *Nezara* eggs in Fukuoka and several others are present elsewhere. The first, *Telenomus gifuensis*, is an effective parasitoid of *Scotinophara lurida* eggs, and also attacks a range of other pentatomids (Hidaka 1958; Hokyo et al. 1966b). The second, *Ooencyrtus nezarae*, the smallest of the three, is known from *Nezara viridula*, *N. antennata* and *Anacanthocoris concoloratus*. The third, *Anastatus japonicus*, is known as an egg parasitoid of the gypsy moth *Lymantria dispar* and other Lepidoptera (Hokyo et al. 1966b).

KIRIBATI

N. viridula was a pest on the islands of Betio and Tarawa in the 1970s. *T. basalis* was released in 1978 and, since 1984, this pest has not been recorded from Tarawa (E. Dharmaraju pers. comm. 1985).

NEW CALEDONIA

Trissolcus basalis was introduced in 1942–43 and became established (Lever 1943; Clausen 1978).

NEW ZEALAND

N. viridula was first recorded in 1944 and soon became a serious pest of many crops. *T. basalis* was introduced from Australia in 1949 and rapidly became widely established. There followed a gradual decline in the severity of plant damage and, although populations continued to fluctuate seasonally, the situation became satisfactory (Cumber 1949, 1951, 1953, 1964). Over this period *T. basalis* extended its host range to other pentatomid bugs (e.g. *Cuspicona simplex* and *Glaucias amyoti*), thereby providing a source of parasitoids to attack any eggs of *Nezara* that became available. Adaptation of *T. basalis* to *Nezara* under New Zealand conditions may also have been responsible for its improved performance (Cumber 1964).

Trichopoda pennipes, originally from Florida, was obtained from Hawaii in 1965 and released over the next 3 summers. Evidence of a generation in the field was obtained in May 1967, but the fly did not become established. In addition to *Nezara viridula,* eggs were deposited on adults of other pentatomids *Antestia orbona*, *Cermatulus nasalis*, *Cuspicona simplex*, *Glaucias amyoti* and *Dictyotus caenosus*, but a parasitoid was reared only from *G. amyoti* whose nymphs are readily parasitised (Cumber 1967).

PAPUA NEW GUINEA

N. viridula is a serious pest in the Markham Valley where *T. basalis* is present, but generally results in less than 30% parasitisation. In 1978 a strain of this parasite from Western Australia was released, but the level of parasitisation did not increase (Young 1982). In Wau *T. basalis* and another scelionid egg parasite are generally effective, although *N. viridula* occasionally increases to pest proportions (Gagne 1979). The tachinid parasites *Trichopoda pennipes* and *T. pilipes* were introduced from Hawaii but failed to become established (J.W. Ismay pers. comm. 1985). *T. giacomelli* is being considered for release.

PHILLIPINES

Three decades ago it was reported that *N. viridula* was not a pest, apparently being controlled by a native egg parasitoid, *Ooencyrtus* sp. (Cendana, in Davis 1967) and it is interesting that *Nezara* was reported as present, but unimportant, in 1993 (Waterhouse 1993b). This may possibly be correlated with the fact that soybean production in the Philippines is rather limited —much lower than in many other Southeast Asian countries, such as Thailand, Indonesia and Vietnam. Two egg parasitoids *Telenomus comperei* and *T. pacificus* have been reported from *N. viridula* eggs laid on groundnuts. Both species parasitised 100% of offered eggs in 24 hours and adults emerged after 12 to 14 days. Adults lived up to 32 days when fed honey (Cadapan and Alba 1987).

POHNPEI

N. viridula became a major pest in the early 1990s on several islands in the Federated States of Micronesia. Following the introduction of *T. basalis* from Hawaii, the green vegetable bug population has become so low that it is rarely seen now on vegetables in Pohnpei (Esguerra et al. 1993; Suta and Esguerra 1993).

SAMOA

Trissolcus basalis was introduced in 1953 and became established (Clausen 1978).

SOLOMON IS

Trissolcus basalis was introduced from Australia in 1940 against the coconut spathe bug *Axiagastus campbelli*. It is said to be established (CSIRO files) and a *Trissolcus* sp. has been recorded from pentatomid eggs (*N. viridula* or *Plautia brunneipennis*) on beans (R. Macfarlane pers. comm. 1985).

Trichopoda pennipes was introduced from Florida via Fiji in 1950 in order to control the coconut bug *Amblypelta cocophaga* and other phytophagous bugs (O'Connor 1950), but it has not been collected since.

SOUTH AFRICA

Trichopoda pennipes was introduced from USA and Italy and liberated in 1994 (Farinelli et al. 1994; van den Berg et al. 1994) but there is no information on establishment. *T. giacomelli* has also been imported for study (D.P.A. Sands pers. comm. 1997).

TAIWAN

T. basalis was introduced in 1983 and, two months after release, parasitisation rates of 90% and 60% respectively of *N. viridula* eggs at two sites was reported (Su and Tseng 1984).

THAILAND

The most abundant egg parasitoid is *Gryon fulviventris*, which exists as a number of biotypes. Under a series of synonyms (*Dissolcus fulviventris*, *Hadronotus fulviventris*, *H. antestiae* and *Gryon antestiae*) it is known from Africa, India, Thailand, southern USSR and Malaysia. It parasitises the eggs of many species of Pentatomidae, Scutelleridae and Coreidae, but was reported by Jones (1988) for the first time in *N. viridula* eggs in Thailand, where it also breeds in the eggs of *Piezodorus hybneri*. In Africa larvae develop in *Nezara viridula* eggs, but adults do not emerge successfully.

Other egg parasitoids are *Telenomus chloropus*, *Ooencyrtus nezarae, Anastatus* sp. (Jones et al. 1983b; Jones 1988), *Telenomus* sp. and *Trissolcus basalis* (Napompeth 1990).

TONGA

Trissolcus basalis was imported in 1941 and became established (Clausen 1978).

USA

The influence of the host plant on which egg rafts of *N. viridula* are laid on the level of both parasitisation and predation was investigated in North Carolina by Shepard et al. (1994). Parasitisation was higher than predation on eggs on tomato and about equal in okra, soybean and cowpea. In one year, predation was higher than parasitisation in soybean towards the end of the growing season, but parasitisation was higher early in the season in okra and cowpea. Parasitisation of egg masses in wild radish reached a peak of nearly 100% during spring and declined to about 30% in autumn. The major parasitoid from all crops was *Trissolcus basalis*, although *Ooencyrtus submetallicus* occured in low numbers. The conclusion was reached that both parasioids and predators may play an important role in regulating populations of *N. viridula* and that their combined action often resulted in the attack of 100% of egg masses in some crops.

VANUATU

N. viridula occurs in Vila where its eggs are heavily parasitised by a wasp *Trissolcus* sp. (not *T. basalis*) (R. Weller pers. comm. 1986).

Biology of the major species

Scelionidae*:* Hymenoptera

This is the most important family of hymenopterous parasitoids emerging from the eggs of *N. viridula* and is dealt with, amongst others, by Nixon (1935, 1936, 1937, 1966).

Trissolcus basalis

Kamal (1937) was the first of many to make a detailed study of the impact of the egg parasite *Trissolcus basalis* on the abundance of *Nezara viridula*: no control measures are needed in Egypt. His work on the biology of the wasp has been supplemented by studies by many later workers (e.g. Wilson 1961; Cumber 1964; Powell and Shepherd 1982; Correa and Moscardi 1993, 1994; Awadalla 1996; Colazza et al. 1996b). The minute female of *T. basalis* oviposits in the side of the bug egg, after which she marks the egg by rubbing an abdominal secretion over it with the ovipositor, as a deterrent to other females from laying in the same egg. The length of the life cycle ranges from 9 to 24 days depending on temperature, the entire egg, larval and pupal stages being passed inside the same eggshell. The adult wasps chew their way out through the lid of the eggshell, males usually emerging first and disputing with one another for possession of the egg batch and thereby the right to fertilise the later-emerging females. In hot weather the females live 4 to 15 days and have considerable dispersive powers, as shown by the rapidity with which they spread through newly colonised areas. The adult wasps overwinter among leaves and litter.

As indicated earlier, there is good evidence for the existence of several different strains of *T. basalis*. Experimental work using strains from three widely separated regions of Australia and from Florida showed that they were not reproductively isolated, that the Australian strains had a higher fecundity, but that adults of the Florida strain lived longer (Powell and Shepherd 1982).

T. basalis is frequently recorded from several other pentatomids, but has a special preference for *N. viridula* (Jones 1988). It appears to be most effective in coastal and subcoastal areas and has been established in Argentina, Australia, Fiji, Hawaii, Kiribati, Papua New Guinea, New Caledonia, Samoa, Solomon Is, South Africa and Tonga and possibly in several other countries (Table 4.12.2).

In Australia two species of the pteromalid *Acroclissodes* are parasitic on *T. basalis* (Clarke and Seymour 1992).

Gryon sp.

Some aspects of mating and reproduction of *Gryon* sp. in India have been investigated by Velayudhan and Senrayan (1989).

Trissolcus mitsukurii

This important egg parasitoid of *Nezara* in Japan also attacks the eggs of several other pentatomids (Kishino and Teixeira 1994) , preferring species that deposit their eggs in small masses. It is bisexual and the first egg deposited by a mated female always produces a male. Both sexes have aggressive behaviour and females drive *Telenomus chloropus* females off a pentatomid egg mass (Hokyo et al. 1966b). The fecundity and longevity of *T. mitsukurii* were found to be less than those of *T. basalis* in laboratory trials at 26°C and 65% RH. *T. basalis* parasitised 82.2% of eggs on the second day of adult life, whereas *T. mitsukurii* parasitised only 51.3%. On average, the former laid 250 eggs and the latter 80, and the longevity of *T. basalis* was 80.1 days and of *T. mitsukurii* 42.6 days (Ferreira and Zamataro 1989).

Too little is known about the dozen other *Trissolcus* species in Table 4.12.1 to form an opinion of their value in biological control.

Telenomus chloropus (= T. nakagawai)

This is one of the most important egg parasitoids of *N. viridula* in Japan and also attacks eggs of *N. antennata*. Females are parthenogenic, lay about 100 eggs and live for 11 days. They have a high searching ability and can parasitise all egss in a raft (Nakasuji et al. 1966). The species is oligophagous and prefers large egg rafts of pentatomids, such as those of *N. viridula* or *N. antennata,* to smaller egg masses of many other pentatomids. When introduced to the laboratory in Louisiana, USA. females lived for 8 days at 24°C, laid on average 60 eggs and developed from oviposition to emergence in 18 days. When reared from eggs of *N. viridula* which had been reared on resistant soybean its fecundity was half that of parasitoids reared on susceptible soybean and its mortality within *Nezara* eggs was higher (Orr et al. 1985b).

Although morphological differences have not been found, it appears that *T. chloropus* exists as a series of biotypes. It is a widespread polyphagous parasitoid of pentatomid eggs throughout the Palaearctic Region, but it is recorded from *Nezara* only in Japan, Korea and Thailand. The Japanese biotype rarely produces males, although males occur elsewhere (Jones 1988). *T. chloropus* from Japan has been released in Australia (Callan 1963; Field 1984), Brazil (Kobayashi and Cosenza 1987) Hawaii (Davis and Chong 1968) and the USA (Jones 1988), but has not become established, possibly due to its requirement for high humidity (85% RH or higher) for successful emergence (Orr et al. 1985a).

Telenomus cyrus

This parasitoid is known from Indonesia, the Philippines and Taiwan. In Taiwan it parasitises up to 19% of eggs in soybean and is the most important egg parasitoid of *N. viridula* in soybean, rice and jute (Taiwan Agricultural Research Institute 1984).

Encyrtidae*:* Hymenoptera

Species of *Ooencyrtus* have been recorded from *N. viridula* eggs from many parts of the world (Table 4.12.1), but are never a major component of the suite of parasitoids.

Ooencyrtus submetallicus

This species ranges from Florida through to West Indies, Brazil and Argentina (Jones 1988). It was found to be inferior to *T. basalis* in host location and dispersal in soybeans in Louisiana (Lee 1979). It was introduced to Australia, Hawaii and New Zealand, but did not become established (Wilson 1960; Davis and Krauss 1963; Davis 1967).

Tachinidae: Diptera

These are clearly important parasitoids of adult *N. viridula* in the Americas and the Ethiopian region. Outside of Japan, where one species attacking the green vegetable bug is known, there appear to be no records of tachinids regularly attacking *N. viridula* in Eastern Asia.

Trichopoda spp*.*

Trichopoda pennipes

T. pennipes in North America is a complex of biotypes or sibling species. In the east its native hosts are the squash bug *Anasa tristis*, other coreids and several pentatomids (Arnaud 1978). In the southeast it occurs regularly in the native pentatomid *Acrosternum hilare*, but seldom in other pentatomids (Jones 1988). In California it does not oviposit on *A. tristis,* but in the field breeds in a pyrrhocorid and a largid bug (Sabrosky 1955; Dietrick and van den Bosch 1957). Salles (1991, 1993) has studied *T. pennipes* in Florida.

The female *Trichopoda pennipes* lays eggs singly on the cuticle, mainly of the undersurface of fourth and fifth instar nymphs and adult bugs. The eggs hatch in 3 to 4 days and the young larvae bore directly into the host, tap the respiratory system of the bug for air and feed on the body fluids and internal organs of the host. When fully fed (16 days), the third instar larvae forces its way out through an intersegmental membrane of the host abdomen and pupates in the soil. After about 14 days the adult fly emerges. Up to 232 eggs are laid by a female and, unlike *Trissolcus basalis*, there is often great wastage, many eggs (up to 237) being laid by several females on one adult bug, although only one parasitoid larva survives (Shahjahan 1968). The reproductive organs of the host bug may or may not be aborted by the feeding of the parasite, and it ultimately dies from mechanical injury caused by the emerging larva. The parasitoid overwinters as a second instar larva inside the hibernating adult bug (Beard 1940; Clausen 1978). Rearing methods are discussed by Gianguiliani and Farinelli (1995). Male *N. viridula* receive more parasitoid eggs than females and are more heavily parasitised (Mitchell and Mau 1971; Todd and Lewis 1976).

In Georgia, USA, female *Nezara* parasitised by *T. pennipes* live about half as long as normal females and lay about a quarter the number of fertile eggs (Harris and Todd 1980).

Trichopoda pilipes

In the West Indies, instead of *T. pennipes,* the closely related *T. pilipes* (sometimes regarded as a subspecies) occurs. Both species have been established in Hawaii and *T. pilipes* is the more important (Davis 1967). Unsuccessful attempts have been made to establish one or both of these species in Australia, Fiji, South Africa and a number of other places, although *T. pennipes* has been established in Italy (Table 4.12.2).

Trichopoda giacomellii

Parasitisation levels by *T. giacomellii* of *N. viridula* in Argentina were 45.3% on sorghum, 42.1% on flax, 29.9% on wheat and 27.9% on soybean. Levels on males were higher than on females, except on soybeans, where there was no significant difference (La Porta 1990). Liljesthröm (1985, 1995) observed that the highest densities of parasitoids and the highest rate of parasitisation occurred in areas with the highest densities of *N. viridula*.

Many fly eggs are laid on some individual hosts and few or none on others. More eggs are deposited on adult *N. viridula* than on 4th or 5th instar nymphs and more on adult males than on females. Some bugs are attacked sufficiently late in their development that they are able to produce at least one normal egg batch which has unaffected egg viability. In one study less than 7% parasitised nymphs died in the 5th instar. This resulted in sufficient eggs being laid to enable *N. viridula* to persist in the environment (Liljesthröm 1992, 1993a,b). In the laboratory at 26°C, 70% RH and a 16-hour day, the egg, larval and pupal stages lasted 2.8, 33.0 and 13.3 days respectively and females laid an average of 29 eggs (La Porta 1987).

On hatching, young larvae penetrate the host cuticle and, on moulting to the 2nd instar, attach their posterior spiracles to one of the host's tracheal trunks. The fully grown 3rd instar larva emerges from the host to pupate in the soil. Most hosts die shortly after the parasitoid larva has left.

In one large field sample the maximum number of living parasitoid larvae found per host was 2 (4% of hosts), whereas only 1 living parasitoid larva was found in 66% of hosts. Small, dead, damaged parasitoid larvae in some hosts provided evidence that there was competition for survival (Liljesthröm 1993b).

Because moulting led to loss of unhatched eggs with the discarded cuticle, eggs laid on nymphs less frequently led to successful parasitisation than eggs laid on adults. With 1 parasitoid egg per adult, success was greater on males than on females whereas, when more than 4 eggs were present, the success rate was higher with females (Liljesthröm 1991). *T. giacomellii* parasitised 100% of *N. viridula* adults for 3 consecutive generations in an uncultivated area near Buenos Aires (Liljesthröm 1981) and it was concluded that *T. giacomellii* could regulate the population of *N. viridula* (Liljesthröm and Bernstein 1990).

T. giacomellii (at times referred to incorrectly as *Eutrichopodopsis nitens*) is also an important parasitoid of *N. viridula* in Brazil. When parasitisation occurred in nymphs or newly moulted adults, adults did not reproduce and longevity was greatly reduced. Female *N. viridula*, parasitised on the 7th day of the adult stage, had their fecundity reduced by 58%, but neither egg fertility nor size was affected (Ferreira et al. 1991). Parasitisation by *T. giacomellii* collected in the field in Brazil from soybean and other crops ranged from 27.1% to 52.7%. More parasitised eggs were found on males than on females and most eggs were on the thorax (Ferreira 1984). High rates of parasitisation of *N. viridula* by *T. giacomellii* were observed on the weed *Leonurus sibericus*, but populations transferred to nearby soybean when this entered the reproductive phase. On the other hand, bugs living on castor, *Ricinus communis,* stayed on this plant all year round. This weed is of low nutritional value to them, but on it they are less liable to attack by the tachinid (Panizzi 1989).

A recent laboratory study of the reproductive attributes of *T. giacomelli* determined the influence of adult food availability and body size on fecundity, and longevity, both relevant to any introduction program (Coombs 1997).

Little is known about other *Trichopoda* species attacking pentatomid bugs: *T. lanipes* in Florida (Drake 1920), *Trichopoda* sp. in Uruguay (Guido and Ruffinelli 1956) and possibly other species in Brazil (Jones 1988).

Bogosia antinorii

This species is widespread in eastern and southern Africa and is known only from *N. viridula* (van Emden 1945; Barraclough 1985). There was apparently an unsuccessful attempt to establish it in Australia from material from Kenya (Greathead 1971).

Ectophasiopsis arctuata

This tachinid is common on *N. viridula* adults in Chile. Following its introduction to Easter Is it brought this bug under successful biological control (Ripa and Rojas 1989).

Gymnosoma rotundata

This tachinid parasitises *N. viridula* in Japan where up to 5% parasitisation is recorded (Kiritani et al. 1963). It is widespread in Palaearctic regions and attacks many hosts, including *Nezara antennata*, in Japan and Korea. *Gymnosoma clavata* has been recorded once from *N. viridula* in Europe (Herting 1960).

One other tachinid has been reported once from *N. viridula*, *Cylindromyia rufifemur* from Australia (Cantrell 1984).

Comments

Although predators are undoubtedly important natural enemies of *N. viridula*, particularly of its early stages, most are generalists which are unlikely to be approved nowadays by quarantine authorities for introduction as biological control agents. This situation is likely to be partly offset by the fact that most countries possess a suite of generalist predators, some of which are likely to attack *N. viridula*.

The species of egg parasitoid most closely associated with *N. viridula* are concentrated in Africa and Japan. Elsewhere its eggs are parasitised by introduced species or by native species that have expanded their activities from native bugs. Indeed, it seems likely that the complex of Japanese parasitoids has probably expanded its host range from the oriental stink bug *N. antennata* of Japanese origin, just as the complex of Central and South American tachinids has clearly expanded to *N. viridula* adults from adults of native bugs.

Successful biological control of *N. viridula* has been achieved in many countries to which it has spread this century. These include a vast area (but not all) of Australia, also New Zealand, Hawaii and several other Pacific islands. The prospects are good for reducing its pest status in many other areas where effective parasitoids are not yet present. This might involve the introduction of additional species or strains of *Trissolcus*. In addition several of the many other parasitoids known to attack eggs (species in the genera *Telenomus* and *Gryon*) are well worth considering. In the Ethiopian region a tachinid (*Bogosia antinorii*) is an important parasitoid of adults and large nymphs and in the Americas there are at least 4 tachinid species worthy of consideration: *Trichopoda pennipes*: USA; *T. pilipes*: West Indies;

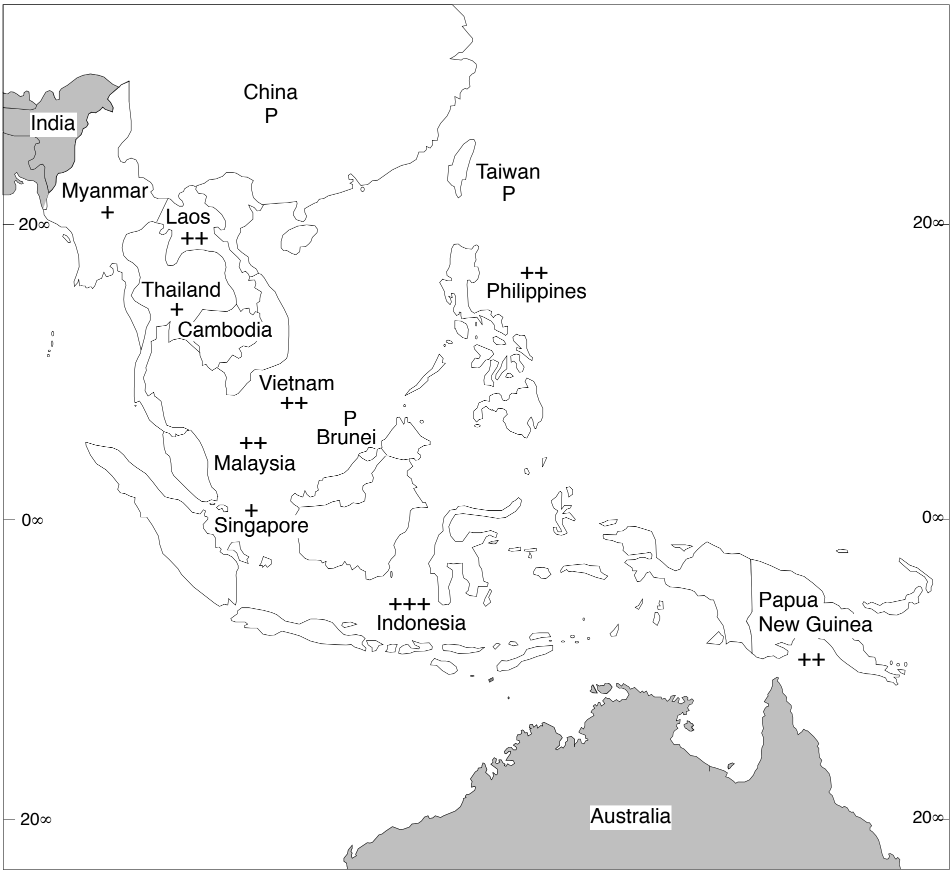
T. giacomelli Argentina; and *Ectophasiopsis arcuata*: Chile. These 4 are reported to be more abundant now on *N. viridula* than on the native bugs they parasitised before the arrival of *N. viridula* (Jones 1988). A problem in their effective use is that location of *N. viridula* hosts is dependent, in some species at least, upon the secretion by *N. viridula* of a specific attractive blend of chemicals. Some biotypes of *N. viridula* that do not produce the appropriate blend largely escape oviposition. There are no records of tachinids regularly attacking *N. viridula* in the East Asian Region, except for the widespread, polyphagous *Gymnosoma rotundata*, which was found to cause up to 5% parasitisation of *N. viridula* in Japan and also to attack *N. antennata* in Japan and Korea (Kiritani et al. 1963).

The main areas where *N. viridula* continues to be an economically important pest in spite of attempts to use natural enemies including *T. basalis* appear, with the exception of certain crops such as macadamia and pecan nuts, to be associated with extensive plantings of soybeans. A detailed re-examination is required of the behaviour of *T. basalis* (and perhaps other egg parasitoids) in relation to ability to parasitise *N. viridula* egg masses laid on soybean. If it is demonstrated that certain physical or chemical characteristics of soybeans are responsible for poorer than usual performance, serious consideration should be given to the selection of varieties that have minimal adverse effects on the parasitoids. This, of course, is different from selecting soybean cultivars that are resistant to *N. viridula*, some of which are known (e.g. Kester et al. 1984; Bowers 1990).

In this context it is relevant that the biology of *Telenomus chloropus*, an egg parasite introduced into southern USA in 1982 from Japan, was studied on eggs of *N. viridula* that had been reared on the stink bug-resistant soybean, PI 717444, or on the susceptible cultivar, Davis. Time of development of the parasite did not differ significantly in eggs from either source, but success of emergence was lower from eggs laid on resistant soybean and fecundity of those that did emerge was about half of that of individuals reared from eggs laid on Davis. The authors (Orr et al. 1985b) point out that, with a marked reduction in emergence and fecundity, combined with decreased host availability, there is the potential for reduction or elimination of resident parasite populations in fields of resistant soybeans.

Comparatively little is known of the range of *Nezara* parasitoids in its centre of origin, namely the Ethiopian region, although at least 6 Scelionidae including *T. basalis* have been recorded, together with the apparently-specific, widespread tachinid *Bogosia antinorii*, whose effectiveness deserves study. It is probable that a thorough investigation in the Ethiopian region would disclose an additional range of potentially valuable species.

4.13 *Ophiomyia phaseoli*



It appears that the bean fly *Ophiomyia phaseoli* originated in Asia. Its most effective natural enemy, the braconid *Opius phaseoli*, is known from eastern Africa, India and the Philippines and has been introduced to Hawaii and Taiwan. This species is capable of parasitisation levels of up to 90% or more and, when introduced to Hawaii, it and the related *O. importatus* resulted in successful biological control of bean fly.

There are good reasons for countries where bean fly is a problem and where parasitisation levels are low, to consider introducing these and other parasitoids to assist in reducing bean fly populations.

Ophiomyia phaseoli (Tryon)

Diptera: Agromyzidae (this species was earlier included in the genus *Agromyza* or *Melanagromyza*) bean fly

Rating

Southeast Asia			China	Southern and Western Pacific		
	+++	Indo			+++	Guam
14	++	Laos, Viet, Msia, Phil		9	++	Fiji, PNG
	+	Myan, Thai, Sing			+	Sam, Sol Is
	P	Brun	P		P	FSM

Origin

Unknown, but presumably in association with one of its current legume host genera in India or possibly Southeast Asia. It was described by Tryon (1895) from specimens causing damage to beans in 1888 in Queensland, Australia and, shortly after, reported to cause similar damage in New South Wales (Froggatt 1899).

Distribution

This was given (CIE 1974a) as **Africa**: Burundi, Congo (Zaire), Egypt, Ethiopia, Kenya, Madagascar, Mauritius, Malawi, Mali, Nigeria, Réunion, Rwanda, Senegal, South Africa, Sudan, Tanzania, Uganda, Zambia, Zimbabwe; **Asia**: Bangladesh, China, Hong Kong, India, Indonesia, Iraq, Israel, Jordan, Malaysia, Myanmar, Nepal, Pakistan, Philippines, Ryukyu Is, Singapore, Sri Lanka, Taiwan, Thailand; **Australia and Pacific Islands**: Australia, Caroline Is, Fiji, Hawaii, Irian Jaya, Mariana Is, Papua New Guinea and Samoa. To the above must be added Israel (Spencer 1990) Brunei, Laos, Singapore (Waterhouse 1993b) and Japan (Makino et al. 1990). It has not been recorded from Europe or the Americas.

A morphologically very similar species, *O. spencerella*, only readily distinguishable from *O. phaseoli* by the male genitalia, occurs in association with it in Kenya, Uganda, Tanzania and Nigeria on *Phaseolus vulgaris* and, less commonly, on several other legumes. There are 3 economically important agromyzid miners other than *Ophiomyia phaseoli* that attack much the same legumes in Asia. *Melanagromyza* (= *Agromyza*) *obtusa* is widely distributed in India as a pest of the developing seeds of chick and pigeon peas. The stem miners *M. sojae* and *M. dolichostigma* are pests of soybean in Indonesia, Japan and Taiwan and damage French beans and cowpeas in Sri Lanka and East Africa (Singh and van Emden 1979).

Biology

The adult *O. phaseoli* is a small fly (females 2.2 mm and males 1.9 mm in length), shiny black in colour except for legs, antennae and wing veins, which are light brown (Abul-Nasser and Assem 1966). Females generally oviposit in bright sunlight in the upper surface of the cotyledons (soybeans) or young leaves of its many hosts, laying from 100 to 300 eggs during a 2–week period (Otanes y Quesales 1918). Not all ovipositor punctures receive an egg, many provide sap which the females ingest (Goot 1930). On hatching from the egg after 2 to 4 days, the young larva forms a short leaf mine before tunneling into the nearest vein. Next the petiole is mined and the larva then moves down the stem (Taylor 1958). In young plants the main feeding takes place in the lower layers of the stem and the tap root may be penetrated. When larvae are numerous, some feed more deeply inside the stem and higher up in the plant.

The larval and pupal stages occupy 7 to 10 days and 9 to 10 days respectively, resulting in a life cycle of about 3 weeks (Taylor 1958; Ooi 1988). However, the life cycle may be as short as 17 days in the field in Malaysia (Khoo et al. 1991) and in the laboratory in India at 24° to 31°C as short as 11 days (Singh et al. 1991). At the other end of the scale, at higher altitudes in Java, the larval stage can be extended from 17 to 22 days and the pupal stage from 13 to 20 days (Goot 1930). Pupation occurs head upwards beneath the epidermis and generally near the base of the stem (Greathead 1969). In older plants, larvae may pupate at the base of the petioles.

Talekar and Lee (1989) have developed a method for mass rearing bean fly on newly-germinated soybean cotyledons, permitting one person to produce 2 000 adults per day.

Host plants

Bean fly is known to attack at least 40 plant species. Most of its important hosts belong to the legume tribe Phaseoleae and particularly to the genus *Phaseolus*. The very susceptible *P. vulgaris* (French, kidney, haricot, runner or snap bean) is of Central American origin as are several other economic species of *Phaseolus*. However, from the point of view of the possible origin of *O. phaseoli* in Asia, all of the Asiatic species formerly placed in the genus *Phaseolus* have now been placed in the genus *Vigna* (Verdcourt 1970) and it is relevant that a number of important *Vigna* species are believed to have originated in India or nearby (Purseglove 1968). These include *V. aconitifolia* (moth bean), *V. aurea* (green or golden gram, mung bean) *V. calcarata* (rice bean) and *V. mungo* (black gram, urd bean). Other important hosts include *Cajanus cajan* (pigeon pea: origin Africa); *Glycine* *max* (soybean: southern China); *Lablab niger* (= *Dolichos lablab*) (hyacinth bean: India); *Pisum sativum* (pea: southwestern Asia); and *Vigna unguiculata* (cowpea: Africa) (Purseglove 1968; Spencer 1973). Wild hosts include *Canavalia ensiformis*, *Crotalaria juncea*, *C. laburnifolia*, *C. mucronata*, *Macroptilium atropurpureum*, *M. lathryoides*, *Phaseolus panduratus*, *P. semierectus* and *Vigna radiata* (Goot 1930; Kleinschmidt 1970; Spencer 1973; Abate 1991).

There is a large variation in susceptibility between different cultivars of susceptible species. This variation affords an important opportunity to select cultivars that suffer comparatively little damage and is being extensively investigated (e.g. Annappan et al. 1984, Gill and Singh 1988; AVRDC 1990, Talekar and Hu 1993; Talekar and Tengkano 1993; Gupta et al. 1995). Both morphological and chemical characteristics are involved (Chiang and Norris 1983).

Damage

O. phaseoli can be a limiting factor in the cultivation of susceptible legumes in Southeast Asia and most other regions where it occurs. Spencer (1973) and many other authors consider it to be one of the most serious of all agromyzid pests. Losses of 50% to 100% of crops are reported from many parts of the world, and are particularly heavy under dry conditions.

Although some leaves may wilt as a result of mining and petiole tunnelling, most damage results from destruction of tissue at the junction of the stem and root. When damage is limited, plants may survive by forming adventitious roots (e.g. with *P. vulgaris* and soybeans) and produce a limited crop. However, seedlings most frequently die. Plants that do not respond rapidly to root damage and develop adventitious roots are liable to break off at ground level during windy periods. When infestations are heavy, the aggregation of puparia within the stem results in it swelling, splitting open and rotting. De Meijere (1922) reported that young plants in Sumatra generally died when they contained 10 to 20 larvae. In Egypt, 25 larvae and pupae have been found in a single bean plant (Hassan 1947) and as many as 320 in a cowpea plant (Abul-Nasr and Assem 1966).

Seed treatments or post emergence sprays with broad spectrum insecticides have been used to control *O. phaseoli* but, *inter alia*, they undoubtedly have serious adverse effects on its parasitoids. Useful control has been obtained by intercropping, the use of resistant varieties, adjusting planting dates, crop rotation and other cultural methods such as planting into rice stubble or covering the newly sown areas with rice straw. It is clear, however, that, in areas where effective parasitoids are already present, these can play an important role in minimising bean fly damage if not interfered with by insecticides.

Natural enemies

More than 50 parasitic Hymenoptera have been reported from bean fly (Table 4.13.1), almost all emerging from pupae, arising from eggs laid in host larvae. No egg parasitoids are known and no dipterous parasitoids have been recorded. Although figures for percent parasitisation are unavailable from many countries where bean fly occurs, the levels recorded are generally unimpressive, often less than 30%. The outstanding exception is the 90% or more, often produced by the braconid *Opius phaseoli* in East Africa and Ethiopia (Greathead 1969; Abate 1991) and similar levels from *Opius phaseoli* and *Eurytoma* sp. in the Agra region of India (Singh 1982).

AUSTRALIA

Although Tryon (1895), who described *Ophiomyia phaseoli* from Queensland specimens, believed it to be native to Australia, it has never been recorded extensively from indigenous plants (Kleinschmidt 1970), so is unlikely to have evolved there. Twelve parasitoids (two of them possibly hyperparasitoids) (Table 4.13.1) emerged from *O. phaseoli* pupae taken mainly from cowpea (*Vigna unguiculata*). A later re-examination of Australasian Chalcidoidea by Bouček (1988) indicates that only 11 species were actually involved and none were hyperparasitoids. Bouček (1988) lists one additional parasitoid, the eurytomid *Plutarchia bicarinativentris,* which also occurs in Papua New Guinea. The braconid *Opius oleracei,* which attacks bean fly, has also been recorded from the widespread agromyzid *Chromatomyia horticola* (= *Phytomyza atricornis*).

EAST AFRICA

Ophiomyia phaseoli was not reported in Uganda until the 1920s, Tanzania until 1937 and Kenya until 1939. It occurs in close association with *Ophiomyia spencerella* and also with *O. centrosematis*, a species which is known also from Indonesia.

The bean fly is very heavily attacked in all climatic zones by the braconid *Opius phaseoli* (usually of the order of 70% to 90% and even up to 94.4% parasitisation), and relatively lightly (3% to 9%) by *Opius importatus*, by a polyphagous pteromalid near *Herbertia* sp. (less than 1%) and by an assemblage of chalcidoids. Puparia are also consumed by ants. Three wasps found in small numbers were considered to be hyperparasitoids, namely *Norbanus* sp. (Pteromalidae), *Eupelmus* sp. nr *australiensis* (= *E.* sp. nr *popa*) (Eupelmidae) and *Pediobius* sp. (Eulophidae). In spite of the heavy parasitisation by *Opius phaseoli*, sufficient bean flies survive in some seasons to cause heavy infestations of plantings. These parasitoids are thus, at times, unable to prevent economic damage (Greathead 1969).

Table 4.13.1 Natural enemies of *Ophiomyia phaseoli*

Species	Country	Reference
HYMENOPTERA		
BRACONIDAE		
Fopius sp.	Thailand	Burikam 1978; Burikam & Napompeth 1979, Napompeth 1994
Opius importatus	East Africa	Greathead 1969, 1975
	Hawaii	Raros 1975
*Opius ?liogaster**	Mauritius	Moutia 1932
	Zimbabwe	Jack 1913; Taylor 1958
Opius oleracei	Australia	Kleinschmidt 1970
Opius phaseoli	Botswana	Greathead 1969
	East Africa	Greathead 1969
	Ethiopia	Abate 1991; Greathead 1969
	Hawaii	Davis 1971, 1972; Fischer 1971a; Greathead 1975; Raros 1975
	India	Fischer 1963; Ipe 1987
	Madagascar	Greathead 1969
	Malawi	Letourneau 1994
	Mauritius	Greathead 1969
	Philippines	Fischer 1971b
	Taiwan	N.S. Talekar pers. comm. 1994
	Zimbabwe	Greathead 1969
Opius sp.	Taiwan	Chu & Chou 1965
CHALCIDIDAE		
1.	East Africa	Greathead 1969
2.	Sri Lanka	Rutherford 1914b
3.	Zimbabwe	Jack 1913

* probably *Opius phaseoli* (Fischer 1971a)

Table 4.13.1 (cont'd) Natural enemies of *Ophiomyia phaseoli*

Species	Country	Reference
HYMENOPTERA		
CYNIPIDAE		
Cynipoide sp.	Indonesia	Goot 1930
Eucoilidea sp.	Taiwan	Chu & Chou 1965
Unidentified	Thailand	Burikam 1978
EULOPHIDAE		
Aprostocetus sp.	Ethiopia	Abate 1991
Chrysonotomyia douglasi	Australia	Bouček 1988; Kleinschmidt 1970
Chrysonotomyia sp. nr *erythraea*	Ethiopia	Abate 1991
Chrysonotomyia formosa	Ethiopia	Abate 1991
Chrysonotomyia sp.	Australia	Dodd 1917
Cirrospilus sp.	Ethiopia	Abate 1991
Euderus sp.	Thailand	Burikam 1978; Napompeth 1994
Hemiptarsenus varicornis	Australia	Dodd 1917; Kleinschmidt 1970; Bouček 1988
Hemiptarsenus sp.	Australia	Kleinschmidt 1970
	Philippines	Litsinger 1987
Meruana liriomyzae	Ethiopia	Abate 1991
Pediobius acantha	Ethiopia	Abate 1991
Pediobius sp.	East Africa	Greathead 1969
Tetrastichus sp.	India	Gangrade 1974; Ipe 1987
Unidentified	Hawaii	Raros 1975

Table 4.13.1 (cont'd) Natural enemies of *Ophiomyia phaseoli*

Species	Country	Reference
HYMENOPTERA		
EUPELMIDAE		
Eupelmus ?australiensis	Ethiopia, East Africa	Greathead 1969; Abate 1991
Eupelmus grayi	Australia	Kleinschmidt 1990
Eupelmus sp. nr *urozonus*	Egypt	Abul-Nasr & Assem 1968
	Ethiopia	Abate 1991
Eupelmus sp.	Australia	Dodd 1917
	Ethiopia	Abate 1991
EURYTOMIDAE		
Eurytoma larvicola	Australia	Kleinschmidt 1970; Bouček 1988
	Egypt	Hassan 1947
Eurytoma poloni	Indonesia	Goot 1930
	Malaysia	Ho 1967; Yunus & Ho 1980
	Philippines	Otanes y Quesales 1918
Eurytoma spp. 2 ×	Australia	Dodd 1917; Kleinschmidt 1970
1 ×	Egypt	Abul-Nasr & Assem 1968
1 ×	Ethiopia	Abate 1991
1 ×	India	Singh 1982; Ipe 1987
1 ×	Indonesia	Goot 1930
1 ×	Taiwan	Chu & Chou 1965
Plutarchia sp.	Malaysia	Ooi 1973
	Philippines	Litsinger 1987
Plutarchia bicarinativentris	Australia, PNG	Dodd 1917; Bouček 1988
Plutarchia indefensa	Thailand	Burikam 1978

Table 4.13.1 (cont'd) Natural enemies of *Ophiomyia phaseoli*

Species	Country	Reference
HYMENOPTERA		
PTEROMALIDAE		
Callitula filicornis	Ethiopia	Abate 1991
Callitula viridicoxa	Australia, PNG	Bouček 1988; Kleinschmidt 1970
Callitula yasudi	Japan	Yasuda 1982
Chlorocytus sp.	India	Kundu 1985
Cryptoprymna sp.	Egypt	Abul-Nasr & Assem 1968
	Taiwan	Chu & Chou 1965
Halticoptera ?circulus	Ethiopia	Abate 1991
Halticoptera patellana	Hawaii	Greathead 1975; Raros 1975
Halticoptera sp.	Egypt	Abul-Nasr & Assem 1968
	Taiwan	Chu & Chou 1965
Herbertia sp.	Ethiopia	Abate 1991
	East Africa	Greathead 1969
Oxyharma subaenea	Australia	Dodd 1917; Kleinschmidt 1970
Polycystus propinquus	Sri Lanka	Waterston 1915
Polycystus sp.	India	Babu 1977
Sphegigaster brunneicornis	Ethiopia	Abate 1991
	India	Peter & Balasubramanian 1984
Sphegigaster hamygurivara	Japan	Yasuda 1982
Sphegigaster rugosa	India	Ipe 1987
	Sri Lanka	Waterston 1915

Table 4.13.1 (cont'd) Natural enemies of *Ophiomyia phaseoli*

Species	Country	Reference
HYMENOPTERA		
PTEROMALIDAE (cont'd)		
Sphegigaster stella	Malaysia	Ho 1967
	Philippines	Otanes y Quesales 1918
Sphegigaster stepicola	Ethiopia	Abate 1991
Sphegigaster voltairei	Australia, PNG	Dodd 1917; Kleinschmidt 1970; Bouček 1988
	Egypt	Hassan 1947
	Indonesia	Goot 1930
Sphegigaster sp.	Japan	Yasuda 1982
	Philippines	Litsinger 1987
	Taiwan	Chu & Chou 1965
Syntomopus shakespearei	Australia	Kleinschmidt 1970
Syntomopus sp.	Japan	Yasuda 1982
Unidentified	Thailand	Burikam 1978
TETRACAMPIDAE		
Epiclerus sp. nr *nomocerus*	Ethiopia	Abate 1991
A NEMATODE	East Africa	Greathead 1969
	Thailand	Burikam 1978

EGYPT

The bean fly was first reported in 1922, together with a parasitoid, later identified as *Sphegigaster voltairei* (= *Trigonogastra agromyzae*) (Pteromalidae). The eurytomid *Eurytoma larvicola* was also recorded (Hassan 1947). Later, Abul-Nasr and Assem (1968) recorded 5 parasitoid species emerging from bean fly puparia in the laboratory (Table 4.13.1), but no information was provided on their effectiveness.

ETHIOPIA

O. phaseoli was first reported in the early 1970s from *Phaseolus vulgaris* (French bean), *Vigna unguiculata* (cowpea) and soybean (*Glycine max*), although economic damage occurred only on French bean. The leguminous bush, *Crotalaria laburnifolia* was the only wild host which supported bean fly and its 17 species of parasitoids throughout the year (Table 4.13.1). Of these parasitoids, the pteromalids *Sphegigaster stepicola* and *S. brunneicornis* were the commonest species, accounting for up to 44.5% (average 26.2%) of total parasitisation on *Crotalaria*. Parasitisation by the braconid *Opius phaseoli* averaged a low 5.6% (range 0% to 23.2%) on *Crotalaria*, but it was the major parasitoid on French bean, accounting for over 87% of the total parasitisation. Abate (1991) concluded from this that the host plant plays an important role in *Ophiomyia phaseoli* population dynamics, although it remains to be shown whether this applies equally to the range of food legumes. It is, perhaps, relevant that the bean fly acts as a true leaf miner on *Crotalaria*, the larvae mining and eventually pupating within the leaf. This behaviour renders both stages more accessible to smaller parasitoids than when larvae are in the deeper tissues of a bean stem. The remaining 14 parasitoids recorded from Ethiopia (Table 4.13.1) were classified as very rare, (defined by Abate (1991) as equal to or less than 10% of total insect emergence) and together on average caused 9.6% mortality. Observations suggested that mortality of French bean seedlings caused by bean fly was much less severe in areas where the wild host, *Crotalaria*, occurred (14.8% in 1987 and 3.8% in 1988) than in its absence (39.1% in 1987 and 36.1% in 1988 (Abate 1991)). This is circumstantial evidence that natural enemies play an important part in regulating bean fly populations.

Negasi and Abate (1986) recorded a pteromalid *Cyrtogaster* sp. from *O. phaseoli* on French beans but, as this was not mentioned in the later, much more detailed paper on parasitoids by Abate (1991), it has not been included in Table 4.13.1.

HAWAII

Damaging populations of *O. phaseoli* built up rapidly and caused widespread damage to cultivated legumes after it was first recorded in 1968. The only parasitoid found attacking it at that stage was the pteromalid *Halticoptera patellana,* a polyphagous European parasite of agromyzids (Greathead 1975).

INDIA

Ophiomyia phaseoli is said not to cause as serious damage to food legumes in India as it does elsewhere, especially in Indonesia and East Africa (Talekar 1990).

The pteromalid *Chlorocytus* sp. was reported to parasitise 8% to 10% of *O. phaseoli* puparia infesting stems of soybean (*Glycine max*) in the New Delhi area (Kundu 1985). In Bangalore, the pteromalid *Sphegigaster brunneicornis*, which emerged from bean fly puparia in cowpea, was the only parasitoid recorded. The extent of parasitisation ranged from 16.7% in July to 85.5% in September, but this did not achieve adequate control because bean fly infestation rose from 12% in July to 68% in September (Peter and Balasubramanian 1984). Ipe (1987) recorded four parasitoids (a eurytomid, *Opius phaseoli*, *Tetrastichus* sp. and *Sphegigaster rugosa*) from Agra. He commented that *Ophiomyia phaseoli* infestations are kept under control by parasitoids and that the percentage of parasitisation reaches appreciable levels each season. Babu (1977) reported *Polycystus* sp. emerging from bean fly puparia and causing parasitisation ranging from 3.4% during February to 61% in August. However, the highest levels of attack are those recorded at Agra by Singh (1982) for *Opius phaseoli* and *Eurytoma* sp.. The parasitisation of bean fly infesting cowpea reached 46.2% during early October, rising to 94% by the end of November. From December to March these parasites effectively controlled *Ophiomyia phaseoli* populations infesting cowpea, garden pea and *Lablab niger* (Singh 1982).

It appears that the different species of bean fly parasitoids in India may not occur at all widely. Whether this is due to climatic limitations, sampling from different hosts, or overall inadequate sampling of populations remains to be determined.

INDONESIA

The most comprehensive account of the biology, hosts and parasitoids of bean fly in Indonesia was published in Dutch by Goot (1930). This was translated into English and republished in 1984 by the Asian Vegetable Research and Development Center Taiwan. A summary appears in Kalshoven (1981).

Three agromyzids are pests of soybean and some other economically important legumes in Indonesia: *Ophiomyia phaseoli* (by far the most important), the soybean stem borer *Melanagromyza sojae* (which bores into the pith of the stem, but seldom kills the plant) and the soybean top borer *M. dolichostigma* (which bores into the tops and causes stunting). The first two species have been known in Java since 1900.

Four bean fly parasitoids are known (Goot 1930: Table 4.13.1), but their combined effect is generally low, parasitisation averaging 5.1%, with a maximum of 42.4%. All species emerge from the host pupa. The most effective species is the pteromalid *Sphegigaster voltairei*, which comprised 59.1% of the parasitoids. It is also the most important parasitoid of *Melanagromyza sojae* and occasionally attacks *M. dolichostigma*. Next in importance is the cynipid *Cynipoide* sp., contributing 10.5%: it also attacks the two other agromyzids. Finally, *Eurytoma poloni* and *Eurytoma* sp. each contribute 0.2% to the total. Both are more frequently bred from the two other agromyzids.

MALAYSIA

The bean fly was first reported in Peninsular Malaysia in 1924 and is regarded as the most important pest of green gram (*Phaseolus aureus*). It can also cause serious damage to French bean and other legume crops. Two parasitoids, which also occur in the Philippines, are *Eurytoma poloni* (Eurytomidae) and *Sphegigaster* (= *Paratrigonogastra*) *stella* (Ho 1967). Ooi (1973) recorded the eurytomid *Plutarchia* sp.

PHILIPPINES

The bean fly was first noticed in 1912, but was thought at the time to have been present for some years. Two parasitoids are known, a more abundant *Eurytoma poloni* (Eurytomidae) and a less abundant *Sphegigaster stella*, in the ratio 60:47. Their joint parasitisation averaged 17% with a range from 6% to 49% (Otanes y Quesales 1918). *Opius phaseoli* was not recorded in this study.

SRI LANKA

Ophiomyia phaseoli was first recorded in 1901. Several unidentified species of hymenopterous parasitoids were bred by Rutherford (1914b) but, although they ‘no doubt do a considerable amount of good’, they were unable to keep the fly in check.

TAIWAN

Chu and Chou (1965) reported a braconid (*Opius* sp.), 4 pteromalids (*Cryptoprymna* sp., *Halticoptera* sp., *Sphegigaster* sp. and *Eucoilidea* sp.) and a eurytomid (*Eurytoma* sp.) parasitoid attacking bean fly infesting soybean and Rose et al. (1976) added another eurytomid (*Plutarchia* sp.).

Chiang et al. (1978) surveyed the parasitoids of three agromyzids infesting mungbean, namely *Ophiomyia phaseoli*, *O. centrosematis* and *Melanagromyza sojae*. Parasitisation fluctuated considerably, surpassing 60% during July, but declining to nearly 0% in December and January. Since there was a negative correlation between agromyzid populations and percent parasitisation it was concluded that parasitoids played a role in controlling agromyzid populations.

THAILAND

Surveys in several regions of Thailand for natural enemies of the major pest of soybean (*Ophiomyia phaseoli*) revealed 5 species of hymenopterous parasitoid and a nematode (Burikam 1978). The most important species were *Plutarchia indefensa* (Eurytomidae) and *Fopius* sp. (Braconidae). A eulophid, a pteromalid and a cynipid were less important (Burikam and Napompeth 1979; Napompeth 1994). Parasitisation by *P. indefensa* averaged 52.8% and two samples gave 7.5% and 5.9% for *Fopius* sp. (Burikam 1978), although Napompeth (1994) later considered the two species to be of equal importance. The cynipid wasp also attacked the bean stem miner *Melanagromyza sojae*. On one occasion pupae containing 20 to 50 nematodes were recorded, with a pupal parasitisation rate of 4.6% (Burikam 1978). A life table analysis showed that there was a density-dependent factor regulating bean fly populations (Burikam and Napompeth 1979).

Unless *Fopius* sp. (Braconidae) proves to be *Opius phaseoli* (Braconidae) (which is present in both India and the Philippines), it appears that *O. phaseoli* may not be widespread throughout Southeast Asia and may be well worth distributing more widely. The identity of the *Fopius* sp. is to be investigated (B. Napompeth pers. comm. 1994).

ZIMBABWE

Phaseolus spp. are the principal host crops damaged, but cowpeas (*Vigna sinensis*) and soybeans (*Glycine soja*) are also attacked. Plantings in late summer are usually only lightly infested and a braconid, identified as *Opius liogaster* (but quite possibly *O. phaseoli*), exercises effective control in most years (Taylor 1958). Earlier Jack (1913) had reported that a braconid larval parasitoid was ineffective in controlling bean fly although it was bred freely from *O. phaseoli* late in the season.

Attempts at biological control

The only introductions for biological control of bean fly (Table 4.13.2) have been of the two braconid parasitoids *Opius phaseoli* and *O. importatus* from Uganda to Hawaii in 1969 (Davis 1971, 1972; Greathead 1975; Funasaki et al. 1988) and of *O. phaseoli* from Hawaii to Taiwan in 1974–75 (N.S. Talekar pers comm. 1994). In Hawaii both species rapidly became established on Oahu and host density was soon markedly reduced. They were introduced to other islands and, by 1971, on Kauai 100% of bean flies sampled produced parasitoids: on Maui rates ranged from 25% to 83%. No differences in the incidence of parasitisation were detected when infestations on French bean and cowpea were compared. By 1973 *O. importatus* had become the dominant parasitoid and the polyphagous *Halticoptera patellana* (which was already present) was only rarely encountered (Greathead 1975). Surveys by Raros (1975) in 1973 and 1974 of three locations on Oahu revealed average parasitisation ranging from 8.3% to 23.5%, a result Talekar (1990) suggested might have been due to the heavy use of insecticides diminishing the earlier effectiveness of the parasitoids. In 1994 the bean fly was reported to be still a problem on young seedlings, so that farmers usually apply one or two insecticide sprays after seedlings emerge above the ground. Once the bean plant has developed a couple of leaves the fly is no longer a problem (W.C. Mitchell pers. comm.). *Opius phaseoli* was not recovered in Taiwan for the first two years after its introduction in 1974–75 from Hawaii, but there have been recent reports of its presence, in spite of the current excessive use of insecticides against bean fly (N.S. Talekar pers. comm. 1994).

Table 4.13.2 Introductions for the biological control of *Ophiomyia phaseoli*

Species	Origin	Liberated	Year	Result	Reference
BRACONIDAE					
Opius importatus	Uganda	Hawaii	1969	+	Fischer 1971a; Davis 1971, 1972; Funasaki et al. 1988; Greathead 1975; Raros 1975
Opius phaseoli	Uganda	Hawaii	1969	+	Fischer 1971a; Raros 1975
	Hawaii	Taiwan	1974–75	+	N.S. Talekar pers. comm. 1994

The more important parasitoids

The names of a number of species are now different from those used by earlier authors. To enable cross referencing with those used in Table 4.13.1, the older names are shown below, together with a summary of information available on the biology of the more important species.

Callitula viridicoxa (= Eurydinotellus viridicoxa = Polycystomyia beneficia) Hym.: Eurytomidae

Chrysonotomyia (= Achrysocharis) douglasi Hym.: Eulophidae

Chrysonotomyia ?erythraea Hym.: Eulophidae

Chrysonotomyia formosa Hym.: Eulophidae

The two latter species are widely distributed primary parasitoids attacking bean fly infesting *Crotalaria* in Ethiopia, parasitisation ranging from 0% to 8.7% (average 2.6%). *C. formosa* has also been recorded from *Liriomyza trifolii* infesting beans in Guam (Schreiner et al. 1986; Abate 1991).

Cynipoide sp. Hym.: Cynipoidea

This parasitoid has only been reported from Java, where Goot (1930) found, from 90 samplings between 1919 and 1923, that it constituted 40% of the parasitoids reared, although the level of parasitisation varied greatly. It also emerged from puparia of *Melanagromyza sojae* and *M. dolichostigma*. It occurred in both tropical lowland and cool highland conditions.

Euderus sp. Hym.: Eulophidae

A tentative assignation as *Euderus* ?sp. was made by Napompeth (1994) of the tiny eulophid recorded by Burikam (1978) and Burikam and Napompeth (1979). More than one parasitoid could be produced per bean fly host. The female parasitoid oviposited in the first instar host larva and pupation occurred during the host's third instar, either within or alongside the host. The pupal stage averaged 7 days (Burikam 1978).

Eurytoma poloni Hym.: Eurytomidae

This parasitoid has been recorded from Indonesia, Malaysia and the Philippines, but little is known of its biology. It was recorded only once in Java from *Ophiomyia phaseoli* so it is clearly not an important parasitoid of the bean fly there. In fact, it generally emerges from *Melanagromyza dolichostigma*. Adults live 22 to 28 days (Goot 1930).

Fopius sp. Hym.: Braconidae

This was referred to as *Biosteres* sp. by Burikam (1978) and Burikam and Napompeth (1979), but altered to *Fopius* sp. by Napompeth (1994). Adults emerged from bean fly puparia (one per host) and mated on the first day. Within two days 27 mature and immature eggs could be counted per female.

Two samples in August revealed parasitisation levels of 5.9% and 7.5% (Burikam 1978).

Halticoptera ?circulus Hym.: Pteromalidae

This is a widespread primary parasitoid of agromyzid leafminers in many parts of the world. It was recorded as very rare (≤ 10% parasitisation) on bean fly in Ethiopia (Abate 1991).

Hemiptarsenus varicornis (= Neodimmockia agromyzae and probably = Hemiptarsenus semialbicornis) Hym.: Eulophidae

This is a very widespread parasitoid of dipterous leaf miners, including *O. phaseoli* and *Liriomyza sativae*. It occurs throughout tropical and southern temperate countries of the eastern hemisphere. In Australia it is common in many places along the eastern and southeastern coast. It also occurs in New Zealand, New Caledonia, Fiji and Vanuatu; Malaysia, Sri Lanka, India, Pakistan and Saudi Arabia; Senegal, Ghana, Sudan, Ethiopia, Kenya and Tanzania (Bouček 1988).

Meruana liriomyzae Hym.: Eulophidae

This species was recorded as rare (≥10% parasitisation) on bean fly infesting *Crotalaria* in Ethiopia (Abate 1991). It is also known from *Liriomyza brassicae* in Mauritius, *L. sativae* in Mauritius and Réunion, from *L. trifolii* in Kenya, *Chromatomyia horticola* (= *Phytomyza atricornis*) in Ethiopia and South Africa, and from unidentified hosts in Australia and Zimbabwe (Bouček 1988; Abate 1991).

Opius importatus Hym.: Braconidae

This species was first recorded from East Africa as *Opius* sp. by Greathead (1975) and later described as *O. importatus* by Fischer (1971b). In nature, it is known only from East Africa and only from *Ophiomyia phaseoli*. When first taken between November 1967 and April 1968 it attained parasitisation levels of 3% to 9% (Greathead 1969). However, later samples taken in Uganda in 1971 contained nearly 50% of *O. importatus* (Greathead 1975).

The first instar larva was found in the third instar host larva and developed rapidly once the host pupated. Adults, that are similar in appearance to dark specimens of *Opius phaseoli*, emerge about 33 days after the appearance of the host plant above the soil. *O. importatus* was inadvertently included in shipments of *Opius phaseoli* to Hawaii, where it soon became the dominant parasitoid of *Ophiomyia phaseoli* (Greathead 1975).

Opius phaseoli (= O. melanagromyzae) Hym.: Braconidae

O. phaseoli was originally described from the Philippines (Manila) without a host by Ashmead (1904) as *Eurytenes nanus*. However, as this name was preoccupied, it was redescribed as *O. phaseoli* by Fischer (1963), who listed its host as *Ophiomyia phaseoli* and its distribution as India (Nagpur) and the Philippines. Later, Fischer (1966) listed it as a parasitoid of the leaf miner *Melanagromyza atomella* in India and Singh (1982) from *Melanagromyza sojae*. Both Singh (1982) and Ipe (1987), working in the area of Agra, considered it to be important in regulating bean fly populations there. No information is available on its presence or effectiveness elsewhere in Asia or Southeast Asia, except for the original record of a single female wasp from Manila (Ashmead 1904).

In East Africa, Greathead (1969, 1975) reported parasitisation levels of *Ophiomyia phaseoli* by *Opius phaseoli* that were frequently above 50%, and sometimes reached 94.4%. Levels of up to 10% on *Ophiomyia spencerella* were also recorded and *Opius phaseoli* was twice reared from *Ophiomyia centrosematis*. He concluded that *Opius phaseoli* was the chief biotic factor limiting the population of bean fly in East Africa. Nevertheless, he reported levels of only 38% parasitisation from 3 bean fly samples taken in Madagascar and only about 20% in Mauritius. He suggested that the latter result might be due to a different strain of the parasitoid or, perhaps, even a different species. In Ethiopia Abate (1991) reported over 93% parasitisation of bean fly on French bean, but much lower levels (average 5.6%) on a wild host *Crotalaria*.

One to five (but generally two or three) eggs are laid at a time, usually in first instar host larvae. Hatching occurs about 2 days later, soon after the host larva has moulted to the second instar. The first instar parasitoid larva grows, but does not moult until its host has pupated. Meanwhile, all except one *Opius* larva are suppressed. Development is rapid in the host pupa, the entire larval period lasting 9 to 10 days, leading to a prepupal period of 1 to 2 days and a pupal period (within the host puparium) of about 3 days (Raros 1975). In East Africa, the pupal period lasts a minimum of 4 days and adults commence emerging about 30 days after the appearance of the host plant above the ground (Greathead 1969). On average, males live 20 and females 23 days. Females mate a day after emergence and, following a preoviposition period of 1 to 2 days, may lay up to 358 eggs throughout life. First instar host larvae are preferred to second instar larvae (62.9:32.8) (Raros 1975). Other host stages are not attacked. Adult parasitoids feed on water droplets and host plant sap resulting from oviposition punctures made either by host adults or by female parasitoids. The male:female sex ratio was about 1:1.4 in Hawaii (Raros 1975).

Oxyharma (= Pterosema) subaenea Hym.: Pteromalidae

Plutarchia indefensa Hym.: Eurytomidae

This wasp was referred to by Burikam (1978) and Burikam and Napompeth (1979) as *Plutarchia* sp. Eggs are laid in third instar larvae of *Ophiomyia phaseoli*, usually at the posterior end. One or two eggs are laid per host and, on hatching after 2 to 3 days, one surviving larva remains in the first instar until the host has pupated. The larval stage lasts 5 to 7 days and the pupal stage (inside the host puparium) 7 to 8 days, giving a development period from egg to adult of 16 to 19 days. Adult males lived 4 to 19 days (average 11.5) and females 10 to 25 days (average 16.9), during which 6 to 14 eggs developed per day (Burikam 1978).

Pteromalid Hym.: Pteromalidae

The unidentified pteromalid recorded from Thailand (Burikam 1978; Burikam and Napompeth 1979; Napompeth 1994) was found parasitising pupae of *O. phaseoli*. The female laid 1 or 2 eggs in the host puparium. These hatched in 2 days and, after 4 days larval development, pupation occurred within the host puparium. The pupal stage lasted 7 to 8 days, resulting in a life cycle of 12 to 14 days. Female wasps lived more than 2 weeks (Burikam 1978).

Sphegigaster brunneicornis Hym.: Pteromalidae

This species has been reported from Ethiopia (Abate 1991), India and Sri Lanka (Peter and Balasubramanian 1984). *O. phaseoli* is its only recorded host.

Sphegigaster (= Trigonogastra) rugosa Hym.: Pteromalidae

Sphegigaster (= Paratrigonogastra) stella Hym.: Pteromalidae

Sphegigaster stepicola Hym.: Pteromalidae

This species is known from *Ophiomyia phaseoli* in Ethiopia (Abate 1991) and from *Phytomyza albiceps* in southern Europe and India (Abate 1991). Combined parasitisation with *S. brunneicornis* of bean fly on *Crotalaria* in Ethiopia ranged from 3.1% to 44.4% (average 26.2%), of which *S. stepicola* accounted for nearly 72% (Abate 1991).

Sphegigaster voltairei (= Sphegigaster agromyzae = Trigonogastra agromyzae) Hym.: Pteromalidae

This species is recorded from Australia, Papua New Guinea, Egypt and especially Indonesia where Goot (1930) reported that, on average, it comprised 60% of emergences from parasitised puparia and that it could be kept alive from 30 to 48 days. It was also the most important parasitoid of *Melanagromyza sojae* and was bred several times from *M. dolichostigma*.

Syntomopus (= Merismorella) shakespearei Hym.: Pteromalidae

Comment

Although *O. phaseoli* occurs in Africa, it now seems unlikely that it evolved there. It was reported in Uganda as recently as the 1920s, in Tanzania in 1937 and in Kenya in 1939. In East Africa, it occurs in close association with the very similar *O. spencerella*, which is generally the dominant species (Greathead 1969). Spencer (1973) postulated that *O. spencerella* evolved in Africa and *O. phaseoli* in Asia. The latter subsequently arrived in Africa to occupy a similar niche in much the same host plants, but isolated reproductively from *O. spencerella*. It is interesting that the major natural enemy of *Ophiomyia phaseoli* in East Africa is the braconid *Opius phaseoli*, which also occurs in India, whereas that of *Ophiomyia spencerella* is a cynipid *Eucoilidea* sp.. Although *Eucoilidea* sp. is not restricted to *Ophiomyia spencerella*, this species nevertheless does not attack *Ophiomyia phaseoli*.

In spite of Asia (and probably India) being nominated as the probable centre of origin of *Ophiomyia phaseoli*, it is interesting that bean fly is even more heavily parasitised in East Africa and Ethiopia than anywhere else — and by 2 braconid parasitoids, one of which is native to the latter regions. These are *Opius phaseoli* and *O. importatus*. *Opius phaseoli* was described from a single female from Manila, but the absence of records of it attacking *Ophiomyia phaseoli* there or elsewhere in Southeast Asia raises doubts that it is native to Southeast Asia.

The rapid control of *Ophiomyia phaseoli* in Hawaii following the introduction of *Opius phaseoli* and *O. importatus* (the latter soon becoming the dominant species) demonstrates that, under favourable circumstances, biological control alone can produce valuable results. It seems probable that this success would be repeated, at least in other Pacific island nations.

In the far more complex ecological environment in Southeast Asia extrapolation from experience in Hawaii is more risky. It is probable that the other components of integrated pest management (varietal resistance, cultural methods, rational pesticide use, etc.) will all be required to supplement the reduction in bean fly density that can be brought about by parasitoids. Nevertheless, any substantial decrease in bean fly populations that can be achieved by introducing additional effective parasitoids is likely to be a valuable contribution towards reduced crop losses.

Table 14

Table 14 shows for weeds what **Table 4** did for invertebrates in relation to the top 10 entries. Since no information was available on the relative rating for the five weeds nominated by Tokelau (shown by an asterisk), each was allocated the median value of 5. The ranking order is only given for species that attain an aggregated value of 10 or more. These are arranged in descending order of importance in **Table 15**.

Table 14 The relative importance given to the top 10 weeds of agriculture (72 species) of each country in the southern and western Pacific .

Name	Family	Col	Fij	FrP	FSM	Gua	Kir	Mar	NCa	Niu	PNG	ASa	WSa	Sol	Tok	Ton	Tuv	Van	W.F.	No. *	Rating	Order
Acacia farnesiana	Mimosaceae								4											1	7	
Acacia nilotica	Mimosaceae																					
Achyranthes aspera	Amaranthaceae																					
Agave americana	Agavaceae																					
Ageratum conyzoides	Asteraceae								2											1	9	
Alternanthera sessilis	Amaranthaceae																					
Amaranthus interruptus	Amaranthaceae																					
Amaranthus spinosus	Amaranthaceae																					
Amaranthus viridis (= A. gracilis)	Amaranthaceae																					
Antigonon leptopus	Polygonaceae					2														1	9	
Argemone mexicana (= A. americana)	Papaveraceae																					
Bidens alba, Bidens pilosa	Asteraceae			7	9	3			8			1							9	6	29	6 =
Blechum pyrimidatum (= B. brownei)	Acanthaceae											8								1	3	
Brachiaria mutica	Poaceae	8																		1	3	
Brachiaria reptans	Poaceae																					
Brachiaria subquadripara	Poaceae																					
Broussonetia papyrifera	Urticaceae													4						1	7	
Canavalia rosea	Fabaceae																		10	1	1	
Cardiospermum halicacabum	Sapindaceae	2																		1	9	
Cassytha filiformis	Lauraceae					7	2										6			3	18	13
Cecropia peltata	Euphorbiaceae			5																1	6	
Cenchrus echinatus	Poaceae						3								*				3	3	21	12
Chamaesyce (= Euphorbia) hirta	Euphorbiaceae	10			10										*					3	7	45=
Chloris barbata	Poaceae																					

Table 14 (cont'd) The relative importance given to the top 10 weeds of agriculture (72 species) of each country in the southern and western Pacific .

Name	Family	Col	Fij	FrP	FSM	Gua	Kir	Mar	NCa	Niu	PNG	ASa	WSa	Sol	Tok	Ton	Tuv	Van	W.F.	No. *	Rating	Order
Chromolaena odorata	Asteraceae				3						7									2	12	21=
Clerodendrum chinense (= *C. philippinum)*	Verbenaceae		2							3			1							3	27	9
Clidemia hirta	Melastomataceae											4							5	2	13	20
Coccinia grandis	Cucurbitaceae					5														1	6	
Commelina benghalensis	Commelinaceae															2				1	9	
Commelina diffusa	Commelinaceae	9										6								2	7	
Cordia subcordata	Boraginaceae																					
Crassocephalum crepidoides	Asteraceae									10										1	1	
Crotolaria pallida	Fabaceae																					
Crotolaria retusa	Fabaceae																					
Cuphea carthagenensis	Lythraceae																					
Cynodon dactylon	Poaceae																					
Cyperus rotundus	Cyperaceae	7	6	8	7	1			1		5		4	1		1	1	9	1	13	98	1
Dactyloctenium aegyptium	Poaceae																					
Desmodium incanum	Fabaceae																					
Digitaria ciliaris	Poaceae																					
Digitaria eriantha (= *D. decumbens)*	Poaceae																					
Digitaria insularis	Poaceae									10										1	1	
Digitaria setigera	Poaceae																					
Echinochloa colona	Poaceae																					
Echinochloa crus-galli	Poaceae																		6	1	5	
Eichhornia crassipes	Pontederiaceae		7								1			2				8		4	26	10
Eleocharis geniculata	Cyperaceae																					
Elephantopus mollis (= *E. scaber)*	Asteraceae			9										3						2	10	26=
Eleusine indica	Poaceae				8	9			6				10		*		10		7	7	21	11
Eleutheranthera ruderalis	Asteraceae																					

Table 14 (cont'd) The relative importance given to the top 10 weeds of agriculture (72 species) of each country in the southern and western Pacific .

Name	Family	Col	Fij	FrP	FSM	Gua	Kir	Mar	NCa	Niu	PNG	ASa	WSa	Sol	Tok	Ton	Tuv	Van	W.F.	No. *	Rating	Order
Emilia sonchifolia	Asteraceae																					
Eragrostis tenella	Poaceae																					
Euphorbia heterophylla (= *E. geniculata)*	Euphorbiaceae					8														1	3	
Fimbristylis cymosa (= *F. atollensis)*	Cyperaceae																7			1	4	
Fimbristylis dichotoma	Cyperaceae																					
Fimbristylis miliacea	Cyperaceae																					
Guettarda speciosa	Cyperaceae						4								*					2	12	21=
Hydrilla verticillata	Hydrocharitaceae																					
Hyptis pectinata	Lamiaceae												3							1	8	
Imperata conferta (= *I. cylindrica)*	Poaceae								10											1	1	
Indigofera suffruticosa	Fabaceae																					
Ipomoea macrantha	Convolvulaceae														*		5			2	11	23 =
Ischaemum spp.	Poaceae		10																	1	1	
Jatropha gossypifolia	Euphorbiaceae																					
Kyllinga brevifolia	Cyperaceae																					
Kyllinga nemoralis	Cyperaceae																					
Kyllinga polyphylla	Cyperaceae		3										9							2	10	26 =
Lantana camara	Verbenaceae		8	6	6				7	1						6		3		7	40	4
Leucaena leucocephala	Mimosaceae			2									8			10				3	13	19
Ludwigia octovalvis (= *Jussiaea suffruticosa)*	Onagraceae						5										2			2	15	15 =
Macroptilium lathyroides	Fabaceae																					
Melaleuca quinquenervia	Myrtaceae																					
Merremia peltata	Convolvulaceae				1													10		2	11	23 =
Miconia calvescens	Melastomataceae			1																1	10	28 =
Mikania micrantha	Asteraceae	6	9			4				8	6	2	6	7			8	5		10	49	3
Mimosa invisa	Mimosaceae	1	1	3	4					7	4	3	7	5				2		10	73	2

Table 14 (cont'd) The relative importance given to the top 10 weeds of agriculture (72 species) of each country in the southern and western Pacific .

Name	Family	Col	Fij	FrP	FSM	Gua	Kir	Mar	NCa	Niu	PNG	ASa	WSa	Sol	Tok	Ton	Tuv	Van	W.F.	No. *	Rating	Order
Mimosa pigra	Mimosaceae										3									1	8	
Mimosa pudica	Mimosaceae				5	6				4				6		9			2	6	40	5
Miscanthus floridulus	Poaceae																					
Momordica charantia	Cucurbitaceae																					
Monochoria hastata	Pontederiaceae																					
Nephrolepis hirsutula	Davalliaceae																					
Ocimum gratissimum	Lamiaceae								5											1	6	
Oxalis corniculata	Oxalidaceae																					
Panicum maximum	Poaceae															3				1	5	
Parthenium hysterophorus	Asteraceae																	7		1	4	
Paspalum conjugatum	Poaceae												5						8	2	9	
Paspalum dilatatum	Poaceae																					
Paspalum paniculatum	Poaceae																					
Paspalum vaginatum	Poaceae											5								1	6	
Passiflora foetida	Passifloraceae																					
Passiflora maliformis	Passifloraceae																					
Pennisetum polystachion	Poaceae				2															1	9	
Pennisetum purpureum	Poaceae									2										1	9	
Phyllanthus amarus	Euphorbiaceae																					
Physalis angulata	Solanaceae																					
Pistia stratiotes	Araceae																					
Pluchea indica	Asteraceae																					
Portulaca oleracea	Portulacaceae	5															3			2	14	18
Premna obtusifolia (= *P. serratifolia)*	Verbenaceae						1													1	10	28 =
Pseudelephantopus spicatus	Asteraceae																					
Psidium guajava	Myrtaceae								3											1	8	
Ricinus communis	Euphorbiaceae						6													1	5	

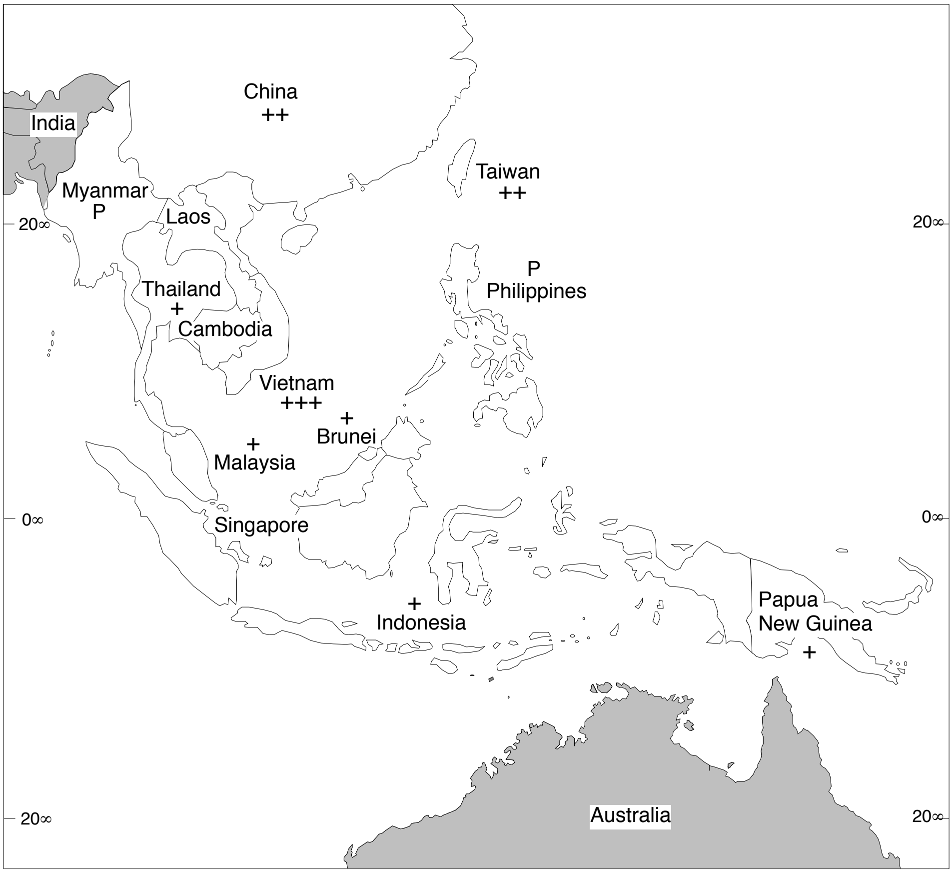
Table 14 (cont'd) The relative importance given to the top 10 weeds of agriculture (72 species) of each country in the southern and western Pacific .

Name	Family	Col	Fij	FrP	FSM	Gua	Kir	Mar	NCa	Niu	PNG	ASa	WSa	Sol	Tok	Ton	Tuv	Van	W.F.	No. *	Rating	Order
Rottboellia cochinchinensis	Poaceae		5								2									2	15	15 =
Ruellia prostrata	Acanthaceae																					
Salvinia molesta	Salviniaceae																					
Scaveola sericea (= S. taccada)	Goodeniaceae						7										4			2	11	23 =
Schinus terebinthifolius	Anacardiaceae																					
Senna (= Cassia) occidentalis	Caesalpinaceae																					
Senna (= Cassia) tora	Caesalpinaceae															8		6		2	8	
Sida acuta	Malvaceae								9		9			8				4		4	14	17
Sida cordifolia	Malvaceae																					
Sida fallax	Malvaceae						8													1	3	
Sida rhombifolia	Malvaceae										8	9				7				3	9	
Solanum americanum (= S. nigrum)	Solanaceae																					
Solanum mauritianum	Solanaceae																					
Solanum torvum	Solanaceae												2	9		5		1		4	27	8
Sonchus oleraceus	Asteraceae																					
Sorghum arundinaceum (= S. verticilliflorum)	Poaceae	4																		1	7	
Sorghum halepense	Poaceae									9						4			4	3	16	14
Sorghum sudanense	Poaceae											10								1	1	
Spathodea companulata	Bignoniaceae		4																	1	7	
Sphaerostaphanos invisus	Thelypteridaceae																					
Sphaerostephanos unitus	Thelypteridaceae																					
Stachytarpheta cayennensis	Verbenaceae																					
Stachytarpheta jamaicensis	Verbenaceae					10				6										2	6	

Table 14 (cont'd) The relative importance given to the top 10 weeds of agriculture (72 species) of each country in the southern and western Pacific .

Name	Family	Col	Fij	FrP	FSM	Gua	Kir	Mar	NCa	Niu	PNG	ASa	WSa	Sol	Tok	Ton	Tuv	Van	W.F.	No. *	Rating	Order
Stachytarpheta urticifolia	Verbenaceae			10						5		7		10						4	12	20
Stictocardia tiliifolia	Convolvulaceae																					
Syndrella nodiflora	Asteraceae																					
Tecoma stans	Bignoniaceae			4																1	7	
Themeda quadrivalis	Poaceae																					
Tournefortia (= Messerschmidia) argentea	Boraginaceae						9													1	2	
Tribulus cistoides	Zygophyllaceae																					
Tridax procumbens	Asteraceae																					
Triumfetta rhomboidea	Tiliaceae																					
Urena lobata	Malvaceae																					
Vernonia cinerea	Asteraceae																9			1	2	
Vigna marina	Fabaceae						10													1	1	
Vitex trifolia	Verbenaceae																					
Wedelia trilobata	Asteraceae																					
Xanthium pungens	Asteraceae	3																		1	8	

4.15 *Planococcus citri*



It is speculated that the citrus mealybug *Planococcus citri* is of south China origin, although it now occurs very widely in tropical, subtropical and temperate regions wherever citrus is grown. Like other mealybugs, it is attacked by a large number of non-specific predators, especially Coccinellidae, but also Chrysopidae. These consume vast numbers of prey when mealybugs are abundant, but often do not reduce host numbers to a level at which economic injury no longer occurs. There are several specific or near specific encyrtid parasitoids that are capable of lowering *P. citri* populations below the economic threshold. These are worth serious consideration for introduction to regions where they do not already occur: *Leptomastix dactylopii* (of Brazilian origin), *Leptomastidea abnormis* and *Anagyrus pseudococci* (of Mediterranean origin) and *Coccidoxenoides peregrinus* (of south China or Indian origin). In some situations (particularly cooler conditions) augmentative releases are necessary if the use of insecticides is to be avoided.

Planococcus citri (Risso)

Hemiptera, Pseudococcidae

citrus mealybug

This account draws heavily on that of Bartlett (1978) and CABI abstracts since then.

Rating

Southeast Asia			China	Southern and Western Pacific		
	+++	Viet				
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	+	Thai, Msia, Brun, Indo			+	Cook Is, PNG, Tong, Sam
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Origin

P. citri was described from citrus in southern France (Risso 1813), but Bartlett (1978) speculates that it is of Chinese origin. However, the fact that it is a widespread and important pest of citrus in 11 of the 14 provinces of southern China casts some doubt on this view (Li Li-ying et al. 1997).

Distribution

The citrus mealybug is extremely widespread, being present in almost all tropical, subtropical and temperate regions of the world and in many glasshouses in cooler parts. Other species of *Planococcus* have often been confused with it, including *P. pacificus* (which does not occur in the Mediterranean but is common in the Pacific: Cox 1981, 1989), *P. ficus* (restricted to fig, pomegranate and grape in the Mediterranean: Tranfaglia 1979; Cox and Freeston 1985; Cox and Ben-Dov 1986) and *P. kenyae* (on *Coffea* in Kenya: Le Pelley 1943a,b). However, their hymenopterous parasitoids discriminate between *P. citri* and *P. kenyae* and biological control fails when the incorrect parasites are used (Rosen and De Bach 1977). The collection data of Pacific specimens suggest that *P. citri* is a recent introduction there (Williams 1982). There may well be different strains of *P. citri*. For example, in Brazil it is rarely found on citrus, but is common on other plants (Compere 1939); and in South Africa it is common on citrus, but seldom found on grape vines (De Lotto 1975).

Biology

P. citri shows considerable morphological variation when reared under different environmental conditions. Small specimens, produced by rearing at high temperatures (32°C), have smaller appendages and lower numbers of cuticular structures than those reared between 17° and 25°C (Cox 1981).

Adult females are oval, flat and yellow to yellowish brown, with a barely visible dorsal line under their waxy covering. Along the edge of the wax cover there are short waxy protruberances, the longest of which are at the posterior end. Yellow eggs are deposited in an ovisac of wax threads and young nymphs are lemon-yellow in colour. Females are oviparous, and possibly parthenogenetic when males are not available.

The development time varies from 20 to 40 days, depending upon the host plant and temperature. The pre-oviposition period is 7 to 10 days, eggs hatch in 3 to 6 days and, 300 to 500 eggs are laid per female. Additional details of developmental periods on coffee and potato sprouts are provided by Bartlett and Lloyd (1958) and Martinez and Suris (1987a, b). Eggs, nymphs and adults are capable of overwintering. There are 3 instars for female nymphs and 2 for male nymphs which then form a waxy puparium. In warm areas there are normally 4 or 5 overlapping generations per year (Bartlett 1978; Kalshoven 1981), but about double this number under laboratory conditions (Gray 1954).

P. citri can be readily reared in the laboratory on potato sprouts (Fisher 1963; Martinez and Suris 1987b), lemons and butternut pumpkins (Samways and Mapp 1983) and a crawler-proof cage has been described (Rao 1989). Dispersal of crawlers is brought about by wind, rain and ants.

Until mated, females secrete a pheromone continously to attract males: (1R-*cis*) (3-isopropenyl-2-2-dimethylcyclobutyl) methyl acetate (Dunkelblum et al. 1986). Synthetic analogues have been tested to reduce populations (Rotundo and Tremblay 1974, 1980, 1982; Rotundo et al. 1979).

Host plants

P. citri has an extremely wide host range, attacking almost every flowering plant and some grasses as well. It is most frequently reported from citrus, and occurs commonly on other fruit trees and grape vines. Other important crops include banana, tobacco, coffee, fig, mango, cocoa, date, casssava, macadamia, passionfruit and cut flowers.

Damage

The citrus mealybug is a widespread and severe pest of citrus; also, in temperate areas, of grape vines and, in tropical areas, of coffee and mango. *P. citri* is the most injurious of 6 species of mealybug in the Mediterranean basin, the damage caused, especially to fruit, being so severe in France that the economic threshold is 2% infestation (Panis 1979). In glasshouses its hosts include bulbs, ferns, gardenias and other ornamentals. It is generally found on the aerial parts of plants, although a root form occurs. Tender growing tips, flower buds and young fruit clusters are favoured aggregating points. Excessive removal of sap by large numbers of mealybugs leads to wilting and death of shoots and flower buds and to drop of fruit. Furthermore, there is abundant growth of sooty moulds on the large amounts of honeydew produced, which may render produce unmarketable. *P. citri* becomes most abundant during the dry season.

P. citri has been incriminated in the transmission of viruses of grape vines, cocoa, cucumber, taro and tobacco (Carpenter et al. 1976; Kenten and Woods 1976; Bartlett 1978; Legg and Lockwood 1981; Dufour 1988; Agran et al. 1990; Pedroso et al. 1991).

Natural enemies

The citrus mealybug, like other mealybugs, is attacked by a wide range of naturally occurring predators, particularly coccinellid beetles and lacewings (Table 4.15.1). Many of these have a wide to very wide host range and thus are less likely nowadays than in the past to be regarded as suitable to introduce to new environments. Nevertheless, those reported in recent literature are recorded, but no attempt has been made to provide an exhaustive list.

The coccinellid predator *Cryplolaemus mountrouzieri* in particular has been very extensively distributed in the past, often with moderate to good success, against a variety of mealybug, scale and aphid pests, including *P. citri*. *C. montrouzieri* and some of the other predators play an important role in greatly reducing the abundance of high populations. In general, however, their searching ability is poor and prey are missed when population densities fall, so their action must generally be supplemented by parasitoids or other means for effective control.

Table 4.15.1 Predators of *Planococcus citri*

Species	Country	Reference
HEMIPTERA		
ANTHOCORIDAE		
Orius minutus	Turkey	Soylu & Urel 1977
NEUROPTERA		
CHRYSOPIDAE		
Brinckochrysa (=*Chrysopa*) scelestes	India	Krishnamoorthy 1984
Chrysopa sp.	Australia	Murray 1978
	USA	Meyerdirk et al. 1982
Chrysoperla carnea	India	Krishnamoorthy & Mani 1989b
	Israel	Berlinger et al. 1979
	USSR	Niyazov 1969
Mallada (= Anisochrysa) basalis	India	Krishnamoorthy & Mani 1989b
Mallada boninensis	India	Krishnamoorthy & Mani 1989b
Odontochrysa (=*Chrysopa* =*Plesiochrysa*) *lacciperda*	India	Mani & Krishnamoorthy 1990
Oligochrysa lutea	Australia	Murray 1978, 1982
Sympherobius barberi	USA	Dean et al. 1971; Meyerdirk et al. 1979, 1982
Sympherobius sanctus	Turkey	Soylu & Urel 1977
COLEOPTERA		
COCCINELLIDAE		
Brumoides lineatus	China	Weng & Huang 1988
Brumus suturalis	Indonesia	Kalshoven 1981

Table 4.15.1 (cont'd) Predators of *Planococcus citri*

Species	Country	Reference
COLEOPTERA		
COCCINELLIDAE (cont'd)		
Chilocorus bipustulatus	Israel	Berlinger et al. 1979
	Turkey	Soylu & Urel 1977
Coccinella californica	California	Bartlett & Lloyd 1958
Coccinella transversalis (= *C. repanda*)	Indonesia	Kalshoven 1981
Coccinella semipunctata	USSR	Niyazov 1969
Cryptolaemus affinis	USA	Meyerdirk et al. 1979, 1982
	Papua New Guinea	Szent-Ivany 1963
Cryptolaemus montrouzieri	Easter Is	Ripa et al. 1995
	India	Chacko et al. 1978
	Mediterranean	Panis 1977
Diomus pumilio	Australia	Meyerdirk 1983
Exochomus flavipes	South Africa	Samways 1983
Exochomus flaviventris	Mediterranean	Kanika et al. 1993
Harmonia octomaculata	Australia	Murray 1978
Hyperaspis lateralis	California	Bartlett & Lloyd 1958
Hyperaspis polita	Turkey	Soylu & Urel 1977
Hyperaspis 2 × spp.	USSR	Niyazov 1969
		Bennett & Hughes 1959
Nephus (= *Scymnus) bipunctatus*	USSR	Niyazov 1969
Nephus (= *Scymnus*) *reunioni*	East Africa	Ershova & Orlinskii 1982
Pullus pallidicollis	India	Prakasan 1987
Scymnus (= *Nephus*) *includens*	Italy	Tranfaglia & Viggiani 1973
Scymnus apetzi	USSR	Niyazov 1969
Scymnus apiciflavus	Indonesia	Kalshoven 1981
Scymnus biguttatus	USSR	Niyazov 1969

Table 4.15.1 (cont'd) Predators of *Planococcus citri*

Species	Country	Reference
COLEOPTERA		
COCCINELLIDAE (cont'd)		
Scymnus binaevatus	South Africa	Smith 1923
Scymnus spp.	South Africa	Samways 1983
	Turkey	Soylu & Urel 1977
Scymnus roepkei	Indonesia	Kalshoven 1981
Scymnus sordidus	California	Bartlett & Lloyd 1958; Bennett & Hughes 1959
Scymnus subvillosus	USSR	Niyazov 1969
DIPTERA		
CECIDOMYIIDAE		
Coccidodiplosis smithi	Indonesia	Kalshoven 1981
Diadiplosis hirticornis	Japan	Yukawa 1978
Dicrodiplosis sp.	India	Chacko et al. 1977
Triommata coccidivora	India	Prakasan 1987
CHAMAEMYIIDAE		
Leucopis alticeps	USSR	Niyazov 1969
	Italy	Raspi & Bertolini 1993
Leucopis bella	California	Bartlett & Lloyd 1958
Leucopis silesiaca	Italy	Raspi & Bertolini 1993
CRYPTOCHETIDAE		
Cryptochetum sp.	India	Chacko et al. 1977
SYRPHIDAE		
Syrphus sp.	Australia	Murray 1982

Table 4.15.1 (cont'd) Predators of *Planococcus citri*

Species	Country	Reference
LEPIDOPTERA		
LYCAENIDAE		
Spalgis epius	India	Chacko et al. 1977; Mani & Krishnamoorthy 1990
HYMENOPTERA		
ENCYRTIDAE		
Achrysophagus sp.	Turkey	Soylu & Urel 1977
Anagyrus bohemani	Spain	Carrero 1980a
	India	Varma 1977
Anagyrus greeni	Indonesia	Kalshoven 1981
Anagyrus pseudococci	Italy	Viggiani 1975a
	Turkey	Soylu & Urel 1977
	USA	Meyerdirk et al. 1982
	USSR	Niyazov 1969
Anagyrus sp. nr *sawadai*	USA	Meyerdirk et al. 1982
Blepyrus insularis	India	Chacko et al. 1977
Blepyrus saccharicola	California	Bennett & Hughes 1959
Chrysoplatycerus splendens	USA	Bartlett & Lloyd 1958; Summy et al. 1986
Clausenia josefi	Mediterranean	Niyazov 1969
Coccidoxenoides (= Pauridia) peregrinus	China	Bartlett 1978
	India	Krishnamoorthy & Mani 1989a; Mani 1994
	Italy	Viggiani & Maresca 1973
	USA	Meyerdirk et al. 1978, 1979, 1982

Table 4.15.1 (cont'd) Predators of *Planococcus citri*

Species	Country	Reference
HYMENOPTERA		
ENCYRTIDAE (cont'd)		
Leptomastidea abnormis	Spain Turkey USA	Carrero 1980a Soylu & Urel 1977 Meyerdirk et al. 1979, 1982
Leptomastix dactylopii	Brazil India USA	Mani 1995 Mani 1995 Meyerdirk et al. 1978, 1979, 1982
Leptomastix nigrocoxalis	India	Prakasan & Kumar 1985
Leptomastix trilongifasciatus	India	Kalshoven 1981
Ophelosia crawfordi		Bartlett & Lloyd 1958
Pseudaphycus angelicus	California	Bartlett & Lloyd 1958
Pseudaphycus maculipennis	USSR	Sinadskii & Kozarzhevskaya 1980
Pseudaphycus perdignus		Bennett & Hughes 1959
Sympherobius barberi	USA	Meyerdirk et al. 1982
Timberlakia gilva	South Africa	Prinsloo 1982
PLATYGASTERIDAE		
Allotropa citri	China	Bartlett & Lloyd 1958
Allotropa kamburovi	South Africa	Annecke & Prinsloo 1977
Allotropa mecrida	USSR	Niyazov 1969

The citrus mealybug is also attacked in most regions by encyrtid and sometimes by platygasterid parasitoids (Table 4.15.2), several of which are capable of having a significant effect in warm climates. If the origin of *P. citri* is really China, it is surprising that there are not reports of a number of specific or near specific parasitoids from that region. Indeed the species most commonly employed for biological control is *Leptomastix dactylopii* which is believed to be native to Brazil.

A few fungi attack *P. citri* under humid conditions (Table 4.15.3).

Attempts at biological control

Any account of the biological control of *P. citri* is complicated by the facts that (i) it has been confused with other species on a number of occasions, so that early records are often unreliable, (ii) documentation of some introductions is poor or lacking, and (iii) natural enemies (that also attack it) have often been introduced in programs aimed at other mealybugs. Table 4.15.4 summarises the main introductions for biological control of *P. citri*.

CALIFORNIA

It is convenient to outline, first, the prolonged attempts against *P. citri* in California, since programs elsewhere almost always draw extensively on experience there. Furthermore, since the first introduction of *Cryptolaemus montrouzieri* from Australia to California in 1891–92, there have been few parasites or predators used in the control of any economically important mealybug anywhere in the world that have not also been tested against *P. citri* in California, in the hope that they might attack it also (Bartlett 1978).

C. montrouzieri was mass reared and released in California against *P. citri* with some success, but repeated releases were required to achieve satisfactory control. Another coccinellid *Nephus* (= *Scymnus) bipunctatus* (under the name of *Cryptogonus orbiculus*) was introduced in 1910 from the Philippines, but did not become established (Bartlett 1978). However, establishment followed the introduction from Sicily in 1914 of the parasitoid *Leptomastidea abnormis*, although control was only partly successful (Viereck 1915; Smith 1917). The coccinellid *Scymnus binaevatus* from South Africa was established in 1921, but persists only in small numbers.

Unsuccessful attempts were made to establish the encyrtid *Coccidoxenoides peregrinus* from Hawaii where it was having a major impact on *P. citri*, misidentified at the time as *Planococcus kraunhiae*. However, progeny of a single female from South China in 1950 allowed the species to become established, although at a low level (Flanders 1957).

Table 4.15.2 Parasitoids of *Planococcus citri*

Species	Country	Reference
HYMENOPTERA		
ENCYRTIDAE		
Achrysophagus sp.	Turkey	Soylu & Urel 1977
Anagyrus bohemani	Spain	Carrero 1980a
	India	Varma 1977
Anagyrus greeni	Indonesia	Kalshoven 1981
Anagyrus pseudococci	Italy	Viggiani 1975a
	Turkey	Soylu & Urel 1977
	USA	Meyerdirk et al. 1982
	USSR	Niyazov 1969
Anagyrus sp. nr *sawadai*	USA	Meyerdirk et al. 1982
Blepyrus insularis	India	Chacko et al. 1977
Blepyrus saccharicola	California	Bennett & Hughes 1959
Chrysoplatycerus splendens	USA	Bartlett & Lloyd 1958; Summy et al. 1986
Clausenia josefi	Mediterranean	Niyazov 1969
Coccidoxenoides (= Pauridia) peregrinus	China	Bartlett 1978
	India	Krishnamoorthy & Mani 1989a; Mani 1994
	Italy	Viggiani & Maresca 1973
	USA	Meyerdirk et al. 1978, 1979, 1982
Leptomastidea abnormis	Spain	Carrero 1980a
	Turkey	Soylu & Urel 1977
	USA	Meyerdirk et al. 1979, 1982
Leptomastix dactylopii	Brazil	Mani 1995
	India	Mani 1995
	USA	Meyerdirk et al. 1978, 1979, 1982
Leptomastix nigrocoxalis	India	Prakasan & Kumar 1985

Table 4.15.2 (cont'd) Parasitoids of *Planococcus citri*

Species	Country	Reference
HYMENOPTERA		
ENCYRTIDAE (cont'd)		
Leptomastix trilongifasciatus	India	Kalshoven 1981
Ophelosia crawfordi		Bartlett & Lloyd 1958
Pseudaphycus angelicus	California	Bartlett & Lloyd 1958
Pseudaphycus maculipennis	USSR	Sinadskii & Kozarzhevskaya 1980
Pseudaphycus perdignus		Bennett & Hughes 1959
Sympherobius barberi	USA	Meyerdirk et al. 1982
Timberlakia gilva	South Africa	Prinsloo 1982
PLATYGASTERIDAE		
Allotropa citri	China	Bartlett & Lloyd 1958
Allotropa kamburovi	South Africa	Annecke & Prinsloo 1977
Allotropa mecrida	USSR	Niyazov 1969

Table 4.15.3 Pathogens attacking *Planococcus citri*

Species	Country	Reference
Aspergillus flavus	Cuba	Martinez & Bravo 1989
Cladosporium oxysporum	South Africa	Samways 1983; Samways & Grech 1986
Entomophthora fresenii	Indonesia	Kalshoven 1981
Entomophthora fumosa	Australia	Murray 1978; Samal et al. 1978
Fusarium sp.	Easter Is	Ripa et al. 1995

The encyrtid *Leptomastix dactylopii*, introduced in 1934 from Brazil, was mass reared and released. Recoveries were made over a number of years following each spring or summer release, but not following the ensuing winter. Eventually, a few managed to overwinter, resulting in a low level population (Compere 1939).

The South China platygasterid, *Allotropa citri*, introduced in 1950, attacked 1st and 2nd instar *P. citri*, but mass releases over some 6 years resulted in few field recoveries and it is not thought to be established (Bartlett 1978).

A somewhat polyphagous encyrtid, *Anagyrus pseudococci*, was unsuccessfully introduced from Brazil in 1934 and 1953. The same or a similar species, *Anagyrus* sp. nr *pseudococci*, was brought in from Italy in 1955, but was established only briefly (Bartlett 1978).

The coccinellid *Exochomus metallicus* from Eritrea was established from introductions in 1954 against citricola scale (*Coccus pseudomagnoliarum*) and black scales and attacks *P. citri* on plants other than citrus (Bartlett 1978).

In spite of this series of introductions, the natural enemies of *P. citri* in California do not, unaided, maintain populations at sub-economic levels, mainly because, it is claimed, climatic conditions permit the overwintering of, at best, inadequate populations. *Cryptolaemus montrouzieri* has often provided spectacular control of high populations, but is unable to maintain its numbers on low prey populations and disappears, requiring reintroduction. Methods are available for its low cost mass production (Fisher 1963).

The encyrtid *Leptomastidea abnormis* is of considerable value in attacking young mealybugs sheltering under citrus fruit sepals in spring and autumn, but is adversely affected by high temperatures. Both *Leptomastix dactylopii* and *Coccidoxenoides peregrinus* build up high numbers following mass releases, but crash over winter and require repeated mass releases to maintain effectiveness.

AUSTRALIA

P. citri can be an important pest of citrus, but also attacks passionfruit and custard apple in warmer regions. The earliest attempts at biological control were in Western Australia, where *Cryptolaemus montrouzieri* was introduced from New South Wales in 1902 and an unidentified coccinellid from Spain in 1903. Only the former was established and it rapidly became an important factor in the successful control of mealybugs there (Wilson 1960).

Before biological control was attempted in Queensland in 1980, six natural enemies were recorded, the coccinellids *Cryptolaemus montrouzieri,* and *Harmonia octomaculata* (= *Coccinella arcuata*) the chrysopids *Chrysopa* sp. and *Oligochrysa lutea* (all 4 native) and the exotic encyrtids *Leptomastidea abnormis* and *Coccidoxenoides peregrinus*. However, they were unable to maintain infestations consistently at acceptable commercial levels. Attack by a fungus similar to *Entomophthora fumosa* caused up to 58.1% mortality of 3rd instar nymphs and adults on passionfruit during wet periods (Murray 1978, 1982; Smith et al. 1988).

The Brazilian encyrtid *Leptomastix dactylopii* was imported from California and approximately 2.5 million adults released between 1980 and 1987. It established readily and became the commonest natural enemy of *P. citri* throughout southeast Queensland, reducing mealybug infestations, averaging 38% of fruit in early December, to an acceptable level of 5% or less at harvest in April. Parasitoid numbers were lowest during winter and spring and augmentative releases of 5 to 10 thousand parasitoids per hectare in spring to early summer advanced parasitoid activity by 6 weeks.

When no releases were made, the parasitoid was first recorded in early February and was present in an average of 55% of mealybug-infested fruit by mid-March. The mealybug infestation peaked at an average of 47% in mid-December but, by late April, only dropped to 10% and the presence of the mealybug on 25% or more fruit from December to March usually resulted in excessive amounts of sooty mould. *C. montrouzieri* was recorded on a maximum of 5% of mealybug-infested fruit, and augmentative release failed to increase this level. Augmentative release of *L. dactylopii* was found to be at least as cheap as pesticides and far more compatible with IPM of other citrus pests (Smith et al. 1988).

Placing sticky bands around the trunks of custard apple trees reduced the numbers of the ant, *Pheidole megacephala*, and lowered, somewhat, the numbers of *P. citri*. Parasitisation of *P. citri* by *Leptomastidea abnormis* was low and unaffected by banding, but there were more predators (especially *Oligochrysa lutea*, *Cryptolaemus montrouzieri* and *Syrphus* sp.). Nevertheless, natural enemies were still unable to maintain *P. citri* at acceptable levels (Murray 1982).

BERMUDA

Seven species of parasitoid and four predators were introduced between 1951 and 1955, mainly from California, but originating elsewhere: *Coccidoxenoides peregrinus* from Hawaii and south China, *Leptomastix dactylopii* (South American race) *Leptomastidea abnormis*, *Pseudaphycus perdignus*, *Anagyrus pseudococci*, *Blephyrus saccharicola* and *Allotropa citri*. Only *C. peregrinus*, *L. dactylopii* and *L. abnormis* were established and, of these, *L. dactylopii* may have been the local form. Of the predators, *Cryptolaemus montrouzieri* was established, but only briefly and two species of *Hyperaspis* and *Scymnus sordidus* failed to breed on *P. citri* (Simmonds 1957; Bennett and Hughes 1959).

BRAZIL

P. citri is common on a range of plants, but citrus is seldom infested. In 1939 *Leptomastidea abnormis* and *Leptomastix dactylopii* were commonly reared from it, and it was attacked by numerous predators, including *Hyperaspis c-nigrum*, *Nephus* sp., *Diomus* sp., lacewings and cecidomyiids. *Anagyrus pseudococci* was not recorded, although it was present in Argentina (Compere 1939).

CHILE

Cryptolaemus montrouzieri was introduced in 1931, 1933 and 1939, but establishment is not recorded, although it is present on Easter Is (Ripa et al. 1995). Extensive releases of two parasitoids from California resulted in establishment: *Leptomastidea abnormis* during 1931–36 and *Leptomastix dactylopii* in 1936 and 1938: both of these and *Coccidoxenoides peregrinus* were also established on Easter Is (Ripa et al. 1995). Attempts failed in 1954 to establish from California: *Allotropa citri*, *Anagyrus pseudococci*, *Coccidoxenoides peregrinus* and *Pseudaphycus perdignus* (Duran 1944; Gonzalez and Rojas 1966).

CHINA

Four species of parasitic wasp were introduced from China to California in 1950: a uniparental species of *Coccidoxenoides* and a biparental species of *Allotropa* from Guangzhou, a biparental species of *Pseudaphycus* from Taiwan and a biparental species of *Coccophagus* from Hong Kong (Flanders 1951).

CUBA

Seven natural enemies attack *P. citri* on coffee including a *Leptomastix* sp.. A cecidomyiid predator was commonest (Martinez et al. 1992). A fungus *Aspergillus flavus* was also detected (Martinez and Bravo 1989).

CYPRUS

Leptomastix dactylopii was introduced from Italy in 1977 and became established, attaining a parasitisation rate of 15% in 1979. At harvest there were far fewer *P. citrus* on the fruit than in a plot that had received 3 applications of insecticide (Krambias and Kontzonis 1980).

FRANCE

Cryptolaemus montrouzieri was introduced from California in 1918 and became established, but overwinter survival was low (Marchal 1921, 1922; Poutiers 1922; Marchal and Pussard 1938). Of the 6 species of mealybug on citrus in the Mediterranean basin, *P. citri* is the most injurious. Damage by it in France is such that an economic injury level of 2% infested fruit has been set. Mass rearing and release of *Leptomastix dactylopii*, which requires the use of fewer mealybugs for laboratory rearing than the coccinellid *C. montruzieri* and is cheaper, is preferred to that of the coccinellid if only one natural enemy is to be used. However, it is preferable to employ both, with *C. moutrouzieri* destroying high populations of females and eggs and *L. dactylopii* parasitising nymphs, even if populations are scattered (Panis 1977, 1979).

GREECE

Cryptolaemus montrouzieri was liberated against *P. citri* on potted orange trees in a glasshouse at 25 to 30°C and 55 to 70% RH and the results compared with the release of *Nephus* (= *Scymnus*) *reunioni* or the application of insecticide. *C. montrouzieri* significantly reduced mealybug populations and was as effective as treatment with methidathion (Hamid and Michelakis 1994).

INDIA

Leptomastix dactylopii was introduced in 1983 to Bangalore and rapidly became established on *P. citri* on mandarins and coffee, causing up to 100% parasitisation (Nagarkatti et al. 1992). Seven years later in 1991, *P. citri* was being attacked on lemon and lime by *L. dactylopii* and the more abundant indigenous *Coccidoxenoides peregrinus*, which was causing 10 to 30% parasitisation. *C. peregrinus* attacks preferentially the early and *Leptomastix dactylopii* the later instars (Krishnamoorthy and Mani 1989a; Mani 1994). In 1984 *L. dactylopii* was released in a lime orchard in Karnataka. Prior to release, infestation by *P. citri* ranged from 38 to 65%, but establishment of the parasitoid led to excellent control within 4 months and no insecticides were required in following seasons. The parasitoid was shown to have migrated about 0.5 km in a 2-year period and a mean of 2.3 adult parasitoids were recovered from each infested fruit in an orange orchard (Krishnamoorthy 1990). Parasitisation of *P. citri* and other mealybugs on coffee ranged, in different years, between 19 and 45% (Reddy et al. 1988) and 0 and 85% (Reddy et al. 1992). Although *L. dactylopii* greatly reduced the population of *P. citri*, augmentative releases were required for continuing control in a coffee plantation (Reddy and Bhat 1993).

Native predators of *P. citri* on coffee include the lycaenid, *Spalgis epius*, the coccinellid, *Pullus pallidicollis*, and the cecidomyiid *Triommata coccidivora* (Prakasan 1987). On citrus the chrysopids *Mallada boninensis*, *Odontochrysa* (= *Chrysopa*) *lacciperda*, *Mallada basalis* and *Chrysoperla carnea* were found (Krishnamoorthy and Mani 1989b); and on guava *Odontochrysa lacciperda*, *Spalgis epius* and *Cryptolaemus montrouzieri* (Mani and Krishnamoorthy 1990).

Releases of *Cryptolaemus montrouzieri* on a coffee estate in Kerala virtually eliminated *P. citri*, but the coccinellid could not be found thereafter for some 6 months, when it reappeared about 10 km distant and virtually eliminated mealybugs from an infestation (Chacko et al. 1978). The requirement that each female consume at least 8 *P. citri* for normal egg production (192 eggs/female) was suggested as the reason for the poor establishment of *C. montrouzieri* when only low populations of *P. citri* are available (Reddy et al. 1991).

ISRAEL

The citrus mealybug is a serious pest of citrus and ornamentals of tropical origin. It develops on the fruit and roots of young trees, the main damage being caused by individuals settling beneath the sepals of citrus fruit and injuring the fruit: honeydew produced also attracts fruit-piercing moths (Mendel et al. 1992).

Two native encyrtids, *Anagyrus pseudococci* and *Leptomastidea abnormis*, attack *P. citri* which is, nevertheless, an important pest of citrus and some other crops (Rosen and Rössler 1966).

Unsuccessful attempts were made to establish *Cryptolaemus montrouzieri* in 1924 from Egypt (Bodenheimer and Guttfeld 1929; Mason 1941) and 1958 (Rosen 1967a), but a Spanish strain introduced in the 1980s finally established (Mendel et al. 1992). *Leptomastix dactylopii* imported from Canada in 1941 was only briefly established (Rivnay 1960). *Clausenia purpurea*, a parasitoid of *Pseudococcus citriculus* introduced from Japan in 1940, attacks *P. citri*, but has little effect on its density (Rosen 1964).

P. citrus became a serious pest on recently established grapefruit in southern Negev. The encyrtid *Anagyrus pseudococci* was present in very low numbers and *Chrysoperla carnea* was active, but only in spring. The coccinellid *Chilocorus bipustulatus* was more abundant and was considered to have potential as a biological control agent (Berlinger et al. 1979). Seven parasitoids and 10 predators have been recorded, of which *Anagyrus pseudococci* (Encyrtidae) and *Sympherobius sanctus* (Chrysopidae) were found in significant numbers by Mendel et al. (1992). However, development of *A. pseudococci* is restricted by winter temperatures. Its development threshold is 13°C and no eggs are laid below 15°C, whereas *P. citri* still lays eggs at 13°C and its development threshold is 8.4°C. By the time in late spring when the population of *A. pseudococci* starts to built up, *P. citri* has already settled under the sepals, where it is well protected from the parasitoid. Climatic conditions were thus regarded as unfavourable for existing natural enemies (Mendel et al. 1992).

ITALY

Infestations of *P. citri* develop on citrus in Sicily, Procida, Sardinia and parts of mainland Italy, especially where it is protected by ants from its native parasitoids, *Leptomastidea abnormis* and *Anagyrus pseudococci* (Zinna 1960). *Cryptolaemus montrouzieri* has been imported a number of times since 1908 and has become established in some warmer areas, but is so reduced in numbers during winter that satisfactory control is not obtained without supplementations (Constantino 1935; Liotta 1965; Liotta and Mineo 1965). *Coccidoxenoides peregrinus* and *Leptomastix dactylopii* were introduced to Procida in 1956–57, but did not survive the winter (Bartlett 1978). *L. dactylopii* was reintroduced in 1974 to this island, to the mainland (Campania, Calabria), and to Sardinia and Sicily. At almost all 15 release sites it afforded, initially, a high level of parasitisation (Viggiani 1975a,b). Small overwintering populations, reduced further by hyperparasitoids and fungus diseases, persisted in some areas, but required supplementation for control (Mineo and Viggiani 1975a,b). *L. dactylopii* was again released in 1979 on Sicily and gave good results (5% of fruit infested), but it is unclear whether or not it is able to overwinter (Barbagallo et al. 1982; Longo and Benfatto 1982). Release of *L. dactylopii* in a mainland orange orchard in Calabria led to a reduction in infested fruit from 80.9% to 12% and only 7.3% of the fruit was unmarketable (Luppino 1979). It now seems that *L. dactylopii* and *Cryptolaemus montrouzieri* are mass reared and released each year against *P. citri* (Raciti et al. 1995).

Insecticides are seldom required against *P. citri* in Sardinia, where *L. dactylopii* may cause 96% cumulative parasitisation and where *Cryptolaemus montrouzieri* and *Nephus* (= *Scymnus*) *reunioni* may increase to more than 100 individuals per tree (Ortu 1982; Ortu and Prota 1983).

PAPUA NEW GUINEA

Mealybugs, including *P. citri*, were causing up to 75% reduction of coffee yield in the highlands near Wau in the mid fifties. Introduction of *Cryptolaemus affinis* in 1957 from the lower Markham Valley resulted in its rapid spread and a substantial reduction of the infestations within one season (Szent-Ivany 1963).

PERU

Very good control of *P. citri* is given in some areas by the encyrtid *Coccidoxenoides peregrinus*, which is restricted to the citrus mealybug and appears to have arrived accidentally in 1963 (Salazar 1972).

SOUTH AFRICA

The history of introductions to South Africa against *P. citri* is confused because of misidentifications of other mealybugs for this species. However, Bedford (1976) reports that *P. citri* is under biological control.

When the ant *Anoplolepis custodiens* was excluded from guava trees bearing *P. citri* at Nelspruit, the population of both ants and mealybugs dropped to half. Without ants, the mealybugs were heavily preyed upon by the ant-intolerant *Exochomus flavipes* and the ant-tolerant *Scymnus* spp. Later, the mealybugs were almost eliminated by the fungus *Cladosporium* sp. nr *oxysporum* (Samways 1983).

SPAIN

P. citri is parasitised by two indigenous encyrtids, *Leptomastidea abnormis* and *Anagyrus bohemani*, but at a low level (Carrero 1980a). *Cryptolaemus montrouzieri* was introduced and established before 1928 and produces control in the warmer months (Gomez 1951; Carrero 1980b). *Leptomastix dactylopii* was introduced in 1948 from California (Gomez 1951) and in 1977 from Italy, but did not become established (Carrero 1980b).

USA (OTHER THAN CALIFORNIA)

Florida

Cryptolaemus montrouzieri was introduced to Florida in 1930 for the control of *P. citri* on citrus and bulbs. It became established but failed to overwinter in sufficient numbers to achieve adequate control (Bartlett 1978; Muma 1954, Watson 1932).

Hawaii

P. citri (originally misidentified as *P. kraunhiae*) was the target of many introductions (Swezey 1931), although not as severe a pest as on the mainland. *Cryptolaemus montrouzieri* was introduced from Australia in 1894, *Leptomastidea abnormis* from California in 1915 and *Leptomastix dactylopii* also from California in 1946. All became established.

Texas

In 1970, *Coccidoxenoides peregrinus* was the dominant parasitoid of 3 present on *P. citri* attacking grapefruit and *Sympherobius barberi* the commonest predator (Dean et al. 1971). In 1977 *Leptomastix dactylopii*, which had been introduced from California in 1970, and *Anagyrus* sp. nr *sawadai* were found for the first time on *P. citri* in Texas. *L. dactylopii* was the most abundant parasite in mid-August (parasitising 20.7% of *P. citri*), the reputedly indigenous *Coccidoxenoides peregrinus* (with 48.5%) the most abundant in late August, whereas *Anagyrus* sp. (with 4.3%) was the only parasitoid recovered in mid-September. A hyperparasitoid *Prochiloneurus dactylopii* attacked 1% of the primary parasitoids in mid-August (Meyerdirk et al. 1978). Release of 5 encyrtid parasitoids on glasshouse citrus resulted in the rapid suppression of *P. citri*. *Leptomastidea abnormis*, *Anagyrus pseudococci* and *Leptomastix dactylopii* persisted for periods between 24 and 32 weeks and maintained the host at low densities, whereas *Chrysoplatycerus splendens* and *Coccidoxenoides peregrinus* persisted for only 20 weeks (Summy et al. 1986). The coccinellid *Diomus pumilio*, whose biology is described, was introduced from South Australia and is a potentially valuable predator (Meyerdirk 1983).

USSR

P. citri can be a serious pest of grape vines, citrus, fig and pomegranate. *Anagyrus pseudococci* from Surkham Dalya and *Leptomastix dactylopii* and *Leptomastidea abnormis* from California were introduced to Uzbekistan commencing in 1959 and resulted in establishment (Roxanova and Loseva 1963). *Anagyrus pseudococci* destroys up to 75% of *P. citri* in areas not treated with insecticides in the south of European Russia and in Soviet Central Asia. The next most important parasitoid, *Allotropa mecrida* attacked up to 20% in Turkmenia in 1967 and in Georgia. In 1960, *Leptomastidea abnormis* and *Leptomastix dactylopii* were introduced from USA into Georgia and Turkmenia. In Transcaucasia and Soviet Central Asia the hyperparasitoid *Thysanus subaeneus* attacks 18 to 20% of *Allotropa mecrida*. Other hyperparasitoids are *Pachyneuron solitarius* and *Neoprochiloneurus bolivari*.

One of the most effective predators of *P. citri* is *Cryptolaemus montrouzieri*, introduced from Egypt in 1932 to the Black Sea area. Others are *Coccinella septempunctata*, *Hyperaspis polita*, *Nephus bipunctatus, Scymnus apetzi*, *S. subvillosus*, and *S. biguttatus* which were recorded in Turkmenia. The larvae of the fly *Leucopis alticeps* and of the lacewing *Chrysoperla carnea* are able to devastate all stages of *P. citri*. The coccinellids were parasitised by *Homalotylus* sp. and the lacewing by *Telenomus acrobates* (Niyazov 1969).

The coccinellid *Nephus reunioni* was introduced into southern areas in 1978 and has reduced *P. citri* on grape vines. It is capable of overwintering, but with high mortality, and is more tolerant of moisture conditions than *Cryptolaemus montrouzieri* (Orlinskii et al. 1989).

Table 4.15.4 Introductions for the biological control of *Planococcus citri*

Species	From	To	Year	Result	Reference
HYMENOPTERA					
ENCYRTIDAE					
Anagyrus kivuensis	Kenya	California	1948	–	Bartlett & Lloyd 1958
Anagyrus pseudococci	Brazil	California	1934	–	Bartlett & Lloyd 1958
	California	Bermuda	1953	+	Bartlett & Lloyd 1958
	California	Chile	1951–54	–	Bennett & Hughes 1959
			1954	–	Gonzalez & Rojas 1966
Anagyrus sp. nr *pseudococci*	Italy	California	1955, 1965	–	Bartlett 1978, Bartlett & Lloyd 1958
Anagyrus sp. nr *sawadai*		Texas		+	Meyerdirk et al. 1978
Blepyrus saccharicola	California	Bermuda	1951–54	–	Bennett & Hughes 1959
Coccidoxenoides peregrinus	Hawaii	California		–	Armitage 1920
	China	California		+	Flanders 1951
	China	Bermuda	1951–54	+	Bennett & Hughes 1959
	California	Chile	1954	–	Gonzalez & Rojas 1966
		Peru	1963	+	Salazar 1972
Leptomastidea abnormis	Sicily	California	1914	+	Viereck 1915; Smith 1917
	California	Chile	1931	+	Gonzalez & Rojas 1966
	California	Bermuda	1951–54	+	Bennett & Hughes 1959
	USA	USSR	1960		Niyazov 1969
Leptomastidea sp. nr *abnormis*	Mexico	California	1956	–	Bartlett & Lloyd 1958

Table 4.15.4 (cont'd) Introductions for the biological control of *Planococcus citri*

Species	From	To	Year	Result	Reference
HYMENOPTERA					
ENCYRTIDAE (cont'd)					
Leptomastix dactylopii	Brazil	California	1934	+	Compere 1939
	California	Chile	1936	–	Gonzalez & Rojas 1966
		Chile	1958	+	Gonzalez & Rojas 1966
	California	Bermuda	1951–54	?	Bennett & Hughes 1959
		Turkey		+	Tuncyurek 1970
	California	Texas	1970	+	Meyerdirk et al. 1978
	California	Australia	1980	+	Smith et al. 1988
		India	1983–85	+	Nagarkatti et al. 1992
		India	1984	+	Krishnamoorthy 1990,
				–	Prakasan & Bhat 1985; Krishnamoorthy & Singh 1987; Prakasan 1987; Reddy et al. 1988; Mani 1994
		Israel			Rivnay 1960
		Italy	1956–7	– (early)	Luppino 1979; Longo & Benfatto 1982
	Italy			+ (later)	Viggiani 1975a,b; Mineo & Viggiani 1976a
		Cyprus	1977	+	Krambias & Kontzonis 1980
		Sardinia	1974	–	Viggiani 1975a,b; Delrio et al. 1981; Ortu & Prota 1981; Ortu 1982
		Sicily	1979	–	Barbagallo et al. 1982 Longo & Benfatto 1982 Viggiani 1975a,b
	Italy	Spain	1977	–	Carrero 1980b
	USA	USSR	1960		Niyazov 1969

Table 4.15.4 (cont'd) Introductions for the biological control of *Planococcus citri*

Species	From	To	Year	Result	Reference
HYMENOPTERA					
ENCYRTIDAE (cont'd)					
Pseudaphycus perdignus	Eritrea	California	1953	–	Bartlett & Lloyd 1958
	California	Bermuda	1951–54	–	Bennett & Hughes 1959
Tropidophryne melvillei	Kenya	California	1948	–	Bartlett & Lloyd 1958
HYMENOPTERA					
PLATYGASTERIDAE					
Allotropa citri	China	California		?	Flanders 1951; Bartlett & Lloyd 1958
	California	Bermuda		–	Bennett & Hughes 1959
	California	Chile	1954	–	Gonzalez & Rojas 1966
COLEOPTERA					
COCCINELLIDAE					
Brumus suturalis	India	California	1955	–	Bartlett & Lloyd 1958
Chilocorus angolensis	Kenya	California	1948	–	Bartlett & Lloyd 1958
Cryptolaemus montrouzieri		Greece		–	Argyriou 1970
		Sardinia	<1980	?	Ortu & Prota 1981, 1985; Ortu 1982
		Turkey	<1970		Tuncyurek 1970
	Egypt	Israel	1924	–	Bodenheimer & Guttfeld 1929
		Israel	1958	–	Rosen 1967a
		USSR	1932	+	Niyazov 1969
		USA	1891–92	+	Bartlett 1978
	NSW	W.A.	1902	+	Wilson 1960
	California	France	1918	+	Marchal 1921

Table 4.15.4 (cont'd) Introductions for the biological control of *Planococcus citri*

Species	From	To	Year	Result	Reference
COLEOPTERA					
COCCINELLIDAE (cont'd)					
	California	Bermuda	1955	+	Bennett & Hughes 1959
	California	Chile	1931	–	Gonzalez & Rojas 1966
			1933	–	Gonzalez & Rojas 1966
			1934	?	Gonzalez & Rojas 1966
		India		+	Prakasan 1987
		Indonesia		–	Kalshoven 1981
	Spain	Israel	1980s	+	Mendel et al. 1992
Diomus pumilio (= *D. flavifrons*)	Australia	Texas		+	Meyerdirk 1983
Exochomus flavipes	Kenya	California	1948	–	Bartlett & Lloyd 1958
Exochomus metallicus	Eritrea	California	1954	+	Bartlett 1978
Hyperaspis jucunda	Trinidad	California	1955	–	Bartlett & Lloyd 1958
Hyperaspis sp. nr *globula*	Mexico	California	1954	–	Bartlett & Lloyd 1958
Hyperaspis sp.	Eritrea	California	1953	–	Bartlett & Lloyd 1958
Hyperaspis 2 × spp.	California	Bermuda	1958	–	Bennett & Hughes 1959
Nephus (=*Scymnus*) bipunctatus	Philippines	California	1910	–	Bartlett 1978
Nephus (=*Scymnus*) *reunioni*	East Africa	USSR	1978	+	Ershova & Orlinskii 1982; Orlinskii et al. 1989
Nephus sp.	Trinidad	California	1958	–	Bartlett & Lloyd 1958
Platynaspis (?) sp.	Eritrea	California	1953	–	Bartlett & Lloyd 1958
Scymnus binaevatus	South Africa	California		+	Smith 1923
Scymnus quadrivittatus	Kenya	California	1948	–	Bartlett & Lloyd 1958
Scymnus sordidus	California	Bermuda	1955	–	Bennett & Hughes 1959

Biology of important natural enemies

Anagyrus pseudococci Hym.: Encyrtidae

This is a solitary endoparasite of 2nd, 3rd and 4th instar mealybugs, but prefers 3rd instar and egg-laying females. It is believed to be native to the Mediterranean. *A. pseudococci* has been known since 1913 in Italy as a widespread parasitoid of *P. citri* and, in Israel, attacking both *P. citri* and *Pseudococcus citriculus* (Rivnay 1960; Rosen 1964). It is common on *P. citri* in Argentina (Compere 1939). In the laboratory it develops successfully on *Pseudococcus fragilis, P. longispinus* and *P. obscurus*.

Females lay about 45 eggs at the rate of 3 to 4 per day. In the laboratory these hatch in 44 hours at 27°C and the life cycle takes 17 to 18 days (Bartlett 1978) or 15.5 days at 25.6°C and 60% RH for a Californian strain, which also had a life span of 8.2 days for virgin and 6.9 days for mated females. Virgin females produce males. *A. pseudococci* is most active in the spring and autumn (Domenichini 1952; Avidov et al. 1967; Rivnay 1968; Chandler et al. 1980).

Progeny production increased and longevity decreased with increase in temperature between 18° and 30°C (Tingle and Copland 1989). Most progeny are produced between 27° and 30°C and the threshold for development is 13.06°C for males and 12.57°C for females (Islam and Jahan 1993). In the laboratory maximum egg production was achieved when 50% honey solution was provided (Islam and Jahan 1992, 1993). Oviposition behaviour is described by Islam (1992). About 40% of parasitoid eggs laid in *P. citri* may be lost due to encapsulation (Blumberg et al. 1995). In Argentina, larvae of *A. pseudococci* are attacked by the hyperparasitoid *Coccophagus heteropneusticus* (Compere 1939).

Coccidoxenoides peregrinus Hym.: Encyrtidae

This parasitoid, earlier widely known as *Pauridia peregrina*, is probably native to southern China (Bartlett 1978), although Meyerdirk et al. (1978) suggest that it is indigenous to Texas. It has been reported, inter alia, from India, Japan, Philippines, Fiji, Hawaii and Uganda. It is a solitary endoparasitoid of 1st, 2nd and 3rd instar female *Planococcus citri* and *P. kenyae* and 1st and 2nd instar males. It is normally parthenogenetic, but there are rare males. In Uganda it parasitises *P. kenyae* (Armitage 1920; Essig 1931) and, in Peru *P. citri* (Beingolea 1969). In India it completed its development only in *P. citri*, although it attacked other mealybugs (Krishnamoorthy and Mani 1989a).

Females commence oviposition shortly after emergence, and continue for about 2 days. At 27°C larval development takes 11 to 12 days and the pupal stage 16 to 18 days (Zinna 1960; Fisher 1963). However, in India, development took 23 to 27 days and adults survived 4 to 9 days at 28 ± 2°C (Krishnamoorthy and Mani 1989a). In 1991 in Karnataka, *C. peregrinus* was more abundant than *Leptomastix dactylopii* on *P. citri* on lemon and acid lime and was responsible for the decline of mealybug populations (Mani 1994).

C. peregrinus has been introduced into California (Flanders 1951), Italy (Bartlett 1978) and Bermuda (Bennett and Hughes 1959).

Cryptolaemus montrouzieri Col.: Coccinellidae

This general predator of mealybugs, which also feeds on some other scales (*Eriococcus* sp., *Pulvinaria* spp.) and aphids, is native to eastern Australia. It is the most widely distributed of all natural enemies of mealybugs, a count in 1978, covering the past 80 years, listing more than 40 countries, geographic areas or islands into which it has been imported. In many instances it was introduced against mealybugs other than *P. citri* and sometimes against coccids such as *Pulvinaria* spp., which produce egg masses similar to those of mealybugs (Bartlett 1978).

Both larvae and adults feed voraciously on all mealybug stages, for example a larva is recorded as consuming an average of 3331 host eggs (Oncuer & Bayhan 1982) and females need to consume at least 8 *P. citri* for normal egg production (Reddy et al. 1991). *C. montrouzieri* does not distinguish between unparasitised *P. citri* and mealybugs parasitised by *Leptomastix dactylopii* (Prakasan and Bhat 1985). Adults mate 1 or 2 days after emergence and, 5 to 6 days later, females begin ovipositing in or near host egg masses. About 100 eggs are deposited in 1 month. These hatch in 4 to 8 days, and wax-covered larvae develop in 12 to 20 days, so that the life cycle can be completed in slightly less than a month (27.7 days at 25.5° ± 1°C: Oncuer and Bayhan 1982), although there are usually only 4 generations a year. Development stops below 10°C and freezing temperatures are lethal. Pupae, and occasionally adults, are capable of hibernating. Hot dry climates are tolerated, but high humidities are said to be detrimental. *C. montrouzieri* thrives when host density is high and, under these conditions, is capable of providing spectacular control. However its searching ability and natural spread is poor, so it often dies out locally when hosts become scarce (Bodenheimer 1928; Cole 1933; Mineo 1967).

Methods have been developed for the production of mealybugs and *C. montrouzieri* that permit the production and release of large numbers of the predators at low cost (Branigan 1916, Smith and Armitage 1920, 1931; Fisher 1963; Chacko et al. 1978; Oncuer and Koldas 1981).

Diomus pumilio Col.: Coccinellidae

Details of the biology and voraciousness of this predator, which was introduced from South Australia to Texas for biological control of *P. citri,* are given by Meyerdirk (1983).

Leptomastidea abnormis Hym.: Encyrtidae

This solitary endoparasite is possibly native to the Mediterranean where it was first recognised attacking *P. citri* (Viereck 1915), although it is now widespread, occurring in eastern USA, Canada, Brazil (Compere 1939) and many other countries.

L. abnormis strongly prefers small 2nd instar mealybugs for oviposition, but also attacks first and third instars. Females begin to search for hosts soon after emergence. The number of eggs laid varies from 57 to over 300, although it is reported that only about 33 survive to the adult stage. Fertilised eggs give rise to females and unfertilised eggs to males.

The inconspicuously stalked eggs are laid free in the haemolymph and hatch in 36 to 72 hours. The larvae consume haemolymph at first but, in the last instar, consume the entire body contents. The tailed larvae complete development in about 8 days and the life cycle may be as short as 17 days in the laboratory at 26°C (or 25 days at 25° to 27°C and 50–70% RH). In the laboratory females attained their maximum progeny production at 24°C and this remained constant up to 34°C (Tingle and Copland 1989). In the field a generation in summer takes about 1 month. There may be 5 or 6 generations a year, adults living 11 days if provided with honey and water (Viereck 1915; Smith 1916, 1917; Perez 1929; Rivnay and Perzelan 1943; Clancy 1944; Viggiani and Maresca 1973).

Leptomastix dactylopii Hym.: Encyrtidae

This solitary endoparasitoid prefers 3rd instar and young (but not egg-laying) females and occasionally attacks 1st and 2nd instars (Bartlett 1978; Mani 1995). It is presumed to be native to Brazil, although found also in the West Indies and parts of southern USA (Compere 1939). In the field it appears to be specific to *P. citri* (Bartlett 1978; Sinadskii and Kozarzhevskaya 1980; Nagarkatti et al. 1992), but it can be reared on *Planococcus lilacinus* (Mani 1995), *P. pacificus* (Nagarkatti et al. 1992), *Phenacoccus solani* (Lloyd 1964) and *Pseudococcus comstocki* (Clancy 1944). Its reported attack on *Dysmicoccus brevipes* in Hawaii and on *Pseudococcus vitis* in USSR was probably on *P. citri* (Kobakhidze 1965; Bartlett 1978).

It has been used in suppression of *P. citri* in USA (Fisher 1963), Procida island and mainland Italy (Luppino 1979), Cyprus (Krambias and Kontzonis 1980) and India (Krishnamoorthy 1990).

Adults live up to 35 days and longer at 15° than at 7° or 25°C (Yigit et al. 1994) although maximum progeny are produced at 30° (Tingle and Copland 1989). Parasitised hosts are generally rejected after simple antennal contact but, if not then, also following defensive behaviour of the host or possibly after detection of the egg stalk emerging from the surface of the host. If not rejected earlier, they may be rejected after insertion of the ovipositor (Baaren and Nenon 1994). About 18 eggs are laid each day, up to a total of 300 per female. These hatch in 1.5 to 2 days at 28°C and there are four larval instars, each of about 2 days. The pupal stage lasts 7 to 8 days. In Italy there are 6 (and a partial 7th) generations per year (Zinna 1959, 1960) and in Tashkent 5 generations (Roxanova and Loseva 1963).

More males than females are produced from young than from old adult *P. citri* (Su and Li 1993; Mani 1995), more females from larger hosts and more males from smaller larval instars (Jong and Alphen 1988, 1989). Additional information on the biology of *L. dactylopii* is given by Lloyd (1958, 1964, 1966) and Tingle and Copland (1989).

The original introduction of *L. dactylopii* from Brazil to California in 1934 was based on a single pair (Compere 1939). The extent to which the progeny of this pair may have had genes from later introductions added to the gene pool is quite unclear. There may thus be good justification for obtaining fresh stock from matching climatic zones in Brazil if new introductions are to be made.

Odontochrysa (= Chrysopa) lacciperda Neu.: Chrysopidae

Details of the biology and voracity of this lacewing predator of *P. citri* are provided by Krishnamoorthy (1988).

Pseudaphycus maculipennis Hym.: Encyrtidae

This species, studied in Ukraine, for the biological control of *P. citri,* is said to be specific (Sinadskii and Kozarzkevskaya 1980).

Scymnus includens Col.: Coccinellidae

The life cycle and rearing details of this important predator of *P. citri* in Italy are described by Tranfaglia and Viggiani (1973).

Spalgis epius Lep.: Lycaenidae

The predatory larvae of this lycaenid butterfly are often the commonest natural enemies of *P. citri* in India. They also attack *Planococcus lilacinus*, *Chloropulvinaria psidii* and *Ferrisia virgata* (Chacko et al. 1977).

Comments

P. citri is frequently only one of several pests of importance on the economic crops that it infests and, if biological control is contemplated, it is advisable to have its identity confirmed by a competent taxonomist. Its abundance is increased when it is tended by ants for its honeydew and often, by the injudicious use of insecticides (against it or accompanying pests). This is mainly because of the adverse effects on natural enemies and sometimes because low levels of insecticide may stimulate egg-laying. There has thus been considerable effort, within an Integrated Pest Management framework and with varying degrees of success, to develop biological control of each of the important pests in a complex, for example on citrus, grape vines and in glasshouses. This has also involved the careful selection of pesticides (if these are still required) that have the least possible adverse effect on the major natural enemies.

Where natural enemies already present are not adequate, the almost universal response has been to introduce the encyrtid *Leptomastix dactylopii* and the coccinellid *Cryptolaemus montrouzieri* (if the latter is not already present as a result of introductions for other pests).

Both species are affected by the winter in temperate zones and survive less well than *P. citri* in the Mediterranean region. Under these circumstances, classical biological control seldom provides economic control alone and requires augmentation of the natural enemies from time to time.

Where *P. citri* is still a problem in the field in warm regions and *Cryptolaemus montrouzieri* is not present, serious thought should be given to introducing the latter. More importantly, however, if not already present *Leptomastix dactylopii* (of Brazilian origin) should be of highest priority, followed by *Leptomastidea abnormis* and *Anagyrus pseudococci* (both of Mediterranean origin and capable of maintaining populations of low levels under slightly cooler conditions). Under Southeast Asian and Pacific conditions, *Coccidoxenoides peregrinus* (of south China or Indian origin) deserves special attention.

If *Planococcus citri* proves to be of south China origin (and this hypothesis requires confirmation) it is surprising that only two parasitoids have been reported—the encyrtid *Coccidoxenoides peregrinus* and the platygasterid *Allotropa citri*. A thorough survey in this region might well reveal additional valuable specific or near specific parasitoids. There are good grounds for optimism that biological control of *P. citri* can be improved in warmer regions by establishing, if missing, any one of the foregoing natural enemies.

P. citri is one of a group of pests that commonly cause problems in glasshouses in Europe and North America. The mass production and release from time to time, almost always of a predator (especially *Cryptolaemus montrouzieri*, but sometimes also *Nephus reunioni*) and one or more encyrtid parasitoids (especially *Leptomastix dactylopii* and *Leptomastidea abnormis* but, on occasion also, *Coccidoxenoides peregrinus*, *Anagyrus pseudococci* and *Chrysoplatycerus splendens*) has generally removed the need to use insecticides. Examples of control in glasshouses include those from Belgium (Ronse 1990), Netherlands (Heanekam et al. 1987), France (Panis and Brun 1971), U.K. (Copland 1983, Hussey and Scopes 1985; Tingle and Copland 1988), Israel (Rubin 1985) and USA (Summy et al. 1986).

4.16 *Trichoplusia ni*

The cabbage looper, *Trichoplusia ni*, of North American origin, attacks cabbage (and other Brassicaceae), cotton, lettuce, tomatoes and a very wide range of other cultivated crops and wild hosts. In North America it is maintained for much of the time at sub-economic levels by a wide range of natural enemies, but damaging outbreaks do occur, particularly when its natural enemies are killed by insecticides applied against other pests in the same crop.

The major predators, which together cause considerable mortality, are widely polyphagous, and hence are unlikely to be considered seriously as classical biological control agents. Several, among its 120 or so parasitoids are somewhat more host specific and are worth serious consideration. They include species of *Trichogramma* egg parasitoid; *Copidosoma truncatellum* (an egg-larval parasitoid); and the larval parasitoids *Hyposoter exiguae*, *Microgaster brassicae* and *Voria ruralis*.

High larval mortality is frequently produced by a valuable, naturally occurring, nuclear polyhedral virus, particularly late in the season when *T. ni* populations are high and rainfall is adequate.

There appear to be good reasons for optimism that the establishment of suitable missing natural enemies in regions into which *T. ni* has spread would assist in maintaining its populations at sub-economic levels.

Trichoplusia ni (Hübner)

Lepidoptera: Noctuidae

cabbage looper

Synonym: In North America *T. ni* has sometimes been referred to as *Autographa brassicae* (Riley).

Rating

Southeast Asia			China	
7	++	Myan, Thai, Camb	+	(all 14 southern Provinces)
	+	Viet		
	P	Indo		

Origin

T. ni is native to the southern half of North America.

Distribution

Widespread in southern Europe, North, East and South Africa, extending eastwards through Pakistan, India and Bangladesh to much of Southeast Asia, to China, Taiwan, Korea and Japan; not yet present in Papua New Guinea, Australia, New Zealand or the oceanic Pacific; present in South America in Argentina, Bolivia, Brazil, Chile, Colombia and Uruguay (Apablaza and Norero 1993; CIE 1974b). In North America, *T. ni* overwinters in the south, re-invading northern States each spring.

Biology

Adult *T. ni* are mottled brownish in colour. The forewings, producing a span of about 3.8 cm, each bear an 8-shaped silvery mark near the middle. Adults are mostly active at night, but also on dull days. By day, they rest on the underside of host plants, in the debris at their base, or in vegetation bordering a cultivated crop. Adults are capable of flying long distances—700 km northwards from southern Texas (Lingren et al. 1993) 161 km from land into the Gulf of Mexico, and up to 1500m in California (Kreasky et al. 1972).

They move readily between cultivated and wild hosts. A female may lay her own bodyweight in eggs, but requires access to nectar and moisture to do so. After emerging from the pupa, there is a pre-ovipositional period of about 4 days, after which mating begins and can occur up to 16 days. A female may produce well over 1000 viable eggs. Peak egg deposition is often correlated with the lunar cycle, a rapid rise in egg density on cotton occurring shortly after full moon. There are 3 generations a year in southern California, but breeding is continuous in the Caribbean (McKinney 1944; Kishaba et al. 1967; Ehler and van den Bosch 1974; Ehler 1977a; Debolt et al. 1984; Mitchell and Chalfant 1984).

In cotton, a single egg is laid on the underside of a mature leaf in the upper half of the plant, but seldom in a terminal. On hatching, the larva generally feeds on the underside of the leaf near the egg, later moving from leaf to leaf as it passes through 5 instars during 2 to 4 weeks (Ehler 1977a). Total development time ranges from 19.9 days at 30°C to 40.4 days at 20°C (Jackson et al. 1969). In India at 25°C the egg stage lasted 2.06 days, the larval stage of 5 instars 12.38 days, the prepupal 1 day, the pupal 7.27 days and the adult 7.32 days (Gaikwad et al. 1983). Additional data are provided by Chi and Tang (1993) and Yadav et al. (1983). Flight and mating activity are diminished at temperatures less than 16°C and the threshold for larval development lies between 10°C and 13°C. The larva has 3 pairs of true legs on the thorax and 3 pairs of fleshy abdominal prolegs near the posterior end. It crawls by doubling up to form a loop, thus projecting the body forward. Larvae are green with a white lateral line and 2 whitish lines along the middle of the dorsal surface. After a brief prepupal period, pupation occurs in a loosely spun cocoon either on the underside of a leaf or in plant debris at the soil surface (Ehler 1977a). There is no diapause (Fye 1979).

Eggs and larvae, but also pupae, of *T. ni* are believed to be readily transhipped in vegetables and cut flowers (Poe and Workman 1984).

Male *T. ni* are powerfully attracted to the sex pheromone emitted by virgin females and will fly long distances upwind under its influence. The pheromone is produced in a gland situated dorsally between the 8th and 9th abdominal segments. Six components have been identified and are required to ensure specificity to *T. ni*. The major component is (Z)-7-dodecenyl acetate, known as looplure, which also attracts males of other looper species. Looplure, with or without other components, has been used for trapping males and also in mating disruption experiments. Male *T. ni* also produce a pheromone (with at least 3 components) which attracts both females (especially when starved) and males. (Bjöstad et al. 1984; McLaughlin 1984; Heath et al. 1992; Dunkelblum and Mazor 1993; Landolt 1995; Landolt et al. 1996).

Host plants

In 1966, larvae of *T. ni* were recorded causing damage to at least 119 species, varieties and cultivars in 29 families of plants (Sutherland 1966) and that number has increased steadily over the years to over 160 species in 36 families, although cultivated brassicas are those most favoured when available (Martin et al. 1976a; Sutherland and Greene 1984). Brassicas and cotton are most frequently cited as being damaged, although the list of economic crops affected also includes asparagus, beans, sugarbeet, cantaloupes, capsicum, carrot, celery, maize (silks), cucumber, lettuce, parsley, pea, potato, soybean, spinach, squash, tobacco, tomato and watermelon.

At times, serious infestations occur, but *T. ni* is generally regarded as a secondary pest whose numbers increase late in the season (Ehler 1977a,b).

Differences in susceptibility to *T. ni* have been found in cabbage and related brassicas, in cotton and in lettuce (Cuthbert and Kishaba 1984), in tomato (Sinha and McLaren 1989) and in soybeans (Luedders et al. 1978; Khan et al. 1986), but these largely remain to be exploited. Transgenic cotton lines containing *Bacillus thuringiensis* toxin genes limited damage to initial feeding sites, compared with more extensive skeletonisation in 2 control cultivars (Flint et al. 1995). Transgenic Bt canola (rape) showed excellent resistance to *T. ni* (Stewart et al. 1996).

Larvae are easily reared on an artificial diet (e.g. Shorey and Hale 1965; Honda et al. 1996).

Damage

The cabbage looper is a major pest of commercial brassicas in North America and many other areas where it occurs and causes significant damage also, in particular, to lettuce, tomatoes, celery and cotton. Indeed, Schwartz (1983) claimed that, if uncontrolled, 92% loss would be sustained in the cotton yield in USA, compared with 30% if controlled. Larvae chew large irregular holes, leaving only main veins, in the outer leaves of cabbage, cauliflower and related plants, often leaving them riddled with holes. Later, the outer layers of cabbage heads are eaten and masses of faecal pellets contaminate the feeding sites. So much leaf tissue is eaten that heads of cabbage and cauliflower are stunted and other leafy vegetables are rendered unfit to eat.

Damage caused to cotton by the larvae consuming leaves is often considered less serious, since it frequently occurs late in the growth of the cotton plant, so that it may not have a major effect on yield. Cabbage looper larvae are essentially foliage feeders and cause their damage in this way.

Natural enemies

Over the last few decades *T. ni* has become a very widely used laboratory insect, particularly in North America. As a result, there are many papers describing laboratory experiments in which parasitoids, predators and/or pathogens have been tested on *T. ni* eggs or larvae. It is often not possible to determine from these accounts whether or not the natural enemy involved has been found attacking eggs or larvae of *T. ni* in the field and hence possibly a useful control agent. If *T. ni* is susceptible to the agent in the laboratory, such records have often been included, although behavioural or other factors might well influence its effectiveness under field conditions. No attempt has been made to include reports of all of the minor natural enemies, especially in the earlier literature.

As will become clearer when the situation is discussed later, many parasitoids (Table 4.16.1), predators (Table 4.16.2) and pathogens (Table 4.16.3) have been recorded attacking the cabbage looper in the field and/or in the laboratory and there is little doubt that looper populations are frequently kept at sub-economic levels by their action. A number of the natural enemies recorded are not widespread in distribution and appear to be incidental records.

Many of the predators are widely polyphagous and attack insect pests in several orders, although a few are considerably more selective than that. Parasitoids, on the other hand, tend to be significantly less polyphagous than predators and some appear to be confined to *T. ni*, at least in certain crops. Where parasitoids have a relatively broad host range, available records indicate that this extends mainly to larvae of other Lepidoptera (generally pest species) in the same crop situation. The extent to which it extends also to non-pest, non-target species is not documented. Nevertheless, there are several species that merit serious consideration as candidates for classical biological control.

All of the *Trichogramma* species oviposit and develop in the host egg. A few others (eg. *Copidosoma truncatellum*, *Chelonus blackburni, Chelonus insularis*) oviposit in the egg and develop in the host larva; and the remainder are larval and/or pupal parasitoids.

Naturally occurring epizootics of nuclear polyhedrosis virus in medium to large *T. ni* larvae are considered to be the major mortality factor affecting them on cabbage in summer and autumn in southern California (Oatman and Platner 1969), on broccoli in Virginia (Hofmaster 1961) and on cabbage in North Carolina (Elsey and Rabb 1970b). Polyhedrosis was seldom a major factor on cotton in southern California (Ehler 1977b), although outbreaks did occur late in the season or at times of high *T. ni* abundance (Ehler and van den Bosch 1974).

Although the mortality produced is probably not significant, birds and bats are known to feed on moths in flight; and earwigs on adults resting beneath host plants (McKinney 1944; Sutherland 1966).

Table 4.16.1 Parasitoids of *Trichoplusia ni*

Species	Country	Reference
HYMENOPTERA		
BRACONIDAE		
Cardiochiles nigriceps	USA	Harding 1976
Chelonus blackburni	USA	Fye & Jackson 1973; Jackson et al. 1979
Chelonus curvimaculatus	USA	Soldevila & Jones 1991, 1994
Chelonus nr *curvimaculatus*	USA	Jones et al. 1981, 1990; Jones 1986
Chelonus formosanus	Taiwan	Chou 1981
Chelonus insularis	USA	Ehler et al. 1973; Ehler & van den Bosch 1974; Jones 1982; Henneberry et al. 1991
Chelonus sp.	USA	Bühler et al. 1985
Cotesia autographae	USA	Muesebeck & Krombein 1951
Cotesia congregata	USA	Riley 1883
Cotesia glomerata	USA	Muesebeck & Krombein 1951; van den Bosch & Hagen 1966; Ehler 1977a
Cotesia laeviceps	USA	Oatman et al. 1983a
Cotesia marginiventris	USA	van den Bosch & Hagen 1966; Ehler & van den Bosch 1974, Harding 1976, Latheef & Irwin 1983; Henneberry et al. 1991
Cotesia plutellae	India	Manjunath 1972; Joshi & Sharma 1974
Cotesia ruficrus	USA India	McCutcheon et al. 1983 Manjunath 1972
Cotesia spp.	USA	Harding 1976
Cotesia yakutatensis	USA India	Miller & West 1987 Manjunath 1972
Meteorus autographae	USA	Muesebeck & Krombein 1951; Grant & Shepard 1984

Table 4.16.1 (cont'd) Parasitoids of *Trichoplusia ni*

Species	Country	Reference
HYMENOPTERA		
BRACONIDAE (cont'd)		
Meteorus laphygmae	USA	Harding 1976
Microgaster (= *Microplitis*) *brassicae*	USA	McKinney 1944; van den Bosch & Hagen 1966; Clancy 1969; Oatman & Platner 1969; Ehler & van den Bosch 1974; Harding 1976; Ehler 1977a; Jones 1982; Oatman et al. 1983a; Henneberry et al. 1991
Microgaster plutellae	USA	Oatman & Platner 1969; Oatman et al. 1983a
Microplitis alaskensis	USA	Butler 1958a
Rogas granulatus	USA	De Gant 1930
Rogas molestus	USA	Butler 1958a
Rogas rufocoxalis	USA	McKinney 1944
Rogas sp.	USA	Wall & Berberet 1975
Snellenius manilae	Taiwan	Chou 1981
CHALCIDIDAE		
Brachymeria intermedia	Italy USA	Dindo 1993 Thompson 1980
Brachymeria lasus	USA	Thompson 1983a,b
Brachymeria ovata	USA	Elsey & Rabb 1970b; Harding 1976; Patana et al. 1978; Chamberlin & Kok 1986; Grant & Shepard 1987
Spilochalcis flavopicta	USA	Harding 1976
Spilochalcis side	USA	Harding 1976
Spilochalcis sp. nr *mariae*	USA	Harding 1976

Table 4.16.1 (cont'd) Parasitoids of *Trichoplusia ni*

Species	Country	Reference
HYMENOPTERA		
ENCYRTIDAE		
Copidosoma floridanum	USA	Strand et al. 1991; Baehrecke et al. 1993; Grbk et al. 1992; Ode & Strand 1995
Copidosoma sp.	USA	Ehler 1977a
Copidosoma truncatellum	Canada	Harcourt 1963
	USA	Riley 1883; McKinney 1944; Pimentel 1961; Oatman 1966; van den Bosch & Hagen 1966; Clancy 1969; Oatman & Platner 1969; , Ehler & van den Bosch 1974; Ehler 1977a; Latheef & Irwin 1983; Oatman et al. 1983a; Roltsch & Mayse 1983; Chamberlin & Kok 1986
	Brazil	Silva & Santos 1980
EULOPHIDAE		
Baryscapus galactopus	USA	Peck 1963
Euplectrus comstockii	USA	McKinney 1944; Harding 1976; Coudron et al. 1994
Euplectrus platyhypenae	USA	Wall & Berberet 1974, 1975; Coudron et al. 1990; Kelly & Coudron 1990,
Euplectrus sp.	Santiago	van Harten & Miranda 1985
Pediobius facialis	USA	Oatman & Platner 1969
Pediobius nr *facialis*	USA	Parkman et al. 1983
ICHNEUMONIDAE		
Angitia insularis	USA	Hayslip et al. 1953; Harding 1976
Campoletis flavicincta	USA	Krombein et al. 1979; Oatman et al. 1983a
Campoletis sonorensis	USA	Cook et al. 1984
Campoletis sp.	USA	Oatman et al. 1983a
Campoletis websteri	USA	Harding 1976
Casinaria infesta	USA	Harding 1976
Cryptus rutovinctus	USA	Krombein et al. 1979

Table 4.16.1 (cont'd) Parasitoids of *Trichoplusia ni*

Species	Country	Reference
HYMENOPTERA		
ICHNEUMONIDAE (cont'd)		
Diadegma insulare	USA	Martin et al. 1982
Diadegma plutellae	USA	Harding 1976
Diadegma spp.	USA	Sutherland 1966
Echthromorpha punctum	India	Manjunath 1972
Enicospilus sp.	India	Manjunath 1972
Gambrus ultimus	USA	Chamberlin & Kok 1986
Gelis tenellus	USA	Sutherland 1966
Hyposoter exiguae	USA	Oatman 1966; van den Bosch & Hagen 1966; Clancy 1969; Oatman & Platner 1969, Ehler & van den Bosch 1974; Ehler 1977a; Jones 1982; Oatman et al. 1983a,
Iseropus stercorator orgyiae	USA	Sutherland 1966
Itoplectis conquisator	USA Canada	Muesebeck & Krombein 1951 Harcourt 1963
Microcharops bimaculata	Brazil	Silva & Santos 1980
Microcharops tibialis	USA	Harding 1976
Nepiera fuscifemora	USA	Clancy 1969; Oatman et al. 1983a
Netelia sp.	USA	Watson et al. 1966
Patrocloides montanus	USA	Clancy 1969; Ehler & van den Bosch 1974; Ehler 1977a; Fox et al. 1996
Pimpla aequalis	USA	Sutherland 1966
Pristomerus sp.	USA	Harding 1976
Pristomerus spinator	USA	Harding 1976

Table 4.16.1 (cont'd) Parasitoids of *Trichoplusia ni*

Species	Country	Reference
HYMENOPTERA		
ICHNEUMONIDAE (cont'd)		
Pterocormus gestuosus	USA	Mitchell 1961
Stenichneumon culpator cincticornis	Canada	Harcourt 1963
	USA	Chamberlin & Kok 1986
Vulgichneumon brevicinctor	USA	Chamberlin & Kok 1986
PTEROMALIDAE		
Pediobius nr *sexdentatus*	USA	Oatman & Platner 1969; Oatman et al. 1983a
SCELIONIDAE		
Telenomus solitus	Guatamala	Johnson 1983; Navasero & Oatman 1989
Telenomus sp.	USA	Martin et al. 1984
TRICHOGRAMMATIDAE		
Trichogramma australicum	India	Manjunath 1972
Trichogramma brevicapillum	Brazil	Hohmann et al. 1988b
	USA	Hoffmann et al. 1990
Trichogramma chilotraeae	India	Manjunath 1972
Trichogramma deion	Brazil	Hohmann et al. 1988a,b
	USA	Hoffmann et al. 1990
Trichogramma evanescens	USA	Oatman et al. 1968
Trichogramma exiguum	USA	Martin et al. 1982; Roltsch & Mayse 1983; Campbell et al. 1991
Trichogramma japonicum	India	Manjunath 1972
Trichogramma minutum	USA	McKinney 1944; Marston & Ertle 1973; Manweiler 1986
Trichogramma platneri	Brazil	Hohmann et al. 1988a,b
	USA	Manweiler 1986

Table 4.16.1 (cont'd) Parasitoids of *Trichoplusia ni*

Species	Country	Reference
HYMENOPTERA		
TRICHOGRAMMATIDAE (cont'd)		
Trichogramma pretiosum	USA	Oatman 1966; Hoffmann et al. 1975, 1990; Martin et al. 1976b; Ehler 1977a; Oatman & Platner 1978; Butler & Lopez 1980; Oatman et al. 1983a
Trichogramma semifumatum	USA	Ehler & van den Bosch 1974
Trichogramma spp.	USA	van den Bosch & Hagen 1966; Harding 1976; Jones 1982
Trichogramma thalense	Brazil	Hohmann et al. 1988b
	USA	Hoffmann et al. 1990
DIPTERA		
SARCOPHAGIDAE		
Sacrodexia sternodontis	USA	Aldrich 1927
Senotainia sp.	USA	Manjunath 1972
TACHINIDAE		
Achaetoneura archippivora	USA	Butler 1958b
Aplomya theclarum	USA	Harding 1976
Archytas californiae	USA	van den Bosch & Hagen 1966
Bessa remota	Malaysia	Jayanth & Nagarkatti 1984
Carcelia sp.	USA	Harding 1976
	India	Manjunath 1972
Chetogena sp.	USA	van den Bosch & Hagen 1966; Chamberlin & Kok 1986
Compsilura concinnata	Canada	Harcourt 1963
	USA	Schaffner & Griswold 1934
Eucelatoria armigera	USA	Butler 1958b, Clancy 1969, Henneberry et al. 1991, Oatman 1966, Oatman & Platner 1969, van den Bosch & Hagen 1966
Eucelatoria nr *armigera*	USA	Harding 1976, Henneberry et al. 1991

Table 4.16.1 (cont'd) Parasitoids of *Trichoplusia ni*

Species	Country	Reference
DIPTERA		
TACHINIDAE (cont'd)		
Eucelatoria rubentis	USA	Watson et al. 1966
Euphorocera spp.	USA	Harding 1976
Euphorocera tachinomoides	USA	Oatman 1966; Harding 1976
Hypantrophaga sp.	USA	Harding 1976
Lespesia achaetoneura	USA	Oatman 1966
Lespesia archippivora	USA	Watson et al. 1966; Oatman & Platner 1969; Henneberry et al. 1991
Lespesia sp.	USA	Clancy 1969; Chamberlin & Kok 1986
Madremyia saundersii	USA	Oatman 1966; Oatman & Platner 1969
Metachaeta (=*Periscepsia*) *helymus*	USA	Clancy 1969
Phorocera sp.	USA	Sutherland 1966
Phryxe vulgaris	USA	Sutherland 1966
Sarcophaga spp.	USA	van den Bosch & Hagen 1966
Schizocerophaga leibyi	USA	Harding 1976
Siphona plusiae	USA	Clancy 1969; Harding 1976; Henneberry et al. 1991
Siphona sp.	USA	Oatman & Platner 1969; Oatman et al. 1983a
Voria edentata	India	Manjunath 1972
Voria ruralis	USA	McKinney 1944; Butler 1958b; Pimentel 1961; van den Bosch & Hagen 1966; Oatman 1966; Clancy 1969; Oatman & Platner 1969; Elsey & Rabb 1970a; Ehler & van den Bosch 1974; Wall & Berberet 1975; Harding 1976; Ehler 1977a; Jones 1982; Latheef & Irwin 1983; Oatman et al. 1983a; Chamberlin & Kok 1986; Gordon et al. 1987; Henneberry et al. 1991; Biever et al. 1992
Winthemia nr *montana*	USA	Harding 1976
Winthemia quadripustulala	USA	Allen 1925

Table 4.16.1 (cont'd) Parasitoids of *Trichoplusia ni*

Species	Country	Reference
DIPTERA		
TACHINIDAE (cont'd)		
Winthemia rufopicta	USA	Chamberlin & Kok 1986
Winthemia spp.	USA	Elsey & Rabb 1970b
Zenilla blanda blanda	USA	West 1925

Table 4.16.2 Some predators of *Trichoplusia ni* in USA

Species	Reference
DERMAPTERA	
LABIDURIDAE	
Labidura riparia	Strandberg 1981a,b Tawfik et al. 1972
HEMIPTERA	
ANTHOCORIDAE	
Orius insidiosus	Lingren et al. 1978
Orius tristicolor	Ehler et al. 1973; Ehler & van den Bosch 1974; Ehler 1977a; Wilson & Gutierrez 1980; Jones 1982; Jones et al. 1983
LYGAEIDAE	
Geocoris pallens	van den Bosch & Hagen 1966; Ehler et al. 1973; Ehler & van den Bosch 1974; Ehler 1977a; Wilson & Gutierrez 1980
Geocoris punctipes	van den Bosch & Hagen 1966; Barry 1973; Barry et al. 1974; Walker & Turnipseed 1976; Wilson & Gutierrez 1980; Reed et al. 1984
NABIDAE	
Nabis alternatus	van den Bosch & Hagen 1966; Barry 1973; Barry et al. 1974
Nabis americoferus	van den Bosch & Hagen 1966; Ehler et al. 1973; Ehler & van den Bosch 1974; Ehler 1977a; Stoltz and Stern 1979; Wilson & Gutierrez 1980
Nabis roseipennis	Reed et al. 1984
PENTATOMIDAE	
Alcaeorrhynchus grandis	McLain 1979
Euthyrhynchus floridanus	McLain 1979

Table 4.16.2 (cont'd) Some predators of *Trichoplusia ni* in USA

Species	Reference
Podisus maculiventris	Hayslip et al. 1953; Ignoffo et al. 1977; Marston et al. 1978; Richman & Whitcomb 1978; McLain 1979; Biever et al. 1982
Stiretrus anchorago	Richman 1977
HEMIPTERA	
REDUVIIDAE	
Sinea complexa	van den Bosch & Hagen 1966
Sinea confusa	van den Bosch & Hagen 1966
Sinea diadema	van den Bosch & Hagen 1966
Sycanus indagator	Greene & Shepard 1974
Zelus bilobus	Hayslip et al. 1953
Zelus exsaguis	Whitcomb and Bell 1964
Zelus renardii	van den Bosch & Hagen 1966
Zelus tetracanthus	van den Bosch & Hagen 1966
NEUROPTERA	
CHRYSOPIDAE	
Chrysopa lanata	Ru et al. 1975
Chrysopa nigricornis	van den Bosch & Hagen 1966
Chrysopa rufilabris	Ru et al. 1976
Chrysopa spp.	Pimentel 1961
Chrysoperla carnea	van den Bosch & Hagen 1966; Barry 1973; Barry et al. 1974; Ehler & van den Bosch 1974; Ehler 1977a; Wilson & Gutierrez 1980
HEMEROBIIDAE	
Hemerobius spp.	van den Bosch & Hagen 1966

Table 4.16.2 (cont'd) Some predators of *Trichoplusia ni* in USA

Species	Reference
COLEOPTERA	
CARABIDAE	
Calosoma affine	van den Bosch & Hagen 1966
Calosoma peregrinator	McKinney 1944
Labia analis	Reed et al. 1984
COLEOPTERA	
COCCINELLIDAE	
Ceratomegilla maculata fuscilabris	Pimentel 1961
Coccinella novemnotata franciscana	van den Bosch & Hagen 1966
Coccinella transversoguttata	Pimentel 1961
Cycloneda sanguinea	van den Bosch & Hagen 1966; Jones 1982
Hippodamia convergens	van den Bosch & Hagen 1966; Jones 1982; Jones et al. 1983
Hippodamia parenthesis	van den Bosch & Hagen 1966
Hippodamia quinquesignata punctulata	van den Bosch & Hagen 1966
Olla v-nigrum	van den Bosch & Hagen 1966
Paranaemia vittegera	van den Bosch & Hagen 1966
MELYRIDAE	
Collops marginellus	van den Bosch & Hagen 1966
Collops vittatus	van den Bosch & Hagen 1966
DIPTERA	
SYRPHIDAE	
Mesograpta marginata	Pimentel 1961
Sphaerophoria cylindrica	Pimentel 1961
Sphaerophoria menthastri	Pimentel 1961

Table 4.16.2 (cont'd) Some predators of *Trichoplusia ni* in USA

Species	Reference
DIPTERA	
SYRPHIDAE (cont'd)	
Sphaerophoria robusta	Pimentel 1961
Several species	van den Bosch & Hagen 1966
HYMENOPTERA	
VESPIDAE	
Mischocyttarus flavitarsis	Bernays & Montelor 1989
Polistes apachus	Cornelius 1993
Polistes metricus	van den Bosch & Hagen 1966; Hunt 1984; Greenstone & Hunt 1993
Vespula pensylvanica	Warren 1990
SPIDERS	
Misumena ratia	Lockley et al. 1989
Oxyopes salticus	Reed et al. 1984; Lockley & Young 1988
Pardosa spp.	Reed et al. 1984
Phidippus regius	Edwards & Jackson 1993, 1994
Phidippus spp.	Edwards & Jackson 1993, 1994
BIRDS	
Dendroica palmarum	Strandberg 1981a
Passerculus sandwichensis	Strandberg 1981a

More than 20 species of microorganism (viruses, bacteria, protozoa and fungi) are associated with *T. ni*, most of them isolated from field populations, but some from laboratory cultures. All were initially isolated from larvae, although at least one species of each group has also been isolated from pupae, adults and even eggs (Table 4.16.3). Details concerning the causative agents and the symptoms they produce are given by Ignoffo and Hostetter (1984). Many papers have been published in recent years to add details to the records in Table 4.16.3, especially in the field of viruses, but also adding to the range of other pathogens, such as a rickettsia-like organism (Browning et al. 1982). Naturally-occurring virus infection has been found to be a major mortality factor of *T. ni* larvae in the field, particularly late in the season when populations are high. A single-embedded nuclear polyhedrosis has been mass produced and applied with excellent results by a number of authors to several crops (Ignoffo and Hostetter 1984).

Table 4.16.3 Major pathogens of *Trichoplusia ni* (Ignoffo and Hostetter 1984)

VIRUSES	single-embedded nuclear polyhedrosis
	multiple-embedded nuclear polyhedrosis
	granulosis
	cytoplasmic polyhedrosis
BACTERIA	*Bacillus thuringiensis*
	Serratia marcescens
PROTOZOA	*Nosema trichoplusiae*
	Thelohania sp. nr. *diazoma*
FUNGI	*Aspergillus flavus*
	Beauveria bassiana
	Entomopthora gammae
	Entomopthora sphaerosperma
	Metarrhizium anisopliae
	Metarrhizium brunneum
	Nomuraea rileyi

Introductions for biological control of *T. ni*

There do not appear to have been any introductions of natural enemies specifically for cabbage looper, but rather for the complex of lepidopterous larvae with which it is almost always associated. Examples of such introductions are shown in Table 4.16.4.

BRAZIL

The natural enemies of *T. ni* larvae on cotton at 3 sites in Paraná Province included the fungus, *Nomuraea rileyi* (which killed 76% of larvae at one site), a virus disease (that killed up to 47% at two sites), the parasitoids *Copidosoma truncatellum* (reared from about 5% of larvae at 2 sites) and *Microcharops bimaculata* (reared from 7.5% of larvae at 1 site) and the fungus *Entomopthora* sp. (which killed 2.5% of larvae at 1 site) (Silva and Santos 1980). The natural enemies of *T. ni* on cotton in Mato Grosso are discussed by Bleicher et al. (1985) and on tomato in Sao Paulo by Gravena (1984).

CARIBBEAN

T. ni is usually a minor pest of Brassicaceae, although outbreaks occasionally cause serious defoliation of crops. A large number of predators attack larvae, in addition to the parasitoids that are listed in Table 4.16.5.

Table 4.16.4 Introductions for the biological control of lepidopterous larvae including *Trichoplusia ni*

Species	From	To	When	Result	Reference
HYMENOPTERA					
BRACONIDAE					
Cotesia marginiventris		Cape Verde Is	1981	+	Lima & van Harten 1985
Cotesia plutellae	India	Barbados, Jamaica	1969	+	Alam 1992
Cotesia ruficrus	Australia	USA	1981	?	McCutcheon et al. 1983
Microplitis (= *Microgaster*) *demolitor*	Australia	USA	1981	?	Shepard et al. 1983; Norlund & Lewis 1985
Microgaster rufiventris	Egypt	USA	1983	–	McCutcheon & Harrison 1987
ENCYRTIDAE					
Copidosoma floridanum	India	Barbados	pre 1985	+	Alam 1992
EULOPHIDAE					
Pediobius nr *facialis*	Japan	USA	pre 1983	*	Parkman et al. 1983

* no indication of field release

Table 4.16.5 Parasitoids and a fungus attacking *T. ni* in the Caribbean (Alam 1992)

Species	**% Parasitisation**	
	Jamaica	**Barbados**
BRACONIDAE		
Cotesia sp. (*glomerata* group)	20.0	
Cotesia plutellae	29.6–70.0	3.5
Glyptapanteles sp. (*vitripennis* group)		0.5– 2.0
CHALCIDIDAE		
Brachymeria sp.	2.4	
Brachymeria ovata		0.5
ENCYRTIDAE		
Copidosoma sp.	12.5	
Copidosoma floridanum		0.5–5.0
Copidosoma (*truncatellum* group)		25.8
EULOPHIDAE		
Euplectrus platyhypenae	4.2	
TACHINIDAE		
Winthemia nr *pinguis* and *Winthemia* nr *pyrrhopyga*		20.2–35.8
Winthemia sp.	1 specimen only	
ENTOMOPHTHORALES	9.5–80.0	

NORTH AMERICA

The cabbage looper is a widespread and often highly destructive pest of cabbage and other Brassicaceae southwards in North America, from about the level of Ontario in Canada. Throughout this range it is associated with up to about a dozen other species of Lepidoptera. It is third in importance to the cabbage white butterfly, *Pieris rapae*, and the diamondback moth *Plutella xylostella* in Canada (Harcourt 1963) and New York State (Pimentel 1961) and about as important as these in southwestern USA (Oatman and Platner 1969; Reid and Cuthbert 1957).

In Ontario the encyrtid wasp *Copidosoma truncatellum* is the most important parasitoid and populations are frequently destroyed by a polyhedral virus (Harcourt 1963). In New York State a polyhedral virus (40% mortality) was the major factor affecting *T. ni* populations in 1957 but less important (7%) in 1958 when predators (especially spiders), caused 2% to 3% mortality (Pimentel 1961). In northwestern USA up to 14% of *T. ni* larvae were parasitised on cabbage by the tachinid fly, *Voria ruralis* (Biever et al. 1992). In southern California up to 39% (av. 7.8%) of *T. ni* eggs were parasitised by *Trichogramma pretiosum*, which was also reared from *Plutella xylostella* eggs. Twelve species of parasitoid were reared from *T. ni* larvae and pupae, 7 of which were Hymenoptera and 5 Diptera (Table 4.16.1). These produced an average of 38.9% mortality, with a maximum of 66.7% in late autumn. The tachinid, *Voria ruralis*, was the dominant parasitoid, especially during autumn and winter months. The ichneumon, *Hyposoter exiguae*, and the encyrtid, *Copidosoma truncatellum*, occurred most commonly during the summer and autumn months, when the latter was associated with a nuclear polyhedrosis virus. Together (and particularly the virus) they were responsible for most of the 60% larval mortality. Pupal mortality was low (2.0%) and was due to the pteromalid *Pediobius sexdentatus* (Oatman and Platner 1969). Also in southern California, Clancy (1969) reared 5 wasps and 5 tachinid flies (Table 4.16.1) from *T. ni* larvae collected from annual weeds (*Malva* sp., *Chenopodium* sp.), mustard, tree tobacco (*Nicotiana glauca*) and lucerne. The fly, *Voria ruralis*, was the most abundant parasitoid in autumn and winter and *Copidosoma truncatellum* the most important wasp, the total parasitisation from all species ranging from 29.5% to 41.1%. A nuclear polyhedrosis virus killed 70.9% of larvae collected in summer from weeds and 63.8% from lucerne (Table 4.16.6). The mortality caused by the various natural enemies varied according to the season and host plant.

Henneberry et al. (1991) recorded 12 species of parasitoid from larvae of the loopers *T. ni* and *Autographa californica* on lettuce, lucerne, sugarbeet and cotton in southern California. Of these, the braconid *Microgaster brassicae* (30%) *Voria ruralis* (23%) and *Copidosoma truncatellum* (23%) were the most abundant, with parasitisation rates ranging from 0% to 91.8% according to season and crop. Average mortality from viral infection ranged between 0.6% and 7.2%, also depending upon the crop.

Thirteen parasitoid species reared from *T. ni* on tomatoes in southern California (Table 4.16.1) caused mean parasitisation rates of larvae of 51.4% and 70.5% and of eggs of 24.6% and 53.4% respectively in two successive years. *Hyposoter exiguae* and *Copidosoma truncatellum* were the most abundant larval parasitoids and *Trichogramma pretiosum* the most important species attacking eggs. The data on population trends and percentage parasitisation suggested that there was a density-dependent relationship between *T. ni* and its parasite complex on tomato (Oatman et al. 1983a).

In Arizona, the most abundant parasitoid of *T. ni* larvae collected from weeds and cultivated crops was *Voria ruralis*, which was present throughout the year, with peak abundance (up to 100%) in late autumn and winter (McKinney 1944; Butler 1958b; Brubaker 1968). Five wasps and 1 tachinid fly were reared from larvae, 1 tachinid from pupae and *Trichogramma*

Table 4.16.6 Natural enemies of *Trichoplusia ni* larvae in southern California from weed hosts, lucerne and tree tobacco (*Nicotiana glauca*) (from Clancy 1969)

Month	No reared	% pupating	% killed by					
			virus	all parasites	*Voria ruralis*	all other Tachinidae	*Copidosoma truncatellum*	all other Hymenoptera
1966			Collections from annual weeds					
May	94	2.1	63.8	34.0	4.3	11.7	10.6	7.4
June	286	12.6	57.3	30.1	7.7	9.8	4.9	7.0
July	327	4.6	70.9	24.2	4.0	10.1	5.5	4.6
Aug	280	6.1	44.3	49.6	16.1	6.4	25.4	1.8
Sept	193	18.6	31.6	49.7	12.4	9.3	30.0	
Oct	267	41.9	37.8	20.2	6.4	3.4	10.5	
Nov	162	47.5	25.9	26.5	9.3	1.2	16.0	
Dec	151	4.6	39.1	56.3	38.4	0.7	16.6	0.7
1967								
Jan	138	31.9	16.7	51.4	34.1	0.7	16.7	
Feb	63	61.9	11.1	27.0	11.1		15.9	
March	7	14.3	28.6	57.1			14.3	42.9
April	12	41.7	33.3	25.0	25.0			
May	120	60.0	15.8	24.2	16.7	1.7		5.8
Totals	2100	22.0	42.5	35.2	13.1	5.9	13.3	2.8
			Collections from lucerne					
	149	6.7	63.8	29.5	6.0	20.8	0.7	2.0
			Collections from tree tobacco, *Nicotiana glauca*					
	479	47.0	11.9	41.1	21.5	1.0	11.7	6.9

minutum from eggs collected from lettuce. In addition, the carabid beetle, *Calosoma peregrinator*, fed readily on *T. ni* larvae (McKinney 1944).

A study in southern Texas of the loopers *T. ni* and *Chrysodeixis includens* on a range of host plants revealed high levels (58% to 71%) of mortality of larvae and pupae by 29 parasitoid species (Table 4.16.1) during all but 4 months of the year, all of which existed at rather low levels (Harding 1976).

Turning to cotton in southern California, *T. ni* is a secondary pest and there is good evidence that natural enemies, in particular several predators, are mainly responsible for its generally low pest status. The 4 major predators there are larvae of the green lacewing, *Chrysoperla carnea* (which consume eggs and larvae) adults and nymphs of the bugs *Geocoris pallens* and *Orius tristicolor* (which prey upon eggs and small larvae) and adults and nymphs of the bug *Nabis americoferus* (which prey upon larvae of all sizes). Spiders, mantids, carabids, vespids and reduviid bugs are among predators that are also present in smaller numbers (Ehler and van den Bosch 1974; Ehler 1977a).

Eleven species of parasitoid have been reported from *T. ni* on cotton, of which the following are most important, although their combined effect is far less than that of the predators: *Trichogramma semifumatum* (an egg parasitoid), *Cotesia marginiventris*, *Hyposoter exiguae* and *Microgaster brassicae* (which attack small larvae and kill hosts when of medium size), *Copidosoma truncatellum* (an egg-larval parasitoid, which emerges from large larvae or prepupae), *Chelonus texanus* (an egg-larval parasitoid which kills medium sized hosts), *Voria ruralis* (which lays eggs on medium sized larvae and kills large larvae or prepupae), and *Patrocloides montanus* (a larval-pupal parasitoid which usually oviposits in large larvae). *Copidosoma truncatellum* is polyembryonic and *Voria ruralis* is often gregarious (Ehler and van den Bosch 1974).

A nuclear polyhedrosis virus was the only pathogen shown to cause *T. ni* mortality, particularly late in the season at peak density of *T. ni* larvae, when levels of 50 to 60% mortality have been observed.

All of the predators mentioned above are widely polyphagous. The first 4 parasitoids listed above had a restricted host range and the last 4 were host specific in the cotton ecosystem.

Disappearance of eggs and small larvae, assumed to be due to predation, was consistently the major mortality factor. Parasitisation of larvae by any parasitoid seldom exceeded 30%, the exception being that by *Copidosoma truncatellum* which often reached 50 to 75%. Detailed life table studies of *T. ni* on cotton were reported by Ehler (1977a).

It was suggested that the temporary nature of the cotton crop, and sufficient time each season for only 3 generations of the host, left parasitoids insufficient time to build up adequate numbers to thoroughly exploit *T. ni* populations. Also, the low density of *T. ni* due to the intense activity of predators early in each generation, impairs successful search by adult parasitoids, particularly those that are host specific (Ehler and van den Bosch 1974; Ehler 1977a).

If the reader is perhaps, somewhat uncertain of what conclusions to draw from the extensive data in the foregoing accounts, the studies of Jones et al. (1983a), dealing with the impact of parasitoids and predators on *T. ni* populations on celery in California, provide valuable insights. He concludes that naturally-occuring entomophagous arthropods do, indeed cause irreplaceable mortality of *T. ni* and that they should be considered a key part of any Integrated Pest Management program for the crop. Although parasitoids (principally *Trichogramma* spp., *Copidosoma truncatellum* and *Voria ruralis*, but also *Hyposoter exiguae*, *Microgaster brassicae*, *Cotesia marginiventris* and *Chelonus insularis*) can explain, for this crop, most mortality of eggs and of both small and medium sized larvae, it should not be concluded that predators are unimportant. It is possible that the additional small amount of mortality due to parasitoids is that required to suppress pest density to just below damaging levels. The parasitoids involved have a more restricted host range than the 2 most important groups of egg predators in celery, namely Coccinellidae (*Hippodamia convergens* and *Cycloneda sanguinea*) and Anthocoridae (*Orius tristicolor*) which are both widely polyphagous.

Major parasitoid species

Laboratory and field studies have been published dealing with many of the parasitoids listed in Table 4.16.1. Several of these species that have emerged as worthy of serious consideration as biological control agents are dealt with below.

Copidosoma truncatellum Hym.: Encyrtidae

Females of this small wasp oviposit in *T. ni* eggs of all ages and polyembryonic development occurs after hatching of the host larva. The host is later killed in the mature larval or prepupal stage. Either one or two eggs are inserted in a host egg during oviposition but, if the latter, generally only one parasitoid egg is fertile. Offspring are unisexual although, when 2 fertile eggs are laid, both males and females may emerge, an average of 1526 wasps per parasitised *T. ni* (Leiby 1926, 1929).

Young female wasps are better than old at searching for eggs. At 14.8°C and 28.9°C the period from egg to first adult emergence was 122.9 and 22.4 days respectively and the duration of a generation was 162.7 and 31.2 days. The life span of a female wasp fed on a diet of 20% levulose solution was 30.3 days at 14.8°C and 28 days at 35.6°C. Synchronisation of the parasite to *T. ni* was found to be nearly perfect at 25°C. At some temperatures the parasitoid killed host eggs and at others, larvae before the 5th instar: this resulted in the death of the contained parasitoids (Stoner and Weeks 1974, 1976).

T. ni larvae parasitised by *C. truncatellum* consumed 35% more food and had a 30% higher maximum weight than unparasitised larvae, which raises a concern for at least the short-term effect of biological control (Hunter and Stoner 1975). The mortality caused by *C. truncatellum* appeared to be density related (Ehler and van den Bosch 1974). Average parasitisation of *T. ni* eggs in the laboratory was 55.3% (McPherson 1993). However, the maximum recorded in cotton fields in southern California was 2.5% (Ehler 1977a).

C. truncatellum has been reported from larvae of Noctuidae, Geometridae, Cossidae and Coleophoridae (Peck 1963). However, Ehler (1977a) points out that it has been reported only from *T. ni* in Californian cotton (van den Bosch and Hagen 1966; Ehler and van den Bosch 1974) and that it appears to be specific in this environment. *C. truncatellum* has a Holarctic distribution, but its native home is not clear (Peck 1963).

Cotesia marginiventris Hym.: Braconidae

More eggs were laid by this generalist larval parasitoid in 2-day-old *T. ni* larvae than in younger or older larvae. The minimum development period from oviposition to adult emergence from the host was 6 days (Boling and Pitre 1970). Females were significantly more responsive to host odors after brief contact with host larval frass or host-damaged cotton leaves (Turlings et al. 1989). *C. marginiventris* from *T. ni* and 4 other species of noctuid larvae were found to contain a non-occluded, filamentous, baculo-like virus (Styer et al. 1987).

Hyposoter exiguae Hym.: Ichneumonidae

This solitary endoparasitoid is one of 3 main parasitoids of *T. ni* on cotton (Ehler 1977a) and other crops in California and has a modest ability to distinguish unparasitised from parasitised hosts (Beegle and Oatman 1975; Browning and Oatman 1984). The female prefers to oviposit in late 1st or 2nd instar *T. ni* larvae, although all instars are acceptable. When early instars are chosen, the host larvae generally die during the 3rd or 4th instar (Ehler 1977a). Parasites commencing their development in hosts 1-day-old took

13.85 days for development, whereas those starting in 10-day-old larvae required only 7.4 days (Smilowitz and Iwantsch 1975; Jowyk and Smilowitz 1978). The influence of temperature on development is discussed by Browning and Oatman (1981). Weight gain of *T. ni* larvae is severely depressed following parasitisation (Smilowitz and Iwantsch 1973; Iwantsch and Smilowitz 1975; Thompson 1982).

Successful parasitisation of *T. ni* larvae was correlated with host age, ranging from 83% to 88% in 1st, 2nd and early 3rd instars and declining in older larvae to 27% in mid 5th instar. Females deposited an average of 2.3 eggs in 1st instar and 1.3 eggs in 2nd instar larvae, superparasitisation declining in later instars (Smilowitz and Iwantsch 1975).

As many parasitoid eggs were laid in virus-infected host larvae as in healthy larvae. Of those females that oviposited in infected hosts, 60% transmitted infective doses of virus to 6% of healthy hosts subsequently exposed to them. Of female parasitoids that developed in virus-infected hosts, 90% transmitted infective doses to an average of 21% healthy host larvae exposed to them. *T. ni* larvae parasitised by *H. exiguae* required twice the dosage of virus for infection and the parasitoid completed development before the host larvae died (Beegle and Oatman 1974, 1975). Washed *H. exiguae* eggs do not develop to maturity on injection into *T. ni* larvae unless virus or fluid from the parasite oviduct is added (Vinson and Stoltz 1986). Because the effects of parasitisation by *H. exiguae* are observable within 24 hours of oviposition and prior to hatching of the parasitoid, it is probable that the *H. exiguae*-associated virus, rather than the developing parasitoid itself, is responsible for the metabolic changes produced (Thompson 1986).

Microgaster brassicae Hym.: Braconidae

This solitary endoparasitoid is an important mortality factor of *T. ni* larvae on both cabbage and cotton. The female usually oviposits in 1st and 2nd instar host larvae and the fully-grown parasite larva leaves through the lateral abdominal wall of the medium-sized host larvae to spin a greenish or grayish cocoon. The host larva often survives for a few days after parasitoid emergence (Ehler 1977a). Duration of parasitoid development from egg to adult ranges from 17.7 days at 21.2°C to 10.7 days at 32.2°C. Adult longevity ranged from 55.5 days at 15.5°C to 12.9 days at 32.2°C for males and from 76.4 days to 13.7 days for females. Total progeny is largest at 21.1°C, averaging 73.2 offspring per female. Rearing methods, mating, searching, ovipositional behaviour and interactions with other parasitoid species have been described (Browning and Oatman 1984, 1985).

M. brassicae is native to North America and appears to be specific to *T. ni* in cotton, although it is also known from the alfalfa looper *Autographa californica* on lucerne (Ehler 1977a).

Trichogramma minutum Hym.: Trichogrammatidae

When attacking eggs of *T. ni*, females reared from *T. ni* eggs were more fecund than those from *Sitotroga cerealella* and searched over larger areas for hosts (Marston and Ertle 1973). At 27°C and 50% RH *T. minutum* populations increased more rapidly than those of *T. platneri*. *T. minutum* does not feed from the host egg nor does it superparasitise eggs even when hosts are in short supply (Manweiler 1986).

Trichogramma platneri Hym.: Trichogrammatidae

After ovipositing in a host egg, females pierce it again and feed from exuding droplets of fluid. *T. platneri* superparasitised hosts when eggs were scarce. At about 27°C and 50% RH, *T. platneri* populations increased more slowly than those of *T. minutum* (Manweiler 1986). The maximum number of progeny bred from a single *T. ni* egg was 3 and 73% of male progeny emerged from the first eggs exposed to a female. Honey was shown to increase parasitoid longevity (Hohmann et al. 1988a, b).

Trichogramma pretiosum Hym.: Trichogrammatidae

This species can be reared from egg to adult in vitro (Hoffman et al. 1975). Females have a preference for young *T. ni* eggs, although eggs of all ages are accepted (Godin and Boivin 1994). A local Missouri, USA strain of *T. pretiosum* successfully parasitised *T. ni* eggs in field experiments, large host eggs producing more adults than small ones and these adults were more fecund and active than those from small eggs (Boldt et al. 1973). A Texan strain was effective in the laboratory against *T. ni* eggs, but not in the field. It was able to develop in the same *T. ni* egg as *Trichogramma evanescens* if eggs of both parasitoids were deposited on the same day (Parker and Pinnell 1972, 1974).

In Texas, naturally occurring *T. pretiosum* assisted in controlling *T. ni* on cotton in field cages (Lingren et al. 1978). In southern California, average parasitisation of *T. ni* eggs ranged from 3 to 47% in tomatoes when releases were made at the rate of 200 000 to 318 000 adult wasps per 0.4 ha (Oatman and Platner 1978). In Florida 3 releases 3 days apart of *T. pretiosum* at about 378 000/acre/release in a 1 acre field cage containing 7 crops resulted in substantial parasitisation of *T. ni* eggs and in suppression of larvae (Martin et al. 1976b). Laboratory and field cage studies with *T. pretiosum* were also carried out in California (Ashley et al. 1974) where female parasitoids produced from *T. ni* eggs were larger, more fecund and lived longer than those from artificial rearing hosts (*Plodia interpunctella* and *Sitotroga cerealella*) (Bai et al. 1992).

Voria ruralis Dip.: Tachinidae

Adults mate soon after eclosion and oviposition commences about 9 days later. Eggs laid on the host surface hatch within a minute and young larvae penetrate the cuticle and enter a muscle fibre. After about 3 days at 24°C the larva pierces a hole in the dorsal wall of the host abdomen through which it inserts its posterior spiracles into the air. After rapid growth of the parasitoid, the host dies and the parasitoid larva pupates within the host integument (Thompson 1915; Brubaker 1968). When *V. ruralis* oviposits on 1st instars, development is slower and mortality higher than in later instars, except the late 5th instar. Development was rarely completed when eggs were laid on 5th instars, unless they were laid on newly moulted individuals. Females laid an average of 310 eggs (Elsey and Rabb 1970a). Development time from egg to puparium ranged from 5.4 to 12 days, depending upon the temperature, and for the pupa 7 to 8 days at 24°C. Time from egg to adult varied from 19.4 days at 20°C to 10.7 days at 30°C (Brubaker 1968; Jackson et al. 1969).

Parasitisation by *V. ruralis* causes large larvae to eat less than normal (an average of 47% reduction (Soo Hoo and Seay 1972). Up to 85% parasitisation was observed in field cages, depending upon the numbers of mated *V. ruralis* released, with significant superparasitism at high parasitoid densities (Soo Hoo et al. 1974).

V. ruralis is one of 3 major parasitoids of *T. ni* on crops in Florida (Martin et al. 1982) and cotton in Arizona (Werner and Butler 1979) but was present only to the extent of 0 to 0.1% in larvae on lucerne in New Mexico (Gordon et al. 1987). In northwestern USA, it was the only parasitoid recovered and occurred in 0 to 14% of *T. ni* larvae (Biever et al. 1992). In Virginia, *V. ruralis* was present in 27% of larvae in 1981 and 17% in 1982 (Chamberlin and Kok 1986).

V. ruralis can survive, develop in, and emerge from virus infected larvae. However, it does not act as a vector, except occasionally as a mechanical one under very restricted conditions (Vail 1981).

V. ruralis is a widespread parasite and has been recorded as far north as Finland and as far south as Trinidad. It has been recorded from a range of Lepidoptera. In the United States it is known mainly from larvae of various Noctuidae, especially *T. ni*, but less frequently from the beet armyworm, *Spodoptera exigua*, and other associated species (Jackson et al. 1969; Ehler 1977a). Ehler and van den Bosch (1974) considered *V. ruralis* to be host specific to *T. ni* in Californian cotton.

Comment

It has not been feasible, except for a rather more comprehensive cover of parasitoids, to include any but the most relevant of the 2000 or so references to *T. ni* in the literature. Further details can be accessed via the bibliographies of Sutherland and Sutherland (1972, 1984) for earlier publications and via Commonwealth Agricultural Bureau Abstracts and Lingren and Green (1984) for much of the more recent literature.

Although *T. ni* is often regarded as a secondary pest of crops in its native North America, damaging numbers, nevertheless, occur from time to time, particularly when its natural enemies are killed or suppressed by broad spectrum insecticides applied for associated primary pests. Predators are often claimed to be more important than parasitoids in maintaining *T. ni* at sub-economic levels.

Regrettably most, if not all, of the major predators involved lack the degree of specificity nowadays considered necessary for introduction as classical biological control agents. For this reason, further consideration is restricted to the potential of parasitoids and viruses. Far more is known from southern California than elsewhere of the parasitoid species present and their interactions. The following discussion is thus somewhat geographically biased and it should be borne in mind that additional species in other regions may well have desirable characteristics, especially for their respective climatic conditions (see later).

In addition to the egg parasitoids (e.g. *Trichogramma pretiosum* and *T. platneri*), there are at least 4 other parasitoids worthy of serious consideration (*Copidosoma truncatellum*, *Hyposoter exiguae*, *Microgaster brassicae* (Hymenoptera) and *Voria ruralis* (Tachinidae)).

If host specificity considerations permit clearance of these species for introduction to a new area, a decision must still be taken on which, if not all, to establish. It may be useful, therefore, to review (and extend) the information presented earlier on their attributes and interactions.

Copidosoma truncatellum oviposits into the host egg, but hatches in the larva and takes about 36 days to develop to adult, so it is present throughout the entire larval period of its host. *Microgaster brassicae* oviposits in 1st and 2nd instar *T. ni* larvae and requires about 14 days to develop to adult. The mature 3rd instar parasitoid larva emerges from late 3rd or early 4th instar hosts after feeding for about 9 days. *Hyposoter exiguae* commonly oviposits into late 1st instar *T. ni* and emerges from late 3rd or early 4th instar hosts. It requires about 16 days from egg to adult at 25°C, the egg-larval period averaging about 10 days. *Voria ruralis* requires about 13 days from egg to adult. It will oviposit on all host instars, but development in most successful when 2nd or 3rd instars are parasitised. Larval development is then completed by the end of the 5th host larval instar (Browning and Oatman 1984). As a result of overlapping life cycles, two or more of these 4 species could inhabit a host larvae simultaneously, unless a species was able to discriminate between parasitised and unparasitised hosts.

As many as 10 adult *Voria ruralis* may emerge from a single host larva. When limited numbers of hosts are present, a female lays more than one egg on each larva. Excess eggs may result in premature mortality of the host larva and any immature parasitoids already within it. External oviposition probably prevents the ovipositing female from receiving sensory information about the presence of parasite eggs or larvae already within the host; and *V. ruralis* females will continue to oviposit as long as the host larva reacts with any movement.

Copidosoma truncatellum parasitises host eggs of all ages following antennal drumming and ovipositor insertion. Females are apparently able to discriminate between unparasitised eggs and those parasitised by other *C. truncatellum* females. *Microgaster brassicae* females insert their ovipositors in all host larvae whether or not parasitised by *Copidosoma truncatellum*, although they are weakly deterred from doing so in larvae already parasitised by other *M. brassicae* females or by *Hyposoter exiguae*. Parasitoid eggs were deposited in 91% of hosts previously unparasitised, whereas those already parasitised by *M. brassicae* or *H. exiguae* showed oviposition levels of 10 and 53% respectively, indicating a response to sensory information after insertion of the ovipositor. When *M. brassicae* oviposited in larvae already parasitised by *C. truncatellum*, the latter emerged from 77.5% of the larvae, whereas *M. brassicae* emerged from only 12.5%. However, when *M. brassicae* oviposited in larvae containing the slower-developing *Hyposoter exiguae*, the latter emerged from 16.7% of larvae and *M. brassicae* from 76.7%. *Hyposoter exiguae* showed little discrimination between unparasitised larvae and those parasitised by any of the other 3 species, although ovipositor insertion did not result in additional eggs in larvae already containing *H. exiguae*. High levels of parasitisation by *H. exiguae* occurred in host larvae already parasitised by *C. truncatellum*, possibly due to the delayed development of the latter. Nevertheless, only *C. truncatellum* emerged from such larvae. Further details of these and other interactions under laboratory conditions are given in the valuable paper by Browning and Oatman (1984). It is interesting that the parasitoid complex attacking *T. ni* on cotton in the field shows little change from season to season in species composition and relative importance. However, this does not enable a simple decision to be made on what impact there would be on abundance of *T. ni* (or on plant damage sustained) if one or more of the species was omitted from an introduction program. This applies particularly to *C. truncatellum*, with its feature of prolonging the feeding period of parasitised larvae.

A further factor to be taken into consideration is the crop or range of crops and the climatic conditions under which *T. ni* control is particularly desired, since the effectiveness of various parasitoid species is affected by both sets of factors.

Relevant to this statement are studies in northwest Florida, which reported that *Cotesia autographae*, *Cotesia marginiventris* and *Meteorus autographae* caused high *T. ni* mortality during spring and early summer in a mixed cropping system (Martin et al. 1982), and work in southern Florida reporting high mortality by *Diadegma insulare* of *T. ni* larvae on brassicas. Furthermore, *Stenichneumon culpator cincticornis* and *Vulgichneumon brevicinctor* appear important in New York State (Sutherland 1966), *Brachymeria ovata* in North Carolina (Elsey and Rabb 1970b), and *Achaetoneura archippivora* and *Eucelatoria armigera* in western United States (Martin et al. 1984).

This suggests that some parasitoid species that are not widely distributed can act as significant mortality factors under certain climatic or crop conditions. They might well have a very restricted host range, and would be available for consideration, if required.

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6 Index of scientific names of insects

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