

# CLASSICAL BIOLOGICAL CONTROL OF THE CITRUS LEAFMINER *PHYLLOCNISTIS CITRELLA STAINTON* (LEPIDOPTERA: GRACILLARIIDAE): THEORY, PRACTICE, ART and SCIENCE

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In any classical biological control program, it is important to know the origin of the pest so that well-adapted, effective natural enemies can be identified from the pest's center of origin. The citrus leafminer, *Phyllocnistis citrella* Stainton (Gracillariidae), is considered to be an Asian species (described in 1856 from India). Heppner (1993) listed the distribution of the citrus leafminer (CLM) as widespread throughout India and southern Asia, including China. However, Tan and Huang (1996) recently suggested that the CLM was first found in China in 1933. It is unclear whether their statement means the CLM had only recently invaded China in the 1930s, or whether it was recognized as a pest only then, or whether it was simply unrecorded in China before the 1930s. John Heppner (pers. comm.) indicated that specimens of the CLM from India collected prior to 1930 are present in the British Museum (Natural History) (BMNH), London, England. Two specimens collected from Sri Lanka were collected during the 1880-90 interval, and three specimens were collected in Malaysia in 1924 and one from South Africa was collected in 1908. No Chinese specimens collected prior to 1930 were found, but that may simply mean that, although the CLM was present there, no specimens were collected prior to 1930. If the CLM only colonized China during the 1930s, then importation of parasitoids of the CLM from China may not involve parasitoids from the center of origin of this pest's distribution unless the natural enemies migrated with the pest into China. If, in fact, the original distribution of the CLM was India, then additional efforts should be directed at examining the parasitoid fauna in that region.

During the 1930s, the CLM also was reported in Korea, Japan, the Philippines, Indonesia, Taiwan, Thailand, and Papua New Guinea, as well Cape Town, South Africa (Clausen, 1931; Hutson and Pinto, 1934; Hill, 1981). The CLM was first recorded in Australia in the Northern Territory in 1917 and was reported to have been eradicated; however, it invaded Australia again in 1940 (Smith and Beattie, 1996). The CLM was reported to be present in Saudi Arabia in 1960 (Ayoub, 1960). The status of the CLM in South Africa is confusing: in 1931 Clausen (1931) indicated that the CLM had arrived in South Africa recently (although a specimen in the BMNH was collected in 1908 in South Africa),

but Kamburov (1986) suggested that the CLM was new to South Africa in 1986, so it appears that it was not a serious pest prior to 1986. The CLM apparently spread to the Sudan, Yemen, Tanzania, and Ethiopia in Africa before 1980 (Badawy, 1967; Ba-Angood, 1977, 1978). The CLM was reported to be widespread on citrus in the Ivory Coast of Africa during the 1970s (Guérout, 1974) and in Nigeria by 1988 (Commonwealth Inst. of Entomology, London, pers. comm.). M. A. Hoy (unpublished) collected the CLM from citrus in Benin in West Africa in December 1996, so its distribution in African countries could be even greater than the above list.

Within the past three years, this pest has moved into additional citrus-growing regions of the world with incredible speed, often colonizing entire countries in less than a year. New invasions have occurred in nearly all citrus-growing countries in the Mediterranean (including Algeria, Cyprus, Egypt, Greece, Israel, Italy, Jordan, Lebanon, Libya, Malta, Morocco, Portugal, Spain, Syria, Turkey, Tunisia), the Caribbean (Bahamas, Cayman Islands, Cuba, Dominican Republic, Jamaica, Puerto Rico), Central America (Belize, Costa Rica, El Salvador, Guatemala, Honduras, Nicaragua, Panama) and South America (Argentina, Brazil, Colombia, Ecuador, Peru, Uruguay, Venezuela). In North America, it invaded Alabama, Florida, Louisiana, Texas, and Mexico. The invasion of the CLM has disrupted integrated pest management (IPM) programs developed for citrus in these locations.

Few other pests have spread over such a large area and have created so much concern in such a short period of time. It remains a mystery as to why the CLM failed to colonize citrus growing regions earlier in the century and why it has spread so far and so rapidly in the past few years. Quarantines and other regulatory barriers appear to have had little effect on restricting the spread of this pest in the past few years. The methods by which the CLM has been able to colonize large areas may be due to several factors: the CLM has a high rate of reproduction with multiple generations (up to 15 per growing season) per year; it can easily be spread by transport of nursery trees or infested foliage; increased global transport via ship and airplane enhance spread of many pest arthropods, perhaps including the CLM; the

CLM thrives in a diversity of climates (Mediterranean as well as subtropical and tropical); and adult moths are thought to have a highly effective dispersal behavior, although we have no detailed information about how far adults can fly.

The citrus leafminer invaded Florida during 1993 and was able to spread throughout the approximately 850,000 acres of citrus within a few months after its arrival despite efforts to delay its spread (Heppner, 1993). Management of the CLM is difficult. Applications of pesticides to control the CLM are seen as a short term solution in Florida (Knapp *et al.*, 1995, 1996a, b), because many pesticides are considered to be disruptive to the currently-effective biological control of numerous other citrus pests, including whiteflies, scales, and mites (for reviews of biological control of citrus pests in Florida see Browning, 1994a, b; Browning and Stimac, 1994; Childers, 1994). As a result, developing an IPM program for the CLM was considered to be critical, with biological control of the CLM having a key role to play.

## BIOLOGY AND EFFECT OF THE CITRUS LEAFMINER

The CLM female deposits eggs singly upon tender young citrus foliage (flush), preferring the midrib on the underneath of the leaf, although she will also deposit eggs on the top of leaves when population densities are high and or when the relative humidity is high. The larva immediately enters the leaf where it feeds on epidermal cells, producing broad serpentine mines in the leaves. High densities of leafminers result in twisted and damaged leaves that dry out, have reduced rates of photosynthesis and, under severe conditions, may defoliate. The prepupa prepares a pupal chamber at the edge of the leaf by folding the edge of the leaf down and binding it together with silk. After pupation, adults emerge and mate to begin the cycle again.

The adult moth is 2-3mm in length with a wingspan of 5-8mm and is greyish-white in color with black spots and four black stripes across each forewing. The length of the life cycle varies with temperature, averaging about 17 days at 25°C. The CLM has no known hibernal or aestival diapause; it appears to survive as larvae within mines in Florida during the winter and populations may be strongly suppressed by cool weather. In Japan, the CLM is reported to pass the winter in the adult stage (Clausen, 1931). In India, the CLM overwinters as larvae and pupae and has 9-13 generations per year (Pandey and Pandey, 1964). In Guangzhou, China, there are five generations a year (Huang *et al.*, 1989a), and predators and parasitoids were determined to be important control agents in late summer and autumn (Huang *et al.*, 1989b). Huang *et al.*, (1989c) reported on the life history of the CLM in Guangxi province, China, where it had 12 generations per year.

In Florida, at least 13 generations a year can occur and populations can become large by September and October. At high population densities, females may deposit eggs on tender stems and on young fruit, producing mines in both stems and fruit (Heppner, 1995). Because young trees produce flushed foliage more frequently, continuous populations can develop and CLM is particularly harmful to nursery plantings and in young groves. Young trees can be severely stunted or even die. On mature trees, the CLM damages new growth, which can have a detrimental effect on the growth and yield of producing orchards.

In China, economic damage is estimated to occur when the CLM damages more than 20% of the leaf area in young flush (Tan and Huang, 1996). The number of larvae required to cause this level of damage was estimated to be 0.74 larvae per tender leaf in southern China. In Thailand, treatments for the CLM are recommended when more than 50% of the flushes in pummelo orchards are infested (Morakote and Nanta, 1996). The economic injury level has not determined in Florida., although preliminary results by Stansly *et al.* (1996) indicate that negative effects were observed after the second year of infestation in Florida.

## MANAGEMENT OPTIONS IN FLORIDA

### Chemical Control

Despite the lack of extensive information on the effect of the CLM on tree growth and yield in Florida, the visual impact of foliar damage initially led many growers to apply insecticides in an effort to mitigate their effect. This tactic is expensive and generally ineffective, because none of the foliar products tested provided control for longer than about two weeks (Knapp *et al.*, 1996a, b; Peña and Duncan, 1993). Chemical control is an inappropriate management strategy for the CLM over the long term in Florida due to high costs, concerns about the development of resistance to pesticides by the CLM and other pests, disruption of biological control agents of other citrus pests, concerns about pesticide residues on food and in the ground water, negative effects on worker safety, and effects on non-target organisms in the environment. Resistance to pesticides has developed in CLM populations in China (Tan and Huang, 1996).

### Cultural Practices

CLM populations could be partially suppressed if tree flushing patterns could be modified so that long intervals occurred without flushes. Unfortunately, it is impossible to achieve this by altering irrigation and fertilization practices under Florida's subtropical climatic conditions because summer rainfall is abundant. In irrigated citrus production regions, this tactic may be feasible. Other management options, such as host plant resistance, were not feasible over the short term and there is no clear evidence that any varieties are intrinsically resistant to attack by the CLM (Villanueva-Jimenez and Hoy, 1996).

### Naturally-Occurring Biological Control

Indigenous natural enemies found attacking the CLM were expected to provide some control in Florida. The movement of parasitoids onto invading pest insects is common and new insect species typically accumulate an average of four parasitoid species (Cornell and Hawkins, 1993). The percentage of parasitism by native species on invading host insects is frequently moderate at high pest population density. However, Cornell and Hawkins (1993) concluded that native parasitoid complexes on introduced hosts ". . . are too young to be considered fully integrated associations. . . In other words, many native parasitoids are not physiologically, behaviorally, or phenologically well adapted to the novel host. . ." and that the ". . . period required for these complexes to attain richness and integration comparable to those on native hosts . . . may require between 100 and 10,000 years."

Browning and Peña (1995), Browning *et al.* (1996) and Peña *et al.* (1996) identified the following native parasitoids, all Eulophidae, on the CLM in Florida during 1993 and 1994:

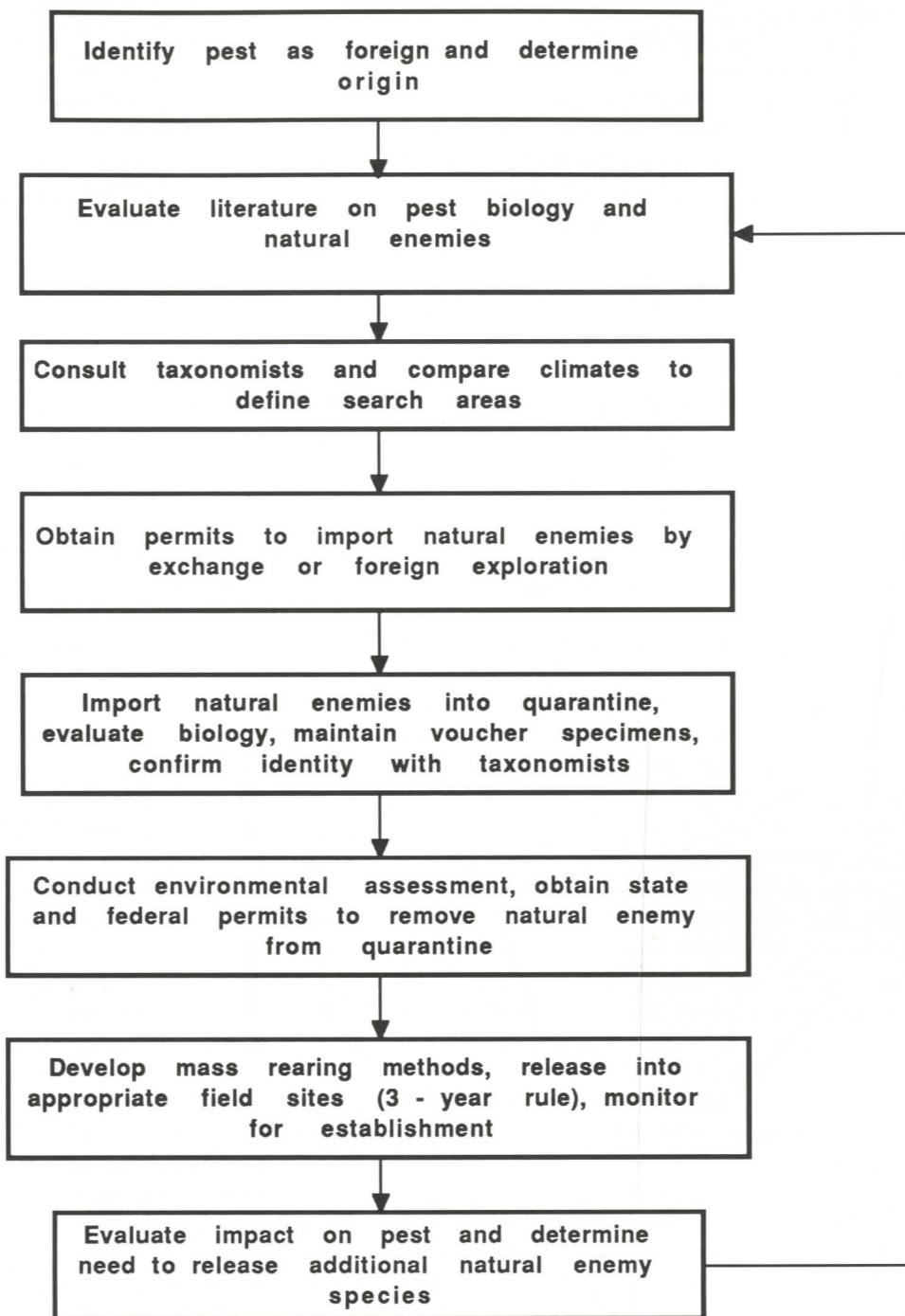


Fig. 1. Steps involved in a classical biological control project.

*Cirrospilus* n. sp., *Pnigalio minio* (Walker), *Closterocerus cinctipennis* Ashmead, *Horismenus* sp., *Elasmus tischeriae* (Howard), *Sympiesis* sp., and *Zagrammosoma multilineatum* (Ashmead). The parasitism levels achieved by native parasitoids varied, ranging up to 60%. Parasitism levels were lowest in late winter and early spring. Indigenous predators in Florida found attacking the CLM include green lacewing larvae (*Chrysoperla rufilabris* Burmeister) (Neuroptera: Chrysopidae), ants (including the red imported fire ant, *Solenopsis invicta* Buren) (Hymenoptera: Formicidae), thrips (Thysanoptera), and spiders (Araneae) (Browning and Peña, 1995).

The original hosts of these indigenous natural enemies are unknown. Some parasitoids are facultative hyperparasitoids, which generally have a broad host range. For example, *Horismenus* spp. are described as having diverse biological relationships with their hosts, some serving as primary parasitoids or hyperparasitoids of small Lepidoptera or as primary parasitoids of bruchids or curculionids, and two Nearctic species are hyperparasitoids in the egg cases of spiders (Burks, 1971). *Pnigalio minio* is the most abundant native solitary ectoparasitoid of larval CLM in south Florida, attacking third instar CLM larvae and prepupae (Duncan and Peña, 1996). We have observed this ectoparasitoid destroying

**Table 1.** When citing a species in the text, we used the name designated by the author of the paper, which means that the valid name is not always used. This list gives synonymized parasitoid names mentioned, as recommended by John LaSalle (pers. comm.).

Cited Name	Current valid name
<i>Chrysonotomyia</i> sp.	Species referred to as <i>Chrysonotomyia</i> sp. will probably refer to either <i>Closterocerus</i> or <i>Neochrysocharis</i> (Hansson 1994)
<i>Cirrospilus quadristriatus</i> (Subba Rao and Ramamani)	= <i>Cirrospilus ingenuus</i> Gahan
<i>Cirrospilus phyllocnistoides</i> Narayanan	= <i>Citrostichus phyllocnistoides</i> (Narayanan)
<i>Teleopterus delucchi</i> Boucek	= <i>Asecodes delucchii</i> (Boucek) The genus <i>Teleopterus</i> was synonymized with <i>Asecodes</i> (Hansson 1996)
<i>Tetrastichus phyllocnistoides</i> (Narayanan)	= <i>Citrostichus phyllocnistoides</i> (Narayanan)
<i>Tetrastichus</i> sp.	The species described in the literature from the CLM are <i>Quadrastrichus</i> sp. (sp. A of Heppner 1993 = <i>Quadrastrichus</i> ) (sp. B of Heppner 1993 = <i>Citrostichus phyllocnistoides</i> ) according to LaSalle
<i>Visnuela</i> sp.	This genus has been synonymized with <i>Zaommomedon</i>

pupae of the introduced endoparasitoid, *Ageniaspis citricola* Logvinovskaya, in Florida (Hoy and Nguyen, unpublished).

#### **Augmentative Biological Control**

The entomopathogenic nematode, *Steinernema carpocapsae* (Weiser), was tested in field trials in Australia, but was unable to provide adequate control of the CLM (Beattie *et al.*, 1995) and has not been studied in detail in Florida.

#### **Classical Biological Control**

Classical biological control was expected to provide additional, possibly more effective, biological control in Florida because host-specific natural enemies were expected to occur in the native geographic range of the pest (Hoy and Nguyen, 1994a). Classical biological control is based on the importation of host-specific natural enemies (parasitoids, predators, or pathogens) from the area of origin of the pest and their subsequent permanent establishment in the new habitat.

Classical biological control projects typically require several years, as a minimum, before their success or failure can be evaluated. For example, there is an unofficial "three year rule" in classical biological control, which means that it is considered prudent to allow a new natural enemy at least that much time to establish and disperse. Only after three years have elapsed without any evidence that an introduced natural enemy species has established is it considered appropriate to list it as a failure. Occasionally, some natural enemy species establish within the

three year interval but remain at extremely low densities so that they are undetected for many years.

The objective in classical biological control is to reduce population levels of the pest, ideally to a level below the economic injury level. Thus, one or more natural enemy species must establish, disperse, and increase sufficiently in density to suppress pest populations. While classical biological control has resulted in hundreds of successful biological control projects (Clausen, 1978; Laing and Hamai, 1976; Luck, 1981; Greathead, 1986; Frank and McCoy, 1993), there is considerable debate over how best to accomplish a successful program. For our program, we have assumed that the CLM is native to India and southeast Asia.

#### **COMPONENTS OF A CLASSICAL BIOLOGICAL CONTROL PROGRAM**

Classical biological control programs require a series of steps and may require many years to complete (Fig. 1). The final program phases (evaluation of natural enemy effect and evaluation of costs and benefits) are rarely conducted because funding is often unavailable. Florida growers' groups may fund a classical biological control project for a few years, but rarely fund efforts to evaluate a program once the natural enemies have become established and appear to have reduced pest populations. Furthermore, if a new pest invades, they may decide that scarce funding

should be diverted to combat the new problem.

During all phases of a classical biological control program, taxonomic services are a critical component (Caltagirone, 1985; Rosen, 1978). This is particularly true for the CLM project because many parasitoids in Asia can be identified only to the genus level. Furthermore, many of the published names of parasitoids have been changed as taxonomic revisions have occurred, making the literature confusing to the novice (Table 1). Identifying appropriate collection sites is also difficult because relatively few faunistic surveys have been conducted on the natural enemies of the CLM in India and southeast Asia. These gaps severely limit the information available for making choices about which species to import.

Once a promising natural enemy species has been identified, imported, evaluated in quarantine, reared, and released, it may fail to establish in the new environment. Sometimes failure to establish may be due to problems in matching climatic requirements of the imported species or biotype. Sometimes, even when a close match in climate appears to have been made, other significant factors essential to the establishment of the species may not be present in the new environment or establishment may be affected by release rates (Hopper and Roush, 1993). Sometimes the process of laboratory rearing results in loss of effectiveness due to genetic, behavioral, or other factors. Depending upon one's viewpoint, the establishment of approximately 30% of species introduced into new environments is either high or low. In any case it is difficult to predict whether a particular natural enemy species will establish or whether it will, after establishment, provide effective control of the target pest (Hassell, 1986; Hawkins *et al.*, 1993; Hopper *et al.*, 1993; Hoy, 1985; Price, 1972; Van Driesche and Bellows, 1993). Furthermore, even after establishment, the new natural enemies may require several years before natural enemy populations stabilize and efficacy can be appropriately evaluated.

## ISSUES TO CONSIDER IN DEVELOPING A CLASSICAL BIOLOGICAL CONTROL PROGRAM

An effective classical biological control program requires effective natural enemies. In choosing which natural enemy species and in what order to import them, a variety of issues should be considered, including issues of environmental risk. Our focus is on the role of parasitoids of the CLM.

### Qualities of Effective Parasitoids

The interactions of natural enemies and pests have been analyzed from various viewpoints in an effort to improve the outcomes of classical biological control projects (Askew and Shaw, 1986; Bellows *et al.*, 1992; Ehler, 1990; Hassell, 1986; Kareiva, 1990; Luck *et al.*, 1988; Waage, 1990). Many analyses have involved examining historical examples of successes and failures. Huffaker *et al.* (1971) noted that "Virtually all of the most outstanding cases of biological control have involved rather host-specific enemies . . ." and that ". . . a species upon which has evolved a highly specific (stenophagous) and effective enemy will, because of that very effectiveness, not be found to support a wide complex of enemies". They also note that in the empirical record there is ". . . ample proof that in general the introduction of a sequence of rather *highly specific* [italics added] species is

a desirable practice."

Other criteria have been associated with effective classical biological control agents (Rosen and Huffaker, 1983), such as a density-dependent relationship between pest and natural enemy. A *density-dependent* natural enemy responds to changes in the population density of the pest, effecting an increasing percentage of kill with increasing pest density. Accordingly, an effective natural enemy should be highly density-dependent, even in the range of low pest densities, so that a low density equilibrium is maintained (Rosen and Huffaker, 1983). An effective natural enemy is defined as capable of responding, both functionally and numerically, to changes in pest population density, as well as to changes in its own density. Other desirable and interrelated attributes are cited by Rosen and Huffaker (1983): *good searching capacity, a high degree of host/prey specificity, a high intrinsic rate of increase relative to that of the pest, and adaptation to the new habitat.*

### Role of Generalist Natural Enemies

Introduced biological control agents should not have an unintended effect on nontarget organisms and should not reduce biodiversity or annihilate native species (Howarth, 1991; Nafus, 1993; Samways, 1988; OTA, 1993). There are no known examples in which arthropod classical biological control agents have resulted in the complete elimination of a nontarget arthropod species. There are, however, sometimes unintended results when polyphagous species are released. For example, of 100 species of exotic organisms introduced into Guam, 27 species were released against seven lepidopterous pests (Nafus, 1993). Nafus identified mortality factors of two nontarget butterfly species and found that introduced *generalist* parasitoids and predators had a significant negative impact on these native butterflies. He cautioned that parasitoids and predators with a broad host range should not be introduced unless they have a demonstrated control potential for the target pest, and have sufficient economic or environmental benefits to offset any negative environmental costs.

Samways (1988) rated the risks of damage to indigenous arthropod species by classical biological control agents and concluded there is a high risk associated with the importation of polyphagous arthropod natural enemies. Despite this concern about potential harm, Samways (1988) noted that, while classical biological control has been widely practiced, it ". . . has to date not thwarted any conservation programme, making the two activities compatible both ethically and economically. Nevertheless, so as to keep natural environments as pristine as possible, new introductions should be highly selective and given the extreme care and planning that such an irreversible exercise demands".

### Role of Hyperparasitoids

Facultative hyperparasitoids are parasitoids that are able to act either as primary parasitoids or as parasitoids of one or more primary parasitoids. Endophagous hyperparasitoids feed inside their host, while ectophagous species feed externally. *Direct hyperparasitoids* attack the primary parasitoid directly by ovipositing in or on it; *indirect hyperparasitoids* attack the primary parasitoid's phytophagous host and thus only attack the primary parasitoid itself indirectly. The female hyperparasitoid oviposits into the phytophagous host whether it is parasitized or

not (Sullivan, 1987).

The role of hyperparasitoids in biological control is highly controversial (Rosen, 1981), with some arguing that facultative hyperparasitoids will be positive additions to a biological control program if their impact on pest density is greater than that obtained in the absence of the facultative hyperparasitoid and if the facultative hyperparasitoid does not have a significant negative impact outside the target pest population. Others argue that facultative hyperparasitoids should never be released.

If facultative hyperparasitoids could discriminate between parasitized and unparasitized hosts and preferred to attack unparasitized hosts, their negative effects on pest population suppression could be limited. The behavior of parasitoids is rarely evaluated sufficiently to determine whether this type of behavior is common, although Moore and Kfir (1995) showed that the gregarious euphorid endoparasitoid *Tetrastichus howardi* (Olliff) is a facultative hyperparasitoid and preferred lepidopteran hosts to their parasitoids. They found that if *T. howardi* had previously experienced parasitizing a particular host its preference for that host increased, and under laboratory conditions *T. howardi* was able to discriminate between parasitized and unparasitized hosts. Under laboratory conditions, *T. howardi* initially preferred parasitized hosts but two days later preferred unparasitized hosts. Whether other euphorid facultative hyperparasitoids behave in this manner is unknown.

There is clear agreement that *obligate hyperparasitoids* should not be introduced in classical biological control programs. Hyperparasitoids (both obligate and facultative) usually have a relatively broad host range, are already usually present in the new habitat, and are thus likely to attack newly-introduced stenophagous primary parasitoids. Little can be done to reduce the negative impact of indigenous hyperparasitoids (Sullivan, 1987).

In the USA, the general consensus is that known *facultative hyperparasitoids* should not be released. Sullivan (1987) concluded that facultative hyperparasitoids, even those in which the hyperparasitic habit is rare, probably should not be introduced until additional information is available. Certainly they should not be introduced as a first option, and Sullivan (1987) suggested that "In a serious pest situation where there are no normal primary parasitoids available for biological control, perhaps a calculated risk should be taken as a last recourse." Such releases may not provide adequate control of the target pest, however, because hyperparasitoids usually lack many of the traits considered valuable in achieving effective pest population suppression, such as a density-dependent response to the pest population.

Bennett (1981) described several examples in which hyperparasitoids have negatively affected classical biological control programs. Recently, *Stenomesius japonicus* (Ashmead), a facultative hyperparasitic euphorid apparently native to Australia, was found parasitizing an introduced biological control agent, *Dialectica scalariella* (Zeller), Gracillariidae, introduced to control the weed *Echium plantagineum* L. in Australia (James and Stevens, 1992). In this case, *S. japonicus* was acting as a parasitoid and not as a hyperparasitoid; *S. japonicus* apparently has a wide host range (as is common in many hyperparasitoids) and has been recorded from the Gelechiidae, Pyralidae, Noctuidae, and various Gracillariidae, including the CLM (Kamijo, 1976). Thus,

if *S. japonicus* were introduced to control the CLM elsewhere in the world, it might have a harmful effect on any biological control program in that country directed against the weed *E. plantagineum*.

Bennett (1981) described some examples of outstanding biological control despite the fact that the primary parasitoids were attacked by hyperparasitoids, but he did not describe any examples in which hyperparasitoids played a beneficial "regulatory role". The effect of indirect hyperparasitoids on classical biological control programs apparently has not been documented.

## BIOLOGICAL CONTROL OF THE CLM

We describe below what we know about the natural enemies of the CLM in Asia, evaluate the current status of the classical biological control program in Florida, and identify research needed to improve our efforts in the classical biological control of this citrus pest. We hope this review will be of value to others interested in classical biological control of the CLM.

### World Fauna of Parasitoids

LaSalle and Schauff (1996) reported on 36 genera of chalcidoid parasitoids in six families identified from the CLM from around the world, including areas in which the CLM has recently invaded. They noted that the recruitment of species and genera of parasitoids by the CLM as it invades new regions is remarkable and of interest not only to researchers in biological control and systematics, but also to scientists studying biodiversity and conservation biology.

The 36 genera identified by LaSalle and Schauff (1996) are primarily from one family, the Eulophidae. Parasitoid species in 30 different euphorid genera have been found attacking the CLM. The asterisks (\*) after the following names indicate that these genera are not known to attack the CLM in Asia, but are new recruits to the CLM in its new geographic range: *Achrysocharoides* Girault, *Apleurotropis* Girault, *Apotetrastrichus* Graham\*, *Ascotolinx* Girault, *Baryscapus* Forster\*, *Chrysocharis* Forster, *Chrysocharodes* Ashmead\*, *Cirrospilus* Westwood, *Citrostichus* Bouček, *Closterocerus* Westwood, *Diglyphus* Walker\*, *Elachertus* Spinola, *Galeopsomyia* Girault\*, *Holcopelte* Forster, *Horismenus* Walker\*, *Kratoysma* Bouček, *Neochrysocharis* Kurdjumov, *Notanisomorphella* Girault\*, *Pediobius* Walker, *Pleurotropopsis* Girault, *Pnigalio* Shrank, *Quadrastichus* Girault, *Ratzeburgiola* Erdos\*, *Semielacher* Bouček, *Stenomesius* Westwood, *Sympiesis* Forster, *Teleopterus* Silvestri, *Tetrastichus* Haliday, *Zagrammosoma* Ashmead\*, and *Zaommomentedon* Girault.

In addition to the Eulophidae, a few genera of parasitoids from the Elasmidae, Encyrtidae, Eupelmidae, Eurytomidae, and Pteromalidae have been found attacking the CLM. In the Elasmidae, only species in the genus *Elasmus* Westwood have been recorded (LaSalle and Schauff, 1996). In the Encyrtidae, only species in the genus *Ageniaspis* Dahlbom have been recorded from the CLM. In the Eupelmidae, only species in *Eupelmus* Dalman have been found attacking the CLM. In the Eurytomidae, only *Eurytoma* Illiger and in the Pteromalidae, only species in the genera *Asaphoideus* Girault and *Pteromalus* Swederus\* have been identified as parasitoids of the CLM (LaSalle and Schauff, 1996).

### Asian Fauna

One or more species of encyrtids (*Ageniaspis citricola* Logvinovskaya from Taiwan and Vietnam and "*Ageniaspis* sp." from Indonesia, Saudi Arabia, and Thailand), two braconids (*Bracon* sp. from the Philippines and *Microbracon phylloconistidis* Muesebeck from Indonesia), two elasmids (*Elasmus* sp. and *Elasmus zehntneri* Ferrière from the Philippines and West Java), one or two eurytomid species (*Eurytoma* sp. from Sri Lanka and Thailand), one pteromalid (*Asphoideus niger* Girault from Australia) and 26 eupophids were recorded as attacking the citrus leafminer in Asia in the review published by Heppner (1993).

Of the 26 eupophids listed by Heppner (1993), some were identified by genus only. For example, the following eupophids were not identified to species in some collection sites, perhaps because they were undescribed species: *Chrysocharis* (Japan), *Chrysonotomyia* (Japan), *Cirrospilus* (Japan), *Holcopelte* (Japan), *Kratosyma* (Thailand), *Pleurotropopsis* (Japan), *Pnigalio* (Japan), *Semielacher* (Papua New Guinea), *Sympiesis* (Australia, Taiwan), *Teleopterus* (Thailand), and *Tetrastichus* (Japan, Taiwan, Thailand).

Nine eupophids listed by Heppner (1993) were identified to species in some locations: *Ascotolinx funeralis* Girault (Australia), *Citrostichus phylloconistoides* (Narayanan) (India, Oman, Afghanistan, Pakistan, S. China, Taiwan, India), *Cirrospilus phylloconistis* (Ishii) (Japan, Taiwan), *Cirrospilus quadrifasciatus* (Rao and Ramamani) [now a synonym of *C. ingenuus* Gahan] (India, Thailand), *C. ingenuus* Gahan (Java and the Philippines), *Closterocerus trifasciatus* Westwood (Japan, Thailand), *Kratosyma citri* Bouček (New Guinea), *Semielacher petiolatus* (Girault) (Australia), *Stenomesius japonicus* (Japan, Korea, China, India, Pakistan, Egypt, Senegal, S. Pacific), *Sympiesis striatipes* (Ashmead) (Japan, Thailand), and *Zaommomentedon brevipetiolatus* Kamijo (Japan, Thailand).

After surveying the literature cited in Heppner's (1993) list, it is difficult to determine which are potentially important natural enemy species for a classical biological control program. Relatively little is known about the biology, ecology, and behavior of these species, including, in some cases, such basic information as which host stage it attacks, which stage it emerges from, its host range, and whether it is a solitary or gregarious endoparasitoid or ectoparasitoid.

Surveys in southeast Asia suggest that different parasitoids predominate in different countries, as described below on a country-by-country basis. The number of species listed by Heppner (1993) may underestimate the number attacking the CLM in Asia. Our experiences in classical biological control programs suggest it is likely that several cryptic species exist. Furthermore, different biotypes may also exist that have important biological attributes that could affect their efficacy as natural enemies (Caltagirone, 1985; Rosen, 1978). Little information is available about the host range of most parasitoids or about their ability to be facultative hyperparasitoids, information which is crucial for evaluating risks of classical biological control programs. Surprisingly little information is available about the ability of these natural enemies to suppress pest populations in Asia. CHINA.—Tan and Huang (1966) reported that the CLM is attacked by four or five parasitoid species in Guangdong Province, and

that at least seven parasitoids attack the larvae and three species attack the pupae in Fujian Province. *Tetrastichus phylloconistoides* (Narayanan), *Elachertus* sp., *Chrysonotomyia* spp., *Apleurotropis* sp., and the pupal parasitoid *Cirrospilus quadrifasciatus* were found, with the dominant species being *T. phylloconistoides* and *C. quadrifasciatus* in Guangdong Province and *Elachertus* sp. in Fujian Province. In addition, predatory lacewings (*Chrysopa boninensis*, *C. sinica*) and the predatory bug *Orius minutus*, ants, and spiders are predators of CLM larvae. If, in fact, the CLM only invaded China in the 20th century (as suggested by the statement of Tan and Huang (1996), noted earlier [p. 1]), it is not clear whether these are indigenous parasitoids that moved on to the CLM in China or whether they moved with the CLM when the CLM invaded China.

Chen and Lee (1986) and Chen and Luo (1987) observed the eupophid *Elachertus* sp. attacking the CLM in Fujian, China. This ectoparasitoid had 14 to 17 generations per year, and exhibited parasitism levels of 40 to 54%. Chen *et al.* (1989) reported on the biology of the green lacewing, *Chrysopa boninensis* Okamoto (Neuroptera: Chrysopidae), as a predator of the CLM.

Ding *et al.* (1989) described the biology of the eupophids *Tetrastichus phylloconistoides* and *Cirrospilus quadrifasciatus*.

**INDIA.**—India is rich in *Citrus* species and it might be the original home of the CLM. If so, we would expect India to have a number of parasitoids well adapted to the CLM, and possibly species that are specific to the CLM. Unfortunately, the literature on parasitoids of the CLM in India appears to be sparse. Batra and Sandhu (1981c) found the eupophids *Cirrospilus quadrifasciatus* (now a synonym of *C. ingenuus*) and *Tetrastichus phylloconistoides* attacking the CLM in the Punjab, with maximal mean parasitism ranging from 30-47% in August and September. Narayanan (1960) described the new eupophid species *Cirrospilus phylloconistoides* from the CLM in India. Rao and Ramamani (1996) described the biology of the two eupophids *Cirrospiloideus phylloconistoides* (Narayanan) and *Scotolinx quadrifasciata* and noted that few parasites have been recorded from the CLM in India.

Little other information is available on the natural enemies of the CLM in this region, and numerous papers report that the CLM is heavily treated with pesticides (Batra and Sandhu, 1981a,b; Bhatia and Joshi, 1991; Bhumannavar, 1987; Maheshwari and Sharma, 1986; Nagalingam and Savithri, 1980; Radke and Kandalkar, 1990; Reddy *et al.*, 1988; Shevale *et al.*, 1987). This suggests either that effective natural enemies of the CLM are absent in India, or that other pests of citrus require chemical control that is disruptive to effective biological control of the CLM.

**INDONESIA.**—Voûte (1935) indicated that *Ageniaspis* was an important parasitoid of the CLM there. He also indicated that parasitism rates were highest where the young trees were shaded.

**JAPAN.**—Kamijo (1990) described the eupophid *Zaommomentedon brevipetiolatus* Kamijo from the CLM in Japan. Ujiye (1988) listed 13 species (one braconid, 11 eupophids, one elasmid) of parasitoids from larvae and pupae of the CLM in Japan. Among the eupophids, *Tetrastichus* sp. were dominant in most areas, with *Chrysocharis* sp. abundant in some. *Sympiesis striatipes*, *Tetrastichus* sp., *Visnuella* sp., and *Chrysocharis* sp. were abundant in some sites.

Ujiye and Adachi (1995) sampled parasitoids of the CLM from Japan and Taiwan during 1984-1987 and 1990-1993. They found 24 chalcidoid parasitoids emerging from larvae and pupae of the CLM, including one encyrtid, one eupelmid, one elasmid, and 21 eulophids. They found that the eulophids *Sympiesis striatipes*, *Quadrastichus* sp. (A), *Chrysocharis pentheus* (Walker), *Achrysocharoides* sp., and *Cirrospilus* sp. were abundant.

**KOREA.**— Catling *et al.* (1977) reported that the CLM was a serious pest in sprayed and unsprayed groves and that they observed no parasitoids.

**PAKISTAN.**— Karimullah (1988) reported on the chemical control of the CLM on citrus in Pakistan but did not provide information on natural enemies.

**PHILIPPINES.**— Barroga (1968) indicated that *Ageniaspis* sp., *Elasmus zehntneri*, *Cirrospilus ingenuus* Gahan, and *Bracon* sp. caused considerable mortality to the CLM between 1961 and 1963.

**TAIWAN.**— Lo and Chiu (1986) reported that *Ageniaspis citricola*, *Cirrospilus ingenuus* and *Tetrastichus* sp. attacked the CLM in Taiwan. Ujiye and Adachi (1995) found that *Citrostichus phylloconistoides* (Narayan), *Cirrospilus quadristriatus* (Rao and Ramamani), and *Quadrastichus* sp. (A) were abundant in Taiwan. Ujiye and Adachi (1995) suggested that because males of *S. striatipes*, *Quadrastichus* sp. (A), *Cit. phylloconistoides*, *Ch. pentheus*, *Achrysocharoides* sp., and *Teleopterus delucchii* Bouček emerged from smaller host larvae than their females, females of these species tend to deposit fertilized eggs on larger hosts and unfertilized eggs on smaller ones.

**THAILAND.**— Ujiye and Morakote (1992) surveyed the parasitoids of the CLM in Thailand, and Ujiye *et al.* (in press) provided a key to parasitoids of the CLM collected in Central and Northern Thailand, Japan, and Taiwan. Morakote and Nanta (1996) reported that three predators and 13 parasitoids attack the CLM in Thailand. The predators are two green lacewings, *Ankylopteryx octopunctata* and *Chrysopa basalis* (Neuroptera: Chrysopidae), and an unnamed ant. The parasitoids include: *Quadrastichus* sp., *Citrostichus phylloconistoides*, *Teleopterus* sp., *Cirrospilus ingenuus*, *Sympiesis striatipes*, *Closterocerus trifasciatus* Westwood, *Zammommentedon brevipetiolus* Kamijo, *Kratoysma* sp., *Ageniaspis citricola* and *Eurytoma* sp. The most abundant species were *A. citricola*, *Quadrastichus* sp., *C. ingenuus*, and *Teleopterus* sp.

Morakote and Ujiye (1992) reported that *Ageniaspis* sp. was the most dominant and important biological control agent. Smith and Papacek (1993) identified at least nine parasitoids in Thailand, and listed the larval parasitoids *Tetrastichus* sp. and *Citrostichus phylloconistoides* and the pupal parasitoids *Cirrospilus quadristriatus* and *Ageniaspis citricola* as the most important. In one location where few pesticides were applied, *A. citricola* parasitized 87% of the CLM present (Smith and Papacek 1993).

#### Parasitoid Communities of Other Leaf-mining Gracillariiid

##### Moths

While relatively little is known about the community structure of parasitoids of the CLM, other gracillariid moths and their assemblage of parasitoids have been studied in some detail. Analysis of their community structure under natural conditions could provide some clues as to the number of parasitoid species

and their host relationships that we might expect with parasitoids of the CLM.

Askew and Shaw (1986) studied the community structure of parasitoids of leafminer (*Phyllonorycter*) complexes on a range of host trees and found that leafminer complexes tend to have large numbers of parasitoids, ". . . which are relatively polyphagous idiobionts, mostly Eulophidae, which very often function as facultative hyperparasitoids."

Sato (1995) studied parasitoids found on *Phyllonorycter* leafminers on two oak species in northern Japan and compared them with those found on two other oak leafminer species in central Japan. He examined species richness, composition, and levels of parasitism at different host stages among the parasitoid assemblages. The mean number of parasitoid species per host species in Japan averaged 3.1, similar to that in the United Kingdom (average = 4.1 parasitoid species/host). Idiobionts (potential generalists) exceeded koinobionts (specialists) in species number, with 63% of the parasitoids being generalists. Thus, the published record suggests that eulophid polyphagous parasitoids of the CLM will be abundant in its native range, with some eulophids functioning as facultative hyperparasitoids.

#### CURRENT STATUS OF CLASSICAL BIOLOGICAL CONTROL OF CLM

##### Florida

A classical biological control project was initiated in February 1994 in Florida (Hoy and Nguyen, 1994a). The encyrtid *Ageniaspis citricola* was identified as a high priority species for introduction into Florida because it had been reared, evaluated, and released by Australian scientists (Beattie and Smith, 1993; Neale *et al.*, 1995). It is an endoparasitoid and appears to have a narrow host range. Its systematics and biology (Logvinovskaya, 1983; Beattie and Smith, 1993) were better known than those of the other species listed by Heppner (1993). Through the assistance of Australian scientists Dan Smith and Dan Papacek, both *A. citricola* and *Cirrospilus quadristriatus* [= *C. ingenuus* Gahan] were collected in Queensland, Australia in March 1994 and successfully imported into quarantine in Florida (Hoy and Nguyen 1994b).

Rearing methods were developed (Smith and Hoy, 1995) and releases of *A. citricola* were begun in early May 1994 throughout Florida with the assistance of Phil Stansly, Jorge Peña, David Hall, Robert Bullock, Harold Browning, and Joe Knapp, who identified appropriate Florida release sites and began to monitor establishment and effect (Hoy *et al.*, 1995). Evaluations during 1994-95 indicated that *A. citricola* established, multiplied, dispersed, and overwintered in the majority of the Florida release sites. In some sites, parasitism of CLM pupae was found to be as high as 99% only 15 months after initial releases and parasitism levels of 60-80% were common (Hoy *et al.*, 1995). As of this writing (October 1996), *A. citricola* appears to have colonized most of Florida's citrus groves, or over 850,000 acres (Hoy and Nguyen, 1994d; Knapp *et al.*, 1995; Hoy *et al.*, 1995, 1997). A late spring and the unavailability of adequate hosts early in the spring of 1996 resulted in a lag in populations of *A. citricola* and the CLM (Robert Bullock and Mark Pomerinke, pers. comm.). Despite the lag in parasitoid and pest populations during the

spring of 1996, the parasitoid clearly overwintered successfully during 1995-96 and rebounded during the 1996 growing season. Parasitism rates of CLM pupae by *A. citricola* in October 1996 averaged 80% in door yard citrus and about 60% in commercial groves. This parasitoid is well established, widely distributed, and abundant. It has multiplied and dispersed long distances and is the dominant natural enemy of the CLM in Florida. The ability of *A. citricola* to suppress CLM populations below an economic injury level has not yet been assessed.

#### Louisiana

*A. citricola* was supplied to Seth Johnson at Louisiana State University for rearing and release in Louisiana citrus groves in March 1995 (Johnson *et al.*, 1996). The parasitoid was allowed to disperse from an open-sided greenhouse, where it had been cultured for one generation, into the adjacent citrus grove on the Citrus Experiment Station at Port Sulphur, Louisiana. By September 1995, *A. citricola* had colonized ca. 1000 acres of citrus in Louisiana and had dispersed at least 42 km north and south of the release site. The rapid establishment and high level of parasitism by *A. citricola* has led to a decision to evaluate the effect of *A. citricola* before additional parasitoid species are introduced so that the effectiveness of *A. citricola* is not lessened (S. Johnson, pers. comm.; Johnson *et al.*, 1996).

#### Bahamas

The remarkable dispersal and colonization record observed in Louisiana and Florida is similar to that which we observed on Andros and Abaco islands in the Bahamas. Within a few months after its release, *A. citricola* multiplied, dispersed, and colonized approximately 700 and 3000 acres, respectively; *A. citricola* was able to reduce CLM populations dramatically on these two islands. In June 1996, a brief survey of citrus by M. A. Hoy on Andros Island indicated that *A. citricola* parasitized nearly 100% of the CLM pupae examined.

#### Honduras

We sent *A. citricola* to Honduras, where it rapidly established, multiplied, and began to spread (Castro *et al.*, 1996; Cave, 1996). At least seven indigenous parasitoids were also found attacking the CLM in Honduras (all Eulophidae), but after *A. citricola* established it became the dominant parasitoid (Cave 1996).

### ADDITIONAL INTRODUCTIONS OF PARASITOIDS INTO FLORIDA?

After *A. citricola* rapidly colonized Florida, Honduras, and the Bahamas, the question arose as to whether *A. citricola* was sufficient to suppress CLM populations by itself. It appears to have all of the attributes of a highly-effective parasitoid, as identified by Rosen and Huffaker (1983): narrow host range (it has not reported from any other host, although Rut Morakote has suggested it may attack another leafminer in Thailand (R. Morakote, pers. comm.)); high reproductive rate (up to 180 progeny per female and a female-biased sex ratio (Edwards and Hoy, unpublished); high dispersal rate (up to 25 miles within two to three months); and high searching rate (which is to be expected for a parasitoid with a narrow host range). It appears to be climatically adapted to the humid tropical and subtropical climates of Louisiana, Florida, Honduras, and the Bahamas, and it has been reported to have established in the Mediterranean climates

of Morocco, Spain, and Syria. The extent of its climatic adaptation remains to be resolved.

The early and rapid establishment, high multiplication rate, effective dispersal, and high rate of parasitism exhibited by *A. citricola*, especially in parts of Florida, Abaco and Andros islands in the Bahamas, and in Louisiana (Hoy and Nguyen, 1994b; Hoy *et al.*, 1995; Pomerinke and Stansly, 1996), suggested that *A. citricola* could be one of the rare "silver bullet" species in classical biological control—a single species capable of providing substantial pest population suppression. If *A. citricola* is eventually shown to be such a species, then the introduction of additional species could be redundant and even, potentially, disruptive to the sustained control of the CLM if the new species interfered with *A. citricola* through hyperparasitism or competition.

Historically, the most dramatic examples of classical biological control have involved the introduction of one or two highly host-specific parasitoids that are collected from a region with a climate similar to that into which they are introduced (Huffaker *et al.*, 1971; Rosen and Huffaker, 1983). These parasitoids are often capable of having a rapid effect on the target pest. DeBach (1964) evaluated 225 cases involving 110 pest species controlled to a greater or lesser degree in approximately 60 countries or islands and concluded "... that a complete case of biological control will occur usually seems to be evident within two or three years..."

*A. citricola* is an endoparasitic koinobiont, which means that it delays its development until its host has matured. This allows *A. citricola* to produce relatively large adults that may be able to locate more hosts in contrast to an idiobiont (which kills its host and develops immediately). In general, the adaptations that allow koinobionts to evade host defenses result in their having a relatively narrow host range and good synchronization with their host. Koinobionts, such as *A. citricola*, generally are poor competitors in comparison with ectoparasitic idiobionts which can function as facultative hyperparasitoids (Godfray 1994). Ujiye *et al.* (in press) reported that *A. citricola* ranked second in average parasitism (25%) in Thailand and was more abundant in orchards with lower densities of the CLM. They also noted it was "... parasitized secondarily by many hyperparasitoids, including *Eurytoma* sp., *Quadrastichus* sp., *Cir. ingenuus*, *Tetrastichus* sp., *Closterocerus* sp. (B) and others." Despite the impact of hyperparasitoids, Ujiye *et al.* (in press) concluded that *A. citricola* was the "... most important parasitoid for natural control of CLM in Thailand." Their observations, and observations by M. A. Hoy while in Thailand and in Australia, suggest that the effectiveness of *A. citricola* could be limited by competition or by facultative hyperparasitism by eulophid parasitoids.

The question of whether to release multiple parasitoid species simultaneously or individual parasitoid species in a specific sequence remains a vexing conundrum in classical biological control and has been the subject of intense debate because it is difficult to predict how parasitoid species will interact in a new environment. Any decision has to be based on a variety of criteria, assumptions, and facts. One approach is to look at the history of other classical biological control programs to determine which have been successful and to determine if any patterns become apparent. How effective are the Braconidae, Encyrtidae, Eulophidae, Elasmidae, Eurytomidae, and Pteromalidae as

biological control agents? As part of an effort to resolve this question, we evaluated the potential of these families as classical biological control agents using historical records.

#### Eulophidae as Biological Control Agents

Many of the euplid species found attacking the CLM in Florida and elsewhere are ectoparasitic idiobionts (Browning and Peña, 1995; Peña *et al.*, 1996). These euplids apparently moved onto the abundant CLM populations from other (generally unknown) hosts shortly after the CLM invaded Florida, and it is likely that they moved onto the CLM from other leafmining species. Parkman *et al.* (1989) surveyed the dipteran leafminers *Liriomyza trifolii* Burgess and *L. sativae* (Blanchard) (Diptera: Agromyzidae) on weeds in south Florida and reported 11 parasitoid species from four families, including Braconidae (4 species), Eulophidae (5 species), Pteromalidae (1 species), and Cynipidae (1 species). The euplid species included *Diglyphus intermedius* (Girault), *Chrysonotomyia punctiventris* (Crawford), *Chrysocharis parksi* Crawford, *Closterocerus* sp., and *Pnigalio flavipes* (Ashmead); parasitoids from most of these genera also attack the CLM in south Florida.

Idiobionts permanently paralyze or kill their host, consume it in the location and state it is in when attacked, and generally have a broad host range, with some species even functioning as facultative hyperparasitoids (Askew and Shaw, 1986). Thus, native euplids (and introduced generalist euplids), if acting as hyperparasitoids, could interfere with the endoparasitic koinobiont *A. citricola*.

*Cirrospilus quadrifasciatus* (recently identified as a synonym of *ingenuus*) (Eulophidae) was collected in Queensland, Australia, evaluated, reared, and released in small numbers in Florida in 1994. There is no evidence it has established (Hoy and Nguyen 1994c). In the evaluation of its taxonomy and biology prior to obtaining permission to release it from quarantine, we noted that this species was recorded from only one host (the mango flea weevil) other than the CLM in the literature. Its ectoparasitic habit raised concerns that it might interfere with *A. citricola*, especially after Harold Browning (pers. comm.) indicated that he observed *C. ingenuus* consuming pupae of *A. citricola* in Thailand during a season when CLM populations were low.

To confirm *C. ingenuus* can act as an indirect hyperparasitoid we conducted experiments in quarantine: cages received citrus trees infested with CLM hosts suitable for parasitism by *A. citricola*. Eight *A. citricola* adults from Australia were released in each cage and two male and two females of *C. ingenuus* were released per cage. After pupal chambers were formed, the proportion containing *Ageniaspis* only or *Cirrospilus* only, both *Ageniaspis* and *Cirrospilus*, and only CLM were determined by opening the intact pupal chambers. A small percentage of the pupal chambers in cages containing both *A. citricola* and *C. ingenuus* contained both pupae, with the *Ageniaspis* pupae damaged, indicating that *C. ingenuus* can kill *A. citricola* and thus serve as an indirect hyperparasitoid (Nguyen and Hoy, unpublished). Because *C. ingenuus* could potentially interfere with *A. citricola*, additional releases have not been made in Florida. If we had known of its ability to serve as an indirect hyperparasitoid we would not have made the original releases. Bouček (1988) noted that the genus *Cirrospilus* develops as parasitoids or as hyper-

parasitoids of leafminers, although some are egg parasitoids.

During July and August 1995, several additional euplid species were collected from the CLM in Asia with the assistance of Rut Morakote and Pimonporn Nanta (Thailand) and K. C. Lo (Taiwan). For that reason a similar experiment was conducted in quarantine with *Quadrastichus* sp. (=*Tetrastichus* sp.). Again, six *Ageniaspis* adults were released first because this parasitoid attacks younger stages of the CLM than *Quadrastichus*. *Quadrastichus* was released four days later (three females and three males) and pupal chambers were later examined. The results indicated that, under quarantine conditions, *Quadrastichus* sp. can act as an indirect hyperparasitoid of *A. citricola* (Nguyen and Hoy, unpublished). Because both *C. ingenuus* and *Quadrastichus* sp. could act as indirect hyperparasitoids of *A. citricola*, we have concluded that additional releases of *C. ingenuus* and releases of *Quadrastichus* sp. in Florida are undesirable.

The Eulophidae contain at least 280 genera and 3,400 described species (Grissell and Schauf, 1990). Hyperparasitism is common in the subfamily Tetrastichinae and is sometimes obligatory; genera with hyperparasitoids include *Tetrastichus* Walker, *Crataepiella* Domenichini, and *Melittobia* Westwood. Hyperparasitism is also extensive in the Entedontinae, including the genera *Horismenus* Walker, *Pediobius* Walker, *Chrysocharis* Foerster, *Neochrysocharis* Kurdjumov, *Achrysocharella* Girault, *Closterocerus* Westwood, and *Teleopterus* Silvestri (Gordh, 1981). Hansson (1985) noted that ". . . species of *Achrysocharoides* are mono- or oligophagous, attacking leaf-mining Gracillariidae on a limited range of plant genera. . ." and that *Chrysocharis* attack ". . . larvae of leaf-mining insects."

Hansson (1994a) reported *Teleopterus delucchii* Bouček, *Teleopterus reticulatus* (Kamijo), and *Teleopterus turcicus* (Nees) as primary parasitoids, while *Teleopterus erxias* (Walker) was identified as both a primary parasitoid and a hyperparasitoid. Hansson (1994a) indicated that *Teleopterus* species appear to be polyphagous. [Hansson (1996) recently transferred five species of the genus *Teleopterus* into the genus *Asecodes*.] Hansson (1994b) evaluated the Nearctic species of the genus *Closterocerus* Westwood and found host records for 11 of 21 species; some species have a very wide host range. Most *Closterocerus* species are primary endoparasitoids, but two host records indicated that *C. trifasciatus* can act as a hyperparasitoid.

*Kratosyma citri* Bouček was identified as a parasitoid of the CLM in Papua, New Guinea by Bouček (1988), who indicated the genus attacks only species of lepidopterous leafminers of the genus *Phyllocnistis*. Bouček (1988) reported that ". . . one *Kratosyma* species was reared from *P. citrella* Stainton in India and another from the same host in New Guinea. Of four *Kratosyma* species, hosts are known for only three. These species are *K. citri* and *K. usticrus*, which have been reared from *Phyllocnistis suffusella* Zeller, another gracillariid moth in Europe (Hansson and Cave, 1993). In addition, *K. gliricidiae* Hansson and Cave, has been reared from a gracillariid in Honduras, and is an endoparasitoid of larvae, with from one to three parasitoids developing per host (Hansson and Cave, 1993).

*Zaommommentedon brevipetiolatus* was identified (under the name of *Visnuella* sp.) as emerging from the fourth instar larva or pupa of the CLM in Japan (Kamijo, 1990).

Historically, relatively few euplophids have been identified as highly-effective natural enemies. Clausen (1940) noted that "In spite of the general occurrence of Eulophidae as parasites of crop pests, very few species have been successfully utilized in biological control." Table 2 summarizes information about euplophids that have been used with some degree of success against a variety of pests.

Nearly all euplophid parasitoids that are credited with substantial impact on the target pest have been endoparasitoid koinobionts—not ectoparasitoid idiobionts (Table 2). One of the most effective euplophids is *Tetrastichus asparagi* Crawford, which is a parasitoid of the asparagus beetle, *Crioceris asparagi* (L.). However, as noted by Capinera and Lilly (1975), *T. asparagi* is an effective natural enemy because adults act as predators and can prey on as many as 50% of the host eggs before subsequently parasitizing the remaining eggs. *T. asparagi* is an egg-larval endoparasitoid but its predatory ability is critical in its success as a natural enemy. Greathead (1986) noted that 36 species of euplophids in 21 genera have been used against 47 pests on 72 occasions and 23 species have provided "effective control". While this success rate is substantial, Greathead (1986) considered only species in two genera, *Tetrastichus* and *Pediobius*, as effective in classical biological control programs.

#### Braconidae As Effective Natural Enemies

The braconid *Microbracon phyllocnistidis* was recorded from 8 females and 9 males of the CLM in Java (Muesebeck, 1933). No additional information on this species was found. This is unfortunate because many braconids, including especially species in the genera *Apanteles*, *Bracon* and *Opius*, have served as highly effective natural enemies in classical biological control programs against other pests (Greathead, 1986).

#### Encyrtidae As Effective Natural Enemies

Encyrtids as a group are considered highly successful classical biological control agents. At least 34 species in 61 genera of Encyrtidae have been used against 40+ pests on 132 occasions, with effective control provided on 53 occasions (Greathead, 1986).

Among the Encyrtidae, species in 13 genera have been used in effective classical biological control programs, especially against scale insect (Pseudococcidae and Coccoidea) pests. Some Encyrtidae are effective against Lepidoptera, such as the polyembryonic larval parasitoid *Copidosoma koehleri* (Blanchard), which is effective against the potato tuber moth, *Phthorimaea operculella* (Zeller). Other encyrtids known as effective parasitoids of Lepidoptera include *Pentalitomastix nacoleiae* (Eady) against the banana scab moth, *Nacoleia octasema* (Meyrick) (Pyralidae); another *Pentalitomastix* sp. against the navel orangeworm, *Paramyelois transitella* (Walker) (Pyralidae); *Ooencyrtus kuwanai* (Howard) as a parasitoid of the gypsy moth, *Lymantria dispar* (L.) (Lymantriidae); and *Paralitomastix pyralidis* (Ashmead) against the peach twig borer, *Anarsia lineatella* Zeller (Gelechiidae) (Clausen, 1978). Another example of a highly successful classical biological control program, but not cited by Greathead (1986), involves the encyrtid *Epidinocarsis lopezi* (De Santis) released against the cassava mealybug *Phenacoccus manihoti* Matile-Ferrero over much of Africa (Herren and Neuenschwander, 1991).

Most encyrtids are primarily endoparasitoid koinobionts (Laing

and Hamai, 1976). Encyrtids include approximately 470 genera and 3,540 described species; only 22 genera are known to be hyperparasitoids of other chalcidooids (J. Noyes, pers. comm.). About 50% of all encyrtid species have been reared from coccid hosts (Noyes and Hayat, 1994).

#### Elasmidae as Biological Control Agents

The Elasmidae are primary parasitoids or hyperparasitoids of Lepidoptera, with hyperparasitoid species attacking both ichneumonids and braconids (Gordh, 1981). Ferrière (1929) noted that species in the genus *Elasmus* ought to be important in biological control because they attack many destructive moths; unfortunately the pests are only attacked just before pupation (after the damage is done) and the female has only a ". . . few victims as her eggs are laid in clusters."

*Elasmus zehntneri* was identified by Heppner (1993) as a parasitoid of the CLM, but species within this genus attack a wide variety of hosts, often as hyperparasitoids (LaSalle and Schauff, 1996). Ujiye *et al.* (in press) reported an *Elasmus* sp. provided only 0.1% parasitism of the CLM in Thailand during 1994. Greathead (1986) did not cite this family as significant in classical biological control programs.

#### Eupelmidae As Effective Biological Control Agents

On the basis of their lack of host specificity, *Eupelmus* species may not be effective natural enemies. Greathead (1986) indicated only four eupelmid species in two genera had been used against three pests on four occasions, but none had provided effective biological control.

#### Eurytomidae As Effective Biological Control Agents

A *Eurytoma* sp. was identified as providing approximately 5% parasitism on the CLM in central and northern Thailand during 1994 (Ujiye *et al.*, in press).

The Eurytomidae consist of about 60 genera and 750 known species, with hyperparasitism restricted to the cosmopolitan genus *Eurytoma* Illiger; some species are phytophagous and some are primary parasitoids (Gordh, 1981). Greathead (1986) did not list any eurytomids as effective natural enemies in classical biological control programs.

#### Pteromalidae As Effective Biological Control Agents

*Asaphoideus niger* Girault is known to attack the CLM in Australia (Bouček, 1988). Pteromalids have a relatively good track record as biological control agents; Greathead (1986) indicated that 26 species in 15 genera have been used against 22+ pests on 49 occasions, with 17 providing "effective control". Pteromalids in the genus *Muscidifurax* are primarily important as parasitoids of house and stable flies, especially *Musca domestica* L. and *Stomoxys calcitrans* (L.). The only pteromalid successfully used against a lepidopteran pest is *Pteromalus puparum* L. against the cabbage white butterfly, *Artogeia rapae* (L.) [=*Pieris rapae* (L.)] (Pieridae) in New Zealand (Greathead, 1986).

#### PROGRAMMATIC LIMITATIONS

In any classical biological control program, we can introduce only a fraction of the natural enemy species identified in the region of origin of the pest. The decisions as to which species, and in what order, should be introduced are influenced by funding, availability, time constraints, level of knowledge of natural enemy biology and taxonomy, and concerns about detri-

Pest	Target	Country	Bulophid species	Origin	Involved of euclopheid	Biology of euclopheid	Comments (References)
(based on evaluations from Claussen 1978, Laiing and Hamai 1976, and Luck 1981).							
Anastrepha ludens	Mexico	<i>Syntomosphyrum</i>	<i>Indicum</i> Silv.	US (Hawaii)	Cregatious endoparasitoid	Substantial (Laiing & Hamai 1976) Four bractonids also established and important (Luck 1981)	
Mexican fruit fly	Lowe						
Bronitispa longistigma	Celebes	<i>Tetrastichus bronitiapse</i>	Java		Attacks larvae & pupae; Parasitoid could be propagated only on species/variety strain from which they originated (Claussen 1978)		(Gesato) Leaf hispa Cocoon leaf hispa
Bronitispa mariana	Maritaina		<i>T. bronitiapse</i>	Malaya &	Dito	Substantial control (Luck 1981).	Spelth cocoon beetle
Martiana cocoon beetle							
Coleophora luteola	USA (N.E.)	<i>Chrysocarhis laricinae</i>		Europe	Solitary endoparasitoid of larvae of host feed	More important as parasitoid of birch leaf-mining sawfly <i>Heterarthrus nemoratus</i> (Fall.) a parasitoid of larch casebearer, <i>Agaethis pumila</i> (Graham) (Braconidae), a parasitoid of birch casebearer. Effective only at high populations of larch casebearers (Luck 1981).	Larch casebearer
Asparagus beetle	USA	<i>Tetrastichus asparagi</i>	(Ohio)	Craw.	Egg-larval endoparasitoid, gregarious; adult females prey on beetle eggs	Established in eastern USA early with the pest.	Crocearis asparagi
Epilachna philippinensis	Guam	<i>Pediobius epilachnae</i> (Roh.)	Philippines	Austria	Cregatious endoparasite attacking larvae	Substantial control (Laiing & Hamai 1976). Partial control (Luck 1981).	Philippine lady beetle
Heterarthrus nemoratus (Fallen)	US	<i>Chrysocarhis insidiator</i> Dalmat	New England	Austria	Not available	Established control attributed to several species, including <i>T. incertus</i> in eastern USA. (Claussen 1978).	Birch leafmining sawfly
Hyperaspis postica	USA	<i>Tetrastichus julus</i> (Willk.)	Europe	Fiji	Not available	Partial control; other parasitoids established and important (Luck 1981).	Oulema melanopus L.
Oulema melanopus L.	USA	<i>Tetrastichus julus</i> (Willk.)	Fiji	Hawaii	Beats Peck.	Partial control; other parasitoids and a predatory mid more important.	Perkinsella saccharicida Kirk.
Allafia weevill (Gyllen)	USA	<i>Tetrastichus incertus</i> (Ratz.)					Sugarcane leafhopper
Perkinsella saccharicida Kirk.	Hawaii	<i>Ooerstachius</i>					Leafhopper

Table 2. A selected list of classical biological control programs in which euclopids provided partial or substantial control under some circumstances (based on evaluations from Claussen 1978, Laiing and Hamai 1976, and Luck 1981).

<i>Phytomyza ilicis</i> (Curt.) Holly leaf miner	Canada	<i>Chrysocharis gemma</i> (Walk.)	England	Host specific solitary endoparasitoid of third instar larvae
<i>Promecotheca coeruleipennis</i> Blanch. Coconut leaf-mining beetle	Fiji	<i>Pediobius parvulus</i> (Ferr.)	Java	Gregarious endoparasitoid of all host stages
<i>P. opacicollis</i> Gestro	New Hebrides	<i>P. parvulus</i>	Java	Very successful (Clausen 1978).
<i>P. papuana</i> (Cziki)	New Britain New Ireland Manus	<i>P. parvulus</i>	New Hebrides & Fiji	Ditto
<i>Pyrharta luteola</i> (Muller) Elm leaf beetle	USA (Calif.)	<i>Tetrastichus brevisigma</i> Gah.	France	Less successful; partial control only due to competition with native parasitoids.
<i>Spodoptera exempta</i> (Walk.) Nutgrass armyworm	Hawaii USA	<i>Euplectrus plathyneae</i> Ashm.	Mexico	Partial control, along with a tachinid parasitoid (Clausen 1978).
				Wide host range on Lepidoptera; ranked third in importance after 2 braconids (Luck 1981, Clausen 1978).

mental effects of facultative hyperparasitoids. Once a parasitoid species has established, its effects are difficult to mitigate should it be detrimental to beneficial species.

Host records from the literature no doubt contain many errors. Many parasitoids are erroneously recorded as emerging from a phytophagous host, but could be emerging from primary parasitoids of the phytophagous species. In other situations, the emergence cages may unknowingly contain several host species and parasitoids are wrongly assigned to the wrong host species. Despite these problems, in many cases historical host records are all that we have and should be considered carefully. Ideally, host ranges should be confirmed under quarantine conditions in classical biological control programs.

Generalist biological control agents may pose threats to native species (Goldson *et al.*, 1994). There are long-standing concerns as to whether inferior natural enemies, introduced first, could prevent subsequent establishment or reduce efficacy of species established subsequently through competition. Natural enemies that are adapted to low host densities should, in theory, provide better control than species adapted to high host densities, but these parasitoids may not be evident if collections are made only in sites with pest population outbreaks. Generalist natural enemies are usually opportunists exploiting pest outbreaks and their introduction can pose a risk to non-target beneficial species such as arthropods used in biological control of weeds (as mentioned above) or to more specialized parasitoid species.

#### PROGRAMS IN OTHER COUNTRIES

In Australia, Neale *et al.* (1995) tested *Ageniaspis citricola*, *Citrostichus phylloconistoides*, and *Cirrospilus quadrastriatus* (now a synonym of *C. ingenuus*) for host specificity on various leafminer hosts before releasing them. Neale *et al.* (1995) found that these natural enemies attacked only the CLM under multiple-choice test conditions. According to Dan Smith (pers. comm.) *C. quadrastriatus* or *C. ingenuus* has had little impact on *A. citricola* in the field in Queensland, Australia. Thus, *C. quadrastriatus* is clearly not an obligate hyperparasitoid and probably qualifies as an indirect hyperparasitoid, attacking the CLM host without concern as to whether it is already parasitized by *A. citricola*. The impact of *C. quadrastriatus* as an indirect hyperparasitoid on *A. citricola* has not been quantified under field conditions.

In the irrigated citrus-growing region in Australia, David James (pers. comm.) has found that the euphorid *Semielacher petiolatus* (Girault) "... is providing good biocontrol at the moment in the southern citrus growing areas". As of March 1996, *A. citricola* had not established in this region of Australia despite repeated releases over several years.

In Israel, Argov and Rossler (1996) have released *A. citricola*, *C. quadrastriatus*, *Quadrastichus* sp., *S. petiolatus* and *Zaommonmentedon brevipetiolatus*. *Semielacher petiolatus* was reported by Bouček (1988) to be an Australian species. If it is an Australian species, it is unlikely to be host specific to the CLM because the CLM is not native to Australia (unless it entered Australia with its host). Bouček (1988) reported three species of *Semielacher* from Australia and two from New Guinea; one undescribed *Semielacher* species was reared as a parasite of the CLM in New Guinea. If *S. petiolatus* is a New Guinean species that came along

with the CLM when it colonized Australia, then *S. petiolatus* could be a specific parasitoid of the CLM. Without additional data on host range of *S. petiolatus* in Australia or evidence that *S. petiolatus* is native to New Guinea, no conclusion can be reached on its potential status as a parasitoid of the CLM in Florida.

Researchers throughout the Mediterranean region are worried that *A. citricola*, which was collected from a humid subtropical climate, will be unable to establish or be effective under the more arid climatic conditions present during the rainless summer months. By conducting simultaneous releases of several parasitoid species, they hope that the establishment of one or more species is not delayed until it can be determined whether *A. citricola* can establish or be effective in a Mediterranean climate. *A. citricola* has been reported to have established in Spain during 1996 (F. Garcia-Mari, pers. comm.). There is some risk that the effectiveness of *A. citricola* could ultimately be reduced by indirect hyperparasitism by the imported euphorids *Cirrospilus ingenuus* and *Quadrastichus*.

#### CONCLUSIONS

We believe that it is appropriate to exercise caution in making releases of euphorid ectoparasitoids of the CLM because some may be facultative hyperparasitoids or indirect hyperparasitoids. Unfortunately, detecting facultative hyperparasitism requires detailed laboratory or field studies, or access to historical records of host ranges of each euphorid species. These studies are time consuming and expensive to conduct and host records are not available for many euphorid species. Relatively few parasitoid species from other families are left for consideration as natural enemies of the CLM because the preponderance of parasitoids collected from the CLM in southeast Asia are euphorids.

Historical analyses indicate that natural enemies that are known to be host-specific and effective at low host densities are more closely synchronized in their habits and better attuned in their nutritional needs, reproductive potential, and searching behavior than generalists. When they can be identified, they are likely to be effective and reliable biological control agents. Unfortunately, the "best" natural enemy may not be found until all natural enemies and their biologies are known. Furthermore, the "best" natural enemy species may differ throughout the geographic range of the target pest due to differences in climate or to interactions with other species such as competition or hyperparasitism.

The importance of identifying natural enemy biotypes that match the climate of the targeted release sites is generally accepted as critical to obtaining establishment in classical biological control programs, although some have questioned the value of "strains" or biotypes (Clarke and Walter, 1995). We know little about biotypes of parasitoids of the CLM, although we could expect that biotypes exist that have different temperature and relative humidity tolerances, or other attributes of potential importance in a classical biological control program. For example, a population, originally identified as *A. citricola*, was collected from Taiwan in 1995 from the CLM. It is genetically distinct from the population collected from the mainland of Asia and subsequently introduced into Australia (Hoy *et al.*, unpublished data). Whether the Taiwan population is a separate species or a

distinct biotype remains to be resolved.

The results of relatively few classical biological control programs have been studied in adequate detail so that the impact of and interactions between different natural enemies are understood. We rarely are able to predict the outcome of a specific release. Lacking critical information, we must conduct classical biological control programs with the best current information. Despite the many uncertainties, we believe that the release of known facultative hyperparasitoids is undesirable early in a classical biological control program. Such releases cannot be justified until substantial efforts have been made to achieve establishment of host-specific primary parasitoids and to evaluate their impact. Because multispecies interactions in new environments are difficult to predict, we are left with the conclusion that effective classical biological control remains something of an art, as well as a science.

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