Parasites of Lepidopteran Stemborers of Tropical Gramineous Plants

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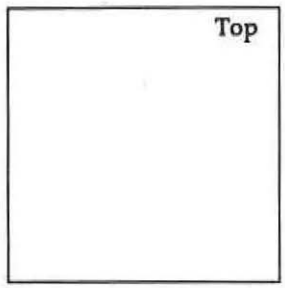
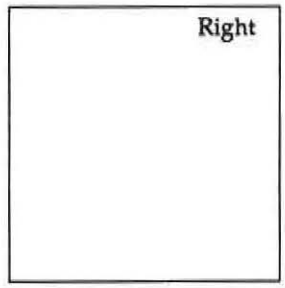
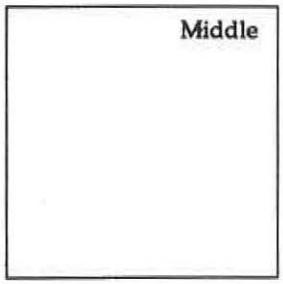
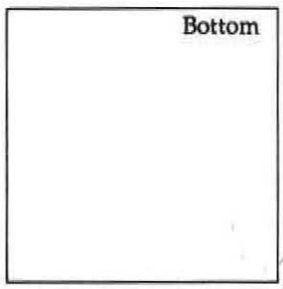
Funded by
Directorate General for International Cooperation (DGIS), Ministry of Foreign Affairs, The Hague, Netherlands and the Texas Agricultural Experiment Station.









Cover: (Top) *Apanteles minator* Muesebeck attracted to frass at the entrance of the larval feeding tunnel of *Diatraea*; (Middle) *Cotesia flavipes* Cameron ovipositing in fifth-instar *Diatraea saccharalis* (F) larva; (Right) *Pediobius furvus* Gahan antennating pupa of *Eoreuma loftini* (Dyar) prior to oviposition. (Photographs by Mike Rose). (Bottom) *Euvipio rufa* Szepligeti probing *Chilo partellus* (Swinhoe) larval entrance hole. (Photograph by W. A. Overholt).

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PREFACE

This publication is primarily intended for biological control practitioners in the tropics, particularly those involved in managing stemborers of gramineous crops. It includes not only information gleaned from the scientific literature, but also draws on the experiences and personal knowledge the authors have gained through years of involvement with biological control of stemborers.

A wealth of information on the biology and ecology of both stemborers and their parasites — as well as tritrophic-level interactions between plants, pests and parasites — is included in the text. Particular attention is given to the generalized hierarchical steps involved in successful parasitization and to the various foraging strategies employed by stemborer parasites. A user-friendly key that incorporates parasite biology and taxonomy is provided to help the user determine the foraging strategy used by the parasites. The key encompasses the primary parasites that are most likely to be encountered when sampling stemborers. The key is not intended to be all inclusive, but rather is a guide that is restricted to those taxa most likely to be found. The intent of the key is to provide tentative identification of the parasite to a useable level, by maximizing the use of ecological information and observational skills, while minimizing taxonomic expertise. Rearing techniques, which acquire their foundation from the foraging strategies, are addressed in the last half of the text.

This publication is intended to be a fairly detailed review of stemborers and their parasites, but is not meant to be the final word. Rather, we intend this to be an initial attempt towards organizing the available information on stemborer parasites in a generalized structure that emphasizes the tritrophic interactions between a gramineous plant, a stemborer, and its parasites. Emphasis is placed on grouping parasites into similar foraging strategies to provide a biological structure for understanding the relationships between taxonomy and biology. Thus, the tables listing parasite genera and the text references to parasite species are not all-inclusive, but representative of the taxa likely to be encountered in field surveys for stemborer natural enemies.

The broad presentation of material has been followed because the authors feel strongly that a basic knowledge of the biology of the hosts and parasites is a prerequisite to pursuit of biological control, and that this basic knowledge is the foundation for successful biological control intervention. Without first presenting the basic knowledge of plant-host-parasite biology and ecology, this publication would result in no more than a cookbook for rearing parasites with limited application. Moreover, we demonstrate that, by knowing the biology and taxonomy of the hosts and parasites, certain generalizations can be made regarding foraging strategies and appropriate rearing procedures. Through the application of these generalizations, practitioners should acquire the knowledge necessary to make field collections of parasites and rear them, regardless of whether specific methods for rearing that species are included. However, whenever generalizations are made there will be exceptions. We have attempted to point out these exceptions whenever possible, but the readers will undoubtedly discover others. The references supplied at the end of sections are not intended to be exhaustive, but rather represent suggested reading for specific information on the subject. Often, citations are made in the text to direct the reader specifically. We have attempted to minimize citations in the text to save space. Undoubtedly we should have made more citations to document the wealth of outstanding information in the literature. We apologize in advance for those omissions.

ACKNOWLEDGEMENTS

In writing this publication, we were helped by numerous individuals. We are especially grateful for the assistance that several colleagues provided: Fred Bennett gave a thorough review with critical comments of the penultimate draft, provided us with obscure references, and freely offered insight from his long and successful career with biological control of stemborers; Robert Wharton listened to our early ideas and offered his viewpoints, provided the correct parasite taxonomy, gave a detailed and critical review of the entire manuscript, and was responsible for writing a large part of the identification key; Harold Browning and Brad Hawkins participated in informative and critical discussions concerning foraging strategies of stemborer parasites during the genesis of these ideas; Andrew Polaszek critically reviewed and suggested changes in the identification key to parasites of stemborers; and A. I. Mohyuddin gave assistance with details on parasite rearing. Many others have graciously provided assistance: Patricia Darnell and Robert Meagher, Jr., read earlier drafts and provided helpful comments; Michael Matthiessen and Tinka Vaughn helped with literature searches; Lourdes Menendez, Imad Bayoun and Mari Decanini produced the illustrations; and Gloria Harvey typed the majority of the text. Because the ideas contained here represent a culmination of many years with biological control of stemborers, numerous scientists, graduate students and technicians have provided insights, thoughtful discussions and rearing technology along the way, including Luis Rodriguez-del-Bosque, Charles Agnew, Tom Fuchs, Seth Johnson, Padmini Malvaganam, Yared Hailemichael, Bart van Leerdam, Bob Pfannenstiel, Patricia Hennier, JoAnn Haselbarth, Lydia Luza, and Patricia Darnell.

We are also grateful for the financial support provided for this publication by the Netherlands Directorate General for International Cooperation and the Texas Agricultural Experiment Station. Funding was made available through the Project "Biological Control of Tsetse and Crops Pests" — a collaborative effort between the International Centre of Insect Physiology and Ecology and Wageningen Agricultural University; and through the Center for Biologically Intensive Integrated Pest Management at Texas A&M University, Projects TEX 09099 and H-6796. Especially important was the long-term commitment to biological control from the Rio Grande Valley Sugar Growers, Inc., Santa Rosa, Texas which provided the opportunity to initiate and, more important, complete studies needed to develop an understanding of stemborers and their parasites. Approved by the Texas Agricultural Experiment Station as TA no. 30977.

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INTRODUCTION

Gramineous crops are of paramount importance for feeding people or providing cash income in tropical countries. In most regions, crop production has been limited due to damage caused by stemborer pests. Stemborers attacking tropical gramineous crops are chiefly Lepidoptera belonging to the families Pyralidae, Noctuidae and Castniidae. The more economically important pyralid genera include *Bissetia, Chilo, Coniesta, Diatraea, Elasmopalpus, Eldana, Eoreuma, Girdharia, Haimbachia, Maliarpha, Ostrinia, Rupela, Scirpophaga, Tryporyza,* and *Xubida. Busseola* and *Sesamia* are the primary noctuid genera of importance, whereas *Castnia* is the only important genus of Castniidae (Table 1). *Castnia, Diatraea, Elasmopalpus, Eoreuma, Rupela* and *Xubida* are Neotropical, the remaining eleven genera are almost exclusively Paleotropical. Jepson (1954) listed 46 species of economically important tropical lepidopteran stemborers and more recently Bleszynski (1969) added a dozen New World species to this list. The majority of the economically important species are members of the Old World genus *Chilo* and the New World genus *Diatraea,* which are closely related and form a monophyletic group that cannot be separated by morphological characters; however the genera are kept distinct for practical reasons (Bleszynski 1969). The New World genera *Eoreuma* and *Xubida* and the Old World genera *Bissetia, Coniesta, Girdharia,* and *Haimbachia* are taxonomically closely related, with *Coniesta* and *Haimbachia* the genera most closely related to *Eoreuma* (Agnew & Smith 1993).

We intentionally omitted discussion of the economically important stemborers in the genus *Ostrinia* for several reasons. First, most species in the genus are primarily temperate in distribution, with the exception of *O. furnacalis* (Guenée), which is distributed throughout

Table 1. Economically important lepidopteran stemborers of tropical gramineous crops.

Pyralidae
Crambinae
Bissetia Kapur, *Chilo* Zincken, *Coniesta* Hampson, *Diatraea* Guilding, *Eoreuma* Ely, *Girdharia* Kapur, *Haimbachia* Dyar, *Xubida* Schaus
Galleriinae
Eldana Walker
Peoriinae
Maliarpha Ragonot
Phycitinae
Elasmopalpus Blanchard
Pyraustinae
Ostrinia Hübner
Schoenobiinae
Rupela Walker, *Scirpophaga* Treitschke, *Tryporyza* Common
Noctuidae
Amphipyrinae
Busseola Thurav, *Sesamia* Guenée
Castniidae
Castnia F.

both temperate and tropical Asia (Mutuura and Munroe 1970). Second, the authors have only a casual familiarity with the voluminous *Ostrinia* literature and little personal experience with biological control of *Ostrinia.* Thus, the lack of experience and the time commitment required precluded inclusion of these mostly temperate stemborers. Readers

interested in discussion of the genus are directed to reviews of biological control of *O. nubilalis* Hübner by Baker et al. (1949) and Clausen (1978), and a recent bibliography of *O. nubilalis* by Brindley et al. (1975). Although we do not discuss parasites of *Ostrinia*, we expect the guilds and foraging strategies to follow the same biological and ecological patterns as those shown for the tropical stemborer species.

With few exceptions, the host range of lepidopteran stemborers appears limited to grasses (Graminae), sedges (Cyperaceae) and cat-tails (Typhaceae) (Jepson 1954). Economically important plants attacked include the tropical staple food crops of rice (*Oryza sativa*), maize (*Zea mays*), sorghums (*Sorghum* spp.) and millets (*Pennisetum* spp.), as well as sugarcane (*Saccharum* spp.), which is grown as a cash crop throughout the tropics and subtropics. Sorghums and millets are grown where rainfall is too uncertain for rice and maize, and sugarcane is an intensively managed plantation crop.

Stemborers are attacked by a diverse group of natural enemies. Historically, studies on the role of natural enemies in stemborer population dynamics have been targeted toward sugarcane because of its value as a cash crop. More recently, the possibilities of biological control of stemborers attacking tropical staple crops has received more attention, especially in the Americas (Overholt & Smith 1990, Rodriguez-del-Bosque et al. 1990a, b, Youm et al. 1990) and Africa (Ingram 1958, Harris 1962, Mohyuddin & Greathead 1970, Appert 1973, Gilstrap 1980, Reyes 1989, Greathead 1990). Although numerous general predators and diseases cause stemborer mortality, parasites have been the primary targets as biological control agents (Jepson 1954, Nickel 1964, Bennett 1969, Mohyuddin & Greathead 1970, Mohyuddin 1978, Ingram 1983), possibly because of their ecological diversity, host specificity and ability to attack hosts that feed cryptically within the plant (Table 2).

Unlike many other types of pests, which become serious pests only after being accidentally introduced into new areas, many stemborers in both the Old World and New World tropics are indigenous to the region in which they cause economic damage. Notable exceptions are *Diatraea saccharalis* (F), which is aboriginal to the Amazon region of Brazil, but which has spread through South and Central America, Mexico and the southern United States, and *Chilo partellus* (Swinhoe), which is aboriginal to Asia but is currently spreading through Africa. Some of the indigenous stemborers have become pests due to suppression of extant natural enemies from inappropriate use of insecticides. Often, elimination or more judicious application of pesticides can help restore the beneficial effect the extant parasites can offer. In other cases, where borers are pests, but not due to suppression of the extant natural enemy fauna by insecticide use, pest status of borers has arisen due to changes in agronomic practices. One way this has occurred is the result of planting a novel crop in a new area, such as the increase in planting of maize in Africa and sugarcane in the neotropics. A second way that agronomic practices has predisposed borers to their pest status is the selective crop breeding for specific morphological characteristics or increased crop yield. For example, breeding for sugarcane, sorghum and maize has led to more robust stems, either to help support larger seed heads (as in the case of maize or sorghum), or for direct yield increases (as in the case of sugarcane). Unfortunately, the increased size of the plant stems may inhibit the ability of naturally occurring parasites to parasitize hosts enclosed within the thicker stems.

Classical biological control, which is the introduction of coevolved natural enemies from a pest's aboriginal home into an area the pest has invaded, is considered to be a potentially effective pest management strategy against exotic pests. But in addition, biological control can provide an opportunity for reducing the damaging impact of native pests as well. A different classical biological control approach is required. This approach, called the "new association" approach (Hokkanen & Pimentel 1984, 1989), unites for the first time efficacious natural enemies that have coevolved with ecologically similar pest

Table 2. Taxa of parasites of tropical stemborers.

HYMENOPTERA

Braconidae

- Agathidinae
  - *Alabagrus* Enderlein, *Bassus* F.
- Braconinae
  - *Bracon* F., *Digonogastra* Viereck, *Euvipio* Szépligeti, *Glyptomorpha* Holmgren, *Habrobracon* Johnson, *Iphiaulax* Foerster, *Myosoma* Brullé, *Stenobracon* Szépligeti, *Tropobracon* Cameron
- Cheloninae
  - *Chelonus* Panzer, *Phanerotoma* Wesmael
- Doryctinae
  - *Allorhogas* Gahan, *Heterospilus* Haliday, *Rhaconotus* Ruthe
- Macrocentrinae
  - *Macrocentrus* Curtis
- Microgastrinae
  - *Apanteles* Foerster, *Cotesia* Cameron
- Orgilinae
  - *Orgilus* Haliday

Bethylidae

- *Goniozus* Foerster

Chalcididae

- *Brachymeria* Westwood, *Invreia* Masi, *Psilochalcis* Kieffer (= *Hyperchalcidia* Steffan) , *Spilochalcis* Thomson

Elasmidae

- *Elasmus* Westwood

Eulophidae

- *Pediobius* Walker, *Tetrastichus* Haliday, *Trichospilus* Ferriere

Ichneumonidae

- Banchinae
  - *Syzeuctus* Foerster
- Campopleginae
  - *Charops* Holmgren, *Venturia* Schrottky
- Cremastinae
  - *Cremastus* Gravenhorst, *Pristomerus* Curtis, *Temelucha* Foerster
- Ichneumoninae
  - *Dentichasmias* Heinrich, *Ichneumon* L., *Procerochasmias* Heinrich
- Phygadeuontinae
  - *Ischnojoppa* Kriechbaumer, *Isotima* Foerster, *Mallochia* Viereck
- Pimplinae
  - *Itoplectis* Foerster, *Pimpla* F., *Xanthopimpla* Saussure

Scelionidae

- *Telenomus* Haliday

Trichogrammatidae

- *Trichogramma* Westwood, *Trichogrammatoidea* Girault

DIPTERA

Tachinidae

- *Descampsina* Mesnil, *Diatraeophaga* Townsend, *Jaynesleskia* Townsend, *Leskiopalpus* Townsend, *Lixophaga* Townsend, *Lydella* Robineau-Desvoidy, *Metagonistylum* Townsend, *Palexorista* Townsend, *Palpozenillia* Townsend, *Paratheresia* Townsend, *Sturmiopsis* Townsend, *Zenillia* Robineau-Desvoidy

species in a different region of the world. Instead of exploring in an exotic pest's aboriginal home to find a coevolved natural enemy, one can peruse the literature to find a parasite that has proven successful against a pest species that occupies the same ecological niche on a different continent or hemisphere. In the case where pest status is not due to insecticide use, but the extant natural enemy fauna is not suppressing native borer species, introduction of a new-association parasite species may be the most fruitful approach to biological control. This new-association approach offers great promise, especially in the case of the many native stemborer pests, which in different regions of the world have coevolved with natural enemies that are similar.

The most notable success of new association biological control against stemborers has involved the movement of the Old World parasite *Cotesia flavipes* Cameron (Hymenoptera: Braconidae) to the New World for use against the pyralid *Diatraea saccharalis*, and the redistribution of *C. flavipes* in the Old World for use against *Chilo* spp. *Cotesia flavipes* has provided substantial to complete biological control of the New World stemborer *D. saccharalis* in sugarcane or maize in several Caribbean islands (Alam et al. 1971, Simmonds, 1972, 1976); in Florida and Texas, U.S.A. (Gifford & Mann 1967, Fuchs et al. 1979); Brazil, S.A. (Macedo et al. 1984); and Mexico (Rodriguez-del-Bosque et al. 1990a). The parasite originated in the Old World and the stemborer in the New World, creating a new host-parasite association that has no coevolutionary history. Trials of *C. flavipes* against other species of *Diatraea*, especially *D. grandiosella* Dyar and *D. lineolata* (Walker), have not been as successful, presumably because of poor host suitability (Overholt & Smith 1990, Rodriguez-del-Bosque et al. 1990b).

Cotesia flavipes is reported to have developed ecological races or strains that are adapted to searching different host plants infested by stemborers and overcoming the host immune system (Mohyuddin et al. 1981, Mohyuddin 1991). For example *C. flavipes*, collected from *Chilo suppressalis* Walker in rice in Japan, was imported into Pakistan and reared on *Chilo partellus* feeding on maize in the laboratory. This "Japanese-rice-maize" strain of *C. flavipes* successfully colonized on *C. partellus* in maize and sorghum, but did not attack *C. partellus* that infested sugarcane. However, "sugarcane adapted" strains of *C. flavipes* from Barbados, Indonesia and Thailand were subsequently established on *C. partellus* in sugarcane (Mohyuddin 1991). Ecological races of *C. flavipes* that possess a propensity to overcome the host immune system (see Successful Parasitization/Host Suitability) have also been demonstrated (Mohyuddin 1991). In Sumatran sugarcane, *Chilo auricilius* Dudgeon encapsulated the "extant strain" of *C. flavipes*, but approximately 25% of the *C. sacchariphagus* (Bojer) were successfully parasitized. Introduction and establishment of *C. flavipes* from sugarcane in Thailand resulted in successful parasitization of 15% of the *C. auricilius* larvae in Sumatra. These experiences in Indonesia and Pakistan show the importance of studying host finding and host suitability for the non-coevolved host-parasite systems utilized in the new-association strategy for biological control.

Whether the efforts include new associations or reunion of coevolved natural enemies with their stemborer hosts, biological control will remain an absolutely integral part of any future strategy to deal with stemborer pests. But biological control of stemborers is not limited to the narrow aspects of identification of a species, details of rearing the parasite, or how to deploy the parasite in the field. Rather, the most crucial part of the process, that is often not considered, is a recognition and identification of the ecological perspective from which to undertake the biological control program. Stemborers have a very complex life history and they have a wide variety of parasites with which they have coevolved. Because different species of parasites attack the same hosts, the parasites have evolved different means of host recognition and utilization that minimizes competitive interactions with other parasites.

When one is in the midst of trying to combat a pest problem, it is easy to get caught up in the exigencies of importing, rearing or releasing one parasite species, and not recognize that similar efforts may have been made against other species. Often, time and economic demands will not permit one to step back and gain the larger perspective. However, we feel from experience that it is absolutely essential for successful biological control of stemborers that we recognize the overall picture of host-parasite relationships. We have written this booklet with that need for recognition as the underlying theme. Rather than a cookbook of rearing methods, or a listing of species known to attack stemborers, we are trying to provide an overall picture and perspective on host-parasite relationships between stemborers and their parasites. We do this by providing an overview of stemborer biology and ecology; the series of steps that are necessary for successful parasitization; the different foraging strategies employed by different guilds of parasites; a means to identify the parasites encountered; and only then, the details of rearing specific parasite taxa. Always, we attempt to keep as the underlying theme the perspective of the broader host-parasite relationship and the ecology and behavior of stemborers and parasites. We are absolutely convinced that this perspective is the most important aspect of biological control of stemborers.

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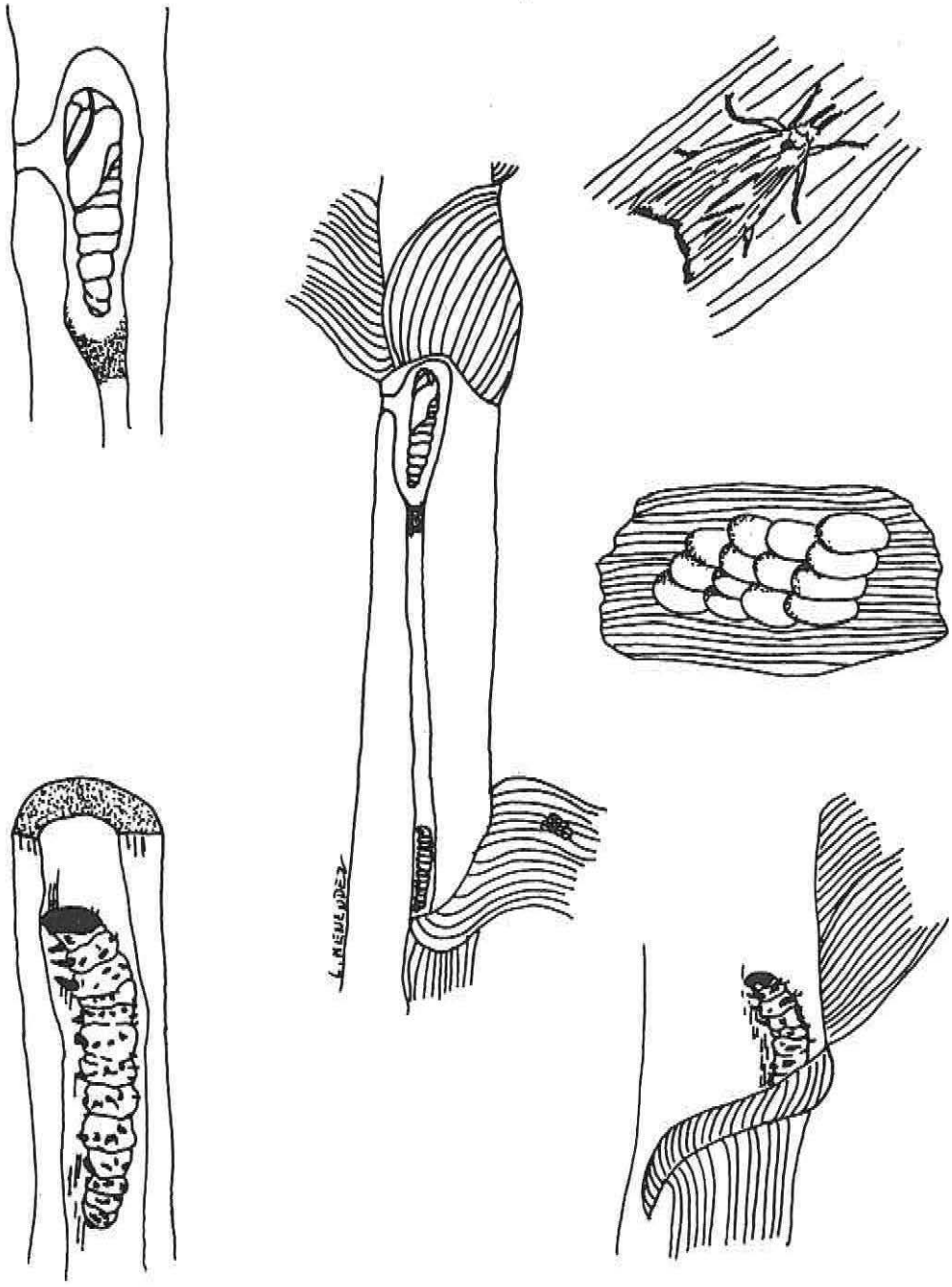
2

LIFE HISTORY OF STEMBORERS

Although each tropical gramineous stemborer has inherent species-specific life-history traits, a generalized life cycle can be developed for this diverse group. The general life cycle constructs a common template for viewing the biological and ecological similarities across



Generalized life cycle of stemborer, showing (clockwise from upper right) adult, egg mass, early-instar larva in leaf sheath, later-instar larva tunneling in stem and pupa in pupal chamber.

taxa and provides the observer with a convenient outline for recognizing subtle differences between the general life cycle and the life history of a specific stemborer. Once these differences in host life history are discerned, modifications in our general understanding of host-finding by parasites can be made to accommodate a particular stemborer species.

With few specific exceptions, all life stages of the more common New and Old World stemborers inhabit the aerial portions of gramineous plants. The drab-colored adult moths oviposit on plant leaves and stems, depositing eggs either singly or (more commonly) in masses. Early-instar larvae feed cryptically on succulent plant tissues in leaf sheaths, whorls, tassels and cobs (of maize), whereas older larvae are found almost exclusively feeding in tunnels inside the plant stem. Pupation normally occurs in the stem in a chamber constructed by the mature larva. The genera *Elasmopalpus* (Pyralidae) and *Castnia* (Castniidae) have significantly different lifestyles and will not be included here. However, because *Elasmopalpus lignosellus* (Zeller) is a serious pest in the New World, we have addressed its life history and its associated parasite fauna in Appendix I.

Adult

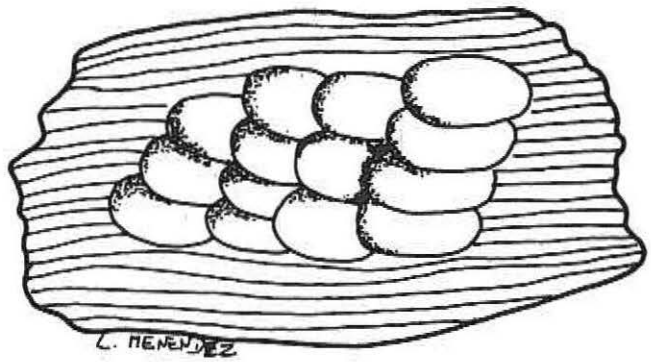
Stemborer moths are generally a drab grey or straw color and usually lack any distinct markings to facilitate field identification. Identification to species often requires examination of genitalia, especially of males (Bleszynski 1969). However, once the field entomologist identifies and becomes familiar with the species occurring in the area of interest, identifications often can be made using external morphology. Moths are nocturnally active and many are attracted to light. The dispersal ability of moths is speculative, but most authors agree that adult movement is most likely local rather than migratory. Crops tend to be infested by adults moving short distances either from within fields, from nearby fields, or from wild host plants in the proximity of fields; the population inoculum is supplied by the previous stemborer generation in crop residue or from wild hosts in the vicinity of the crop, either from continuously breeding or diapausing populations. The adult female life-span ranges from a few days to two weeks, normally with a 1–3 day preoviposition period. Moths lay 100 to 800 eggs, depending upon the species, in a series of ovipositions over three to seven days. Adult Crambinae have a reduced proboscis and probably do not feed as adults, whereas noctuid adults are known to feed on nectar and water.

Adult stemborer moth

Egg

Oviposition occurs on the aerial parts of the host plant, usually on the leaves. Eggs are commonly deposited in clusters that may vary in number from a few eggs to several hundred eggs. The range in cluster size is characteristic for a species, but the specific number of eggs per cluster may vary within a species. The eggs of pyralids are oval, flattened and scale-like, and are laid in imbricated rows. Noctuid eggs are semi-globular, laid singly or in rows. Individual stemborer eggs are creamy white when first laid and

darken before eclosion. The head capsule of the neonate larva is usually visible as a dark spot through the egg chorion just prior to hatching. These eggs are typically referred to as being in the "black-head stage". Usually 3–6 days are required for eggs to hatch under tropical temperatures.

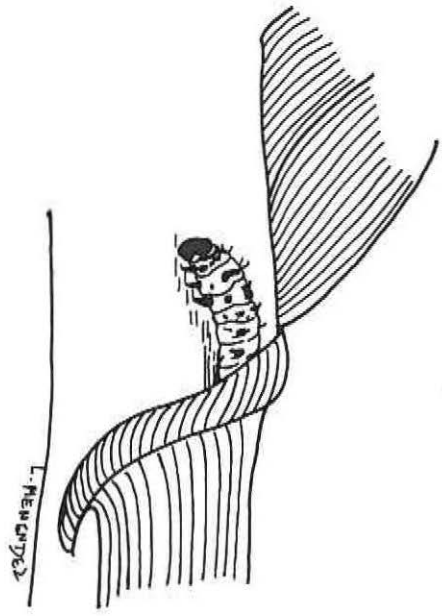


Stemborer egg mass

Most stem-boring Crambinae oviposit on the green, flat surfaces of host plants. Eggs are deposited on leaves and stems and are covered with a fine waxy layer. Eggs are usually exposed and not hidden or covered with camouflaging material. Several variations of this behavior are worth mentioning. *Eoreuma loftini* (Dyar) and *Coniesta ignefusalis* (Hampson) (both Crambinae), and *Eldana saccharina* (Walker) (Galleriinae) lay their eggs in the crevices of leaf folds and leaf sheaths. Oviposition by *E. loftini* and *E. saccharina* is further restricted to dry plant material, as opposed to the green plant material that is utilized as oviposition sites by most other stem-boring pyralids. Ovipositional behavior may be anticipated by examining the ovipositor architecture. The ovipositor of *E. loftini* is laterally compressed, which allows oviposition in crevices, whereas the ovipositor of *Diatraea saccharalis* is vertically depressed, which facilitates oviposition on flat surfaces. Egg masses of *Tryporyza* (Schoenobiinae), are covered with hairs and scales shed from the anal tuft of the abdomen. In contrast to the exposed eggs of most Pyralidae, noctuid eggs are usually concealed in the leaf sheaths.

Larva

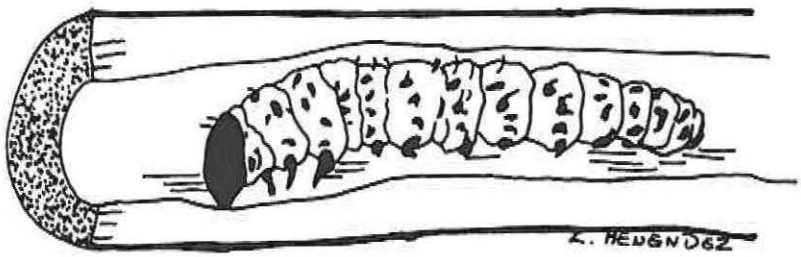
The larval stages of stemborers require approximately 25–45 days to complete development. Most stemboring pyralids have six larval instars, whereas stemboring noctuids generally have 6–8 instars. Stemborer larvae occupy two distinct microhabitats as a result of age-related feeding behavior. Early-instar larvae superficially mine leaves, leafsheaths, and other succulent plant tissues, which confines feeding to the periphery of the stem. During this period, the young larvae are cryptic and cannot be seen without dislodging the leaf sheath or whorl from the stem and exposing the mining activity. Early-instar larvae of some species (e.g., *Chilo partellus*), are known to disperse from the oviposition site by spinning threads and ballooning in the wind (Berger 1989).



Early-instar stemborer larva in leaf sheath

In contrast to the behavior of early-instar larvae, older larvae excavate extensive feeding tunnels inside the stem. Tunnel size, length and architecture vary among species. Some species tunnel through plant internodes, others exit a tunnelled internode to bore into new internodes, and some species tunnel only within one internode. Tunnel architecture can be longitudinal, transverse or a combination of both. For example, in the neotropics, most species of *Diatraea* tunnel through internodes, excavating an extensive longitudinal tunnel. Tunnels may traverse 3–5 internodes in maize and 5–10 internodes in sugarcane. In contrast, *Eoreuma loftini* tends to tunnel both longitudinally and transversely, but only within 1–2 internodes.

Many borer larvae maintain relatively clean feeding tunnels. *Diatraea* larvae regularly deposit their frass outside the entrance of the tunnel. Large mounds of frass accumulate near the tunnel entrance, particularly when the tunnel entrance is just above a leaf sheath. In contrast, *Eoreuma loftini* larvae maintain closed tunnels by plugging the traversed area with frass and detritus, thus packing the tunnel. The clean tunnels typical of *Diatraea* allow access to the tunneling larvae by some natural enemies, whereas the tightly packed tunnels of *Eoreuma* greatly limit natural enemy access to the borer larvae.



Later-instar stemborer larva in feeding tunnel

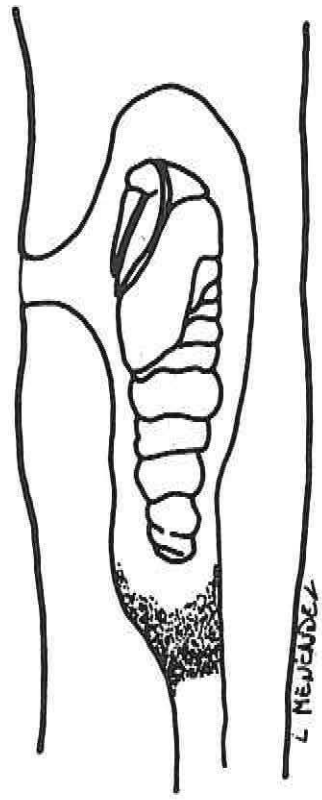
Stem-girdling behavior by larvae of *Diatraea lineolata* and *D. grandiosella* is associated with diapause by the borers in maize. Just prior to entering diapause, the mature larva girdles the maize stem a few centimeters above the newly constructed pupal chamber, causing stems to lodge. The exact advantage to the borer of this behavior is unknown, but the behavior likely provides a survival advantage. When the larva girdles the plant and creates a very weak point in the stem above the pupal chamber, the stem will have a greater propensity to break at the girdle rather than at the pupal chamber, thus decreasing exposure of the diapausing larva to a harsh environment.

Stemborers pass periods of environmental hostility by a prolonged mature larval development. *Diatraea saccharalis* and *D. grandiosella* diapause in the winter as mature larvae in the host stem in the more temperate regions. *Diatraea lineolata*, *Coniesta ignefusalis*, *Chilo orichalcociliellus* (Strand), *C. partellus*, and *Busseola fusca* (Fuller) exhibit a mature larval diapause (aestivation) that is induced by host plant maturity and drought, and is usually broken by the return of rains. Diapause by the mature stemborer larvae is spent in the pupal chamber, which is constructed by the pest prior to entering diapause.

Pupa

Mature stemborer larvae construct a pupal chamber at the terminus of the feeding tunnel just prior to pupation. The pupal chamber is excavated slightly larger than the feeding tunnel and access to the feeding tunnel is packed with frass and detritus. Pupal chambers are lightly lined with silken threads. To facilitate egress from the stem at moth

emergence, the mature larva constructs an exit tunnel from the pupal chamber to the outside of the stem. The outer layer of epidermis on the outside of the stem is left intact and forms a conspicuous "window" on the green stem as the thin epidermal layer dehydrates. The integrity of this moth emergence window varies with borer species and host plant. Some windows are intact and very sturdy, whereas others are fragile and tattered. Intact, sturdy windows can prevent entry of some natural enemies. After completion of the pupal chamber, feeding and movement cease, and the mature larva merges into the prepupal stage. The inactive prepupal stage may last several days before pupation. The noctuid genus *Sesamia* and the pyralid genus *Eldana* pupate differently from this norm. Instead of being totally sheltered in the stem like other stemborer pupae, *Sesamia* and *Eldana* pupate at least partially outside the stem. Mature *Sesamia* larvae normally vacate the feeding tunnel and pupate between the stem and leaf sheath. Pupae are secured in position by loose silken threads. *Eldana saccharina* spins a tough cocoon that partially protrudes through the moth exit hole. Pupation requires 7–10 days for both pyralids and noctuids.



Stemborer pupa

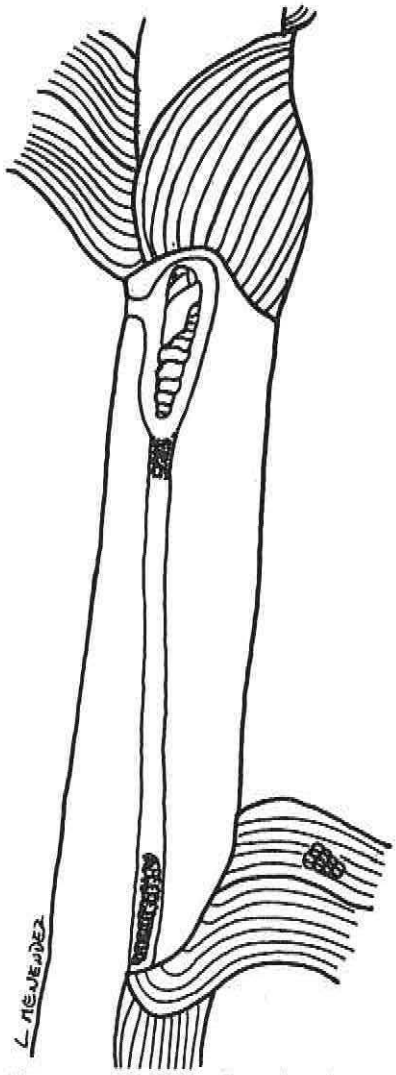
Plant Damage

Excellent, extensive reviews of damage to gramineous crops and yield losses from stemborers are available in the literature (Israel & Abraham 1967, Metcalfe 1969, Walker 1987, Seshu Reddy & Walker 1990), and will not be repeated here. The purpose of this brief section on plant damage is to provide general information on plant attack with regard to larval feeding behavior and how the plant will likely respond to the damage inflicted by the stemborer larvae. Good examples of intensive studies of borer dynamics and damage in a specific locality are provided by Rodriguez-del-Bosque et al. (1988, 1990a, b) and Kfir (1992).

Crop attack by stemborers is usually seasonal and controlled by rainfall in tropical zones, as opposed to being controlled by temperature in the more temperate zones. Crop damage is caused by stemborer larvae feeding on plant tissue. Young larvae feed exclusively on the leaves and stem periphery and only under extreme conditions of very high stemborer density and poor crop growth would we expect to sustain yield losses from peripheral feeding. Crop losses are mainly attributed to the stem tunneling habit of the later-instar larvae. Tunneling in young gramineous plants usually destroys the apical meristem and stops growth of the injured shoot. The terminal leaves actively growing from the apical meristem area die, become faded or brown, creating a "deadheart" condition. Tunnel excavation by larvae in older, larger plants restricts translocation of water and nutrients and weakens the stem. Extensive larval tunneling in the stem also provides sites for invasion by plant pathogens (Holloway et al. 1928, Manser 1959, Minja 1990, Ogunwolu et al. 1991), which can further damage the plant and reduce yields. Lodging of mature plants is also associated with weakening of the tunnelled stem (Rodriguez-del-Bosque et al. 1988). Tunneling in older plants is usually restricted to the formed internodes below the apical meristem and, thus, deadhearts are not common. Exceptions to this generalization of borer damage to older plants are the "top borers" of

sugarcane (Metcalfe 1969), and extensive tunneling in small, yet maturing, plants such as rice. Top borers of sugarcane specifically attack the growing points of older sugarcane, creating deadhearts (Gupta 1959, Kalra & Chaudhary 1964). Deadhearts are created in rice because the plant stem is short and boring larvae destroy the apical meristem during normal feeding and tunneling.

Young maize plants are especially susceptible to deadheart because of the habits of plant growth. Because maize does not tiller like sorghums, millets, rice and sugarcane, maize cannot compensate for the death of the main stem by producing additional lateral shoots. Thus, young maize plants manifesting deadheart cease growth and do not produce grain. Severe attacks of plants that tiller may reduce the plant stand, whereas light infestations may stimulate tillering and potentially increase grain production. Regardless of the intensity of the borer attack, the recovery period of an individual plant manifesting deadheart by tillering will be added to the normal maturity period and delay the anticipated harvest date.



Plant stem showing larval and pupal chamber

Laboratory Rearing

As with the references on plant damage, there is an extensive number of publications in the literature on rearing many different stemborers (see references below); the intention of this section is not to duplicate the material found in those references. However, because rearing stemborers is requisite to rearing their parasites, some basic rearing methods that we have found are appropriate and work well in our laboratory are included to provide the reader with a starting point for rearing stemborers. Our most recent experience with rearing stemborers has been primarily with *Diatraea saccharalis*, *D. grandiosella*, *D. lineolata* and *Eoreuma loftini*, and so most of the methods detailed below will reflect the methods we have found work well for rearing these species. Our rearing techniques rely heavily on methods associated with using artificial diet, but the reader can decide what modifications are necessary for rearing stemborers using live host-plant material.

Adults and Oviposition

For an oviposition cage, a cylindrical cardboard (ice cream) container (approximately 2-1 volume), with the top covered with organdy cloth, is adequate. Containers are kept at approximately 24–26°C, with artificial lighting on a 14:10 (L:D) photoperiod. Approximately every seven days, 50 mature borer pupae are placed in the container, and allowed to emerge and mate. For laboratory cultures, we have not needed to pre-determine the sex of the stemborer pupae. Cotton balls are soaked in a 20% sugar-water solution and placed

in the container, and the organdy cover of the container is sprayed every other day with distilled water to provide free water for the adult moths and to maintain high humidity to avoid desiccation of deposited eggs. In nature, *Diatraea* spp. oviposit on smooth, waxy surfaces, such as lush, green leaves of host plants; this natural smooth surface needs to be replicated for laboratory rearing. Therefore, for rearing *D. saccharalis*, the sides and bottom of the oviposition container are lined with commercially available waxed paper, which approximates the preferred smooth surfaces. *Chilo partellus* prefers to oviposit along the mid-veins of green leaves, rather than on the smoother leaf surface. Thus, for rearing *C. partellus*, making a pleat or a fold in the waxed paper provides an adequate substrate on which the females will oviposit. Unlike *C. partellus* and *D. saccharalis*, *Eoreuma loftini* and *Eldana saccharina* do not oviposit on smooth or exposed surfaces, but oviposit in the crevices of dried plant material (Atkinson 1978, 1979, van Leerdam et al. 1984, 1986). To induce *E. loftini* and *E. saccharina* to oviposit in the laboratory, a substitute for the natural oviposition site must be created. One available substitute is rough-surfaced paper toweling that is folded. Another method that has proven even more effective is to take three, 7.5 by 12.5 cm index cards, aligned and placed atop each other, and staple them together along the two long margins. With scissors or a knife, cuts are made through the stapled cards perpendicular to the stapled edges, and to within approximately 1 cm of the staples. These cut edges simulate the crevices in dried plant material in the field, and *E. loftini* readily oviposits in the crevices.

Whether waxed paper, paper toweling or index cards are used for the oviposition substrate, egg production can be optimized if the ovipositional substrate is removed and replaced every other day for approximately 7–10 days, after which time the surviving moths are destroyed. We use two oviposition containers concurrently, offset by 3–5 days, which allows a completely continuous production of stemborer eggs and larvae. After removing the substrate from the oviposition container, the paper or card is cut into smaller pieces, of a size that can be placed into a plastic bag and held. After 24 h, the eggs (which are now 48–72 h old), are removed from the bag and rinsed with a mild sodium hypochlorite solution before being placed onto an artificial diet for larval emergence and rearing. Rinsing the eggs minimizes much of the fungal growth that can occur during rearing. For rinsing, place the eggs into a 9 cm diameter Petri dish, which has been half-filled with a 2% solution of 0.05% sodium hypochlorite (commercially available household bleach) in distilled water. Eggs are rinsed in the solution for only a few seconds, then the bleach solution is poured off, and the eggs are washed three times with distilled water. After rinsing the eggs, the paper substrates are spread onto paper toweling for air-drying for approximately 15 min. In our experience, rinsing eggs before they are 24–48 h old decreases emergence of larvae. However, eggs that are to be used for exposure to egg parasites, such as *Chelonus* or *Trichogramma*, should not be rinsed before exposure, as the bleach rinse may remove some of the chemicals that provide important cues for the host-recognition process by the female parasites.

Larvae

After the eggs have been dried, the wax paper, paper towels or index cards are cut into smaller sections that contain masses of stemborer eggs. A sufficient number of sections to contain approximately 100 eggs are placed into a 9 cm Petri dish, containing artificial diet, and the dishes covered. Eggs will hatch within a few days, and first-instar larvae are highly positively phototropic and negatively geotropic. Therefore, to avoid losses of larvae through the top of the Petri dish, a thin layer of petroleum jelly (Vaseline) is applied along the inside rim of the Petri dish above the artificial diet. Stacks of Petri dishes (often up to 12–16 dishes) are taped securely together for storage. Once borer larvae reach the third-instar stage, they are removed from the diet (and the accumulated frass) and a maximum

of 15–25 are placed in a new Petri dish with diet.In the later larval instars, too many larvae per dish will produce a large amount of frass, which leads to high humidity and increased incidence of mold. By changing the diet dishes after larvae are in the third instar and avoiding a high density of later-stage larvae, the dishes need to be changed only once per generation. Changing larval dishes is a labor-intensive process and the artificial diet is expensive, thus changing larval dishes on this schedule optimizes costs of labor and materials without sacrificing production of stemborers. If either labor or materials are not limiting, others may find a more optimal schedule or density of larvae per dish. For rearing *D. grandiosella*, first-instar larvae should be separated after emergence and placed individually into diet cups, as later-stage larvae of this species are cannibalistic. Other species may be cannibalistic if kept at high densities, and this should be considered before attempting rearing on a larger scale. For all species, if larvae are reared in small cups, the ultimate-instar larvae will often chew a hole through thin containers, or the cardboard or thin plastic lid of the diet cup prior to pupation, and larvae may be lost.

Pupae

The pupal stage is the most impervious to rinsing with solvents and soaps. We routinely surface-sterilize pupae with the same 2% household bleach solution as used for eggs, to remove surface contaminants. Again, after a quick dip into a Petri dish with the bleach solution, pupae are rinsed three times with distilled water. As with eggs, pupae to be exposed to pupal parasites should not be rinsed with the bleach solution. The pupal stage of many pyralids lasts about 7–10 days. For the purpose of providing pupal hosts for parasites such as *Xanthopimpla* or *Pediobius*, removing new pupae daily or every other day from Petri dishes and separating them by the date collected gives the approximate age of the pupae; production of pupal parasites may be enhanced by avoiding the use of very new or very old pupae. Unparasitized pupae of a known age can be placed in the oviposition cage within a day or two of predicted moth emergence.

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3

SUCCESSFUL PARASITIZATION

Successful parasitization requires a sequence of distinct and consecutive processes (Salt 1935, Doutt 1959, Vinson 1975). Initially, the adult female parasite must locate the habitat that harbors its host and then, within the habitat, the female must find a host. Once a host is located, it must be acceptable to the female for oviposition and be suitable for completion of parasite development. Finally, the parasite must be able to regulate the host physiology to enhance and maintain host suitability. This sequence of events leading to successful parasitization occurs under natural conditions. Recognition of how this sequence of processes occurs in a natural setting is critical, especially with regard to the tritrophic interaction between gramineous plant, stemborer and parasite. Organizing and implementing biological control intervention relies heavily upon a general understanding of these processes.

Habitat Finding

The first process, habitat finding, requires the female parasite to locate the habitat that her host has colonized. Cues for locating an appropriate habitat are usually emitted by the host plants within the plant community in which the stemborer resides. Although very little research has been conducted on habitat location by stemborer parasites, the parasites likely respond to long-distance cues emanating from the habitat of their hosts, i.e., wild and cultivated grasses. Plants may actually be induced by stemborer feeding to release volatile chemicals (synomones) that attract stemborer parasites, as has been found in other tritrophic systems (Vet & Dicke 1992). Thus, the grass communities provide the long-range cues for habitat location by the searching parasite. The area a parasite must traverse to locate the proper habitat depends upon the condition of the habitat where she completed her life cycle. If this local habitat has remained favorable for continuous reinfestation by the stemborer, it should be attractive to the parasite, and only trivial movement within the habitat will be necessary. However, if the habitat has degraded and become unfavorable for the host, the parasite must move to a more suitable habitat occupied by stemborers, and thus the parasite will traverse a greater area to find the appropriate habitat.

In laboratory rearing, the process of habitat finding is usually fulfilled by placing the parasite and host in close proximity within a rearing cage or container. However, parasitization will not proceed further unless the receptive female parasite receives the proper cues that lead to finding hosts.

Host Finding

Once the female parasite has located the host habitat she must locate the host itself. Cues that can be exploited by the parasite for host finding include chemical cues, either as by-products of normal host activity or as a response by the plant to host attack; or physical cues, such as discoloration or deadheart of stems, host frass, larval tunnels or an emergence window, or the host itself.

Chemical by-products of normal host activity such as oviposition, feeding, defecation, or silk production can act as kairomones that provide chemical stimuli to guide the searching female parasite and reduce the searching pattern that eventually leads to host location. For example, the braconid parasite *Cotesia flavipes* is attracted to the larval frass of *Chilo* (Kajita & Drake 1969, Mohyuddin 1971) and *Diatraea* (van Leerdam et al. 1985). Fresh host frass stimulates a host-seeking response in *C. flavipes* that guides the female to the entrance of the host feeding tunnel. Traversing the feeding tunnel then directs the female to the host larva (van Leerdam et al. 1985).

The physical microhabitat of the host also plays an important role in host recognition and finding. This is especially true for stemborer parasites attacking the older larvae and pupae, because hosts are often cryptic and the host alone does not provide the appropriate cues for host recognition. Physical cues such as the larval feeding tunnel, frass deposited outside a tunnel (though this may provide both physical and chemical cues), moth emergence window, or the larva or pupa enclosed in a stem are required for host recognition when hosts are naturally hidden in cryptic microhabitats. Although the exact role a specific physical cue may contribute to parasite success is unknown, we need to recognize that these cues often must be present for successful host finding.

Physical and chemical cues associated with host finding in the natural setting also need to be recognized and often need to be included in the laboratory culturing procedures. Some host finding cues are essential for parasitization, whereas others may simply enhance productivity of the parasite colony. Recreating the natural host microhabitat and normal activity in the laboratory setting usually will provide the essential cues for host recognition. These cues are usually associated with the physical components of the host microhabitat or host *per se* and from the by-products associated with normal host activity.

For parasites in nature, the behavioral events elicited by kairomones usually are complex, and their intricacies need not be totally understood for successful rearing, only that the gross action/reaction process must not be violated. Whereas host frass may be critical for host finding by *C. flavipes* in the field, in the laboratory the absence of fresh host frass does not preclude parasitization by *C. flavipes*. The host finding step initiated by frass is by-passed in laboratory rearing when the parasite and host are placed in close proximity. However, fresh frass, especially from plant stems, may enhance recognition, acceptance, and successful parasitization by *Cotesia* spp. and *Apanteles diatraeae* Muesebeck in the laboratory.

Often, artificial physical microhabitats that mimic the natural situation can be successfully substituted in the rearing process (Melton & Browning 1986, Hawkins & Smith 1986, Smith et al. 1990). Parasitism of stemborer larvae by *Allorhogas pyralophagus* Marsh provides a good example of the role the physical microhabitat plays in host recognition. In nature, *A. pyralophagus* females first locate host larvae in the feeding tunnels and then drill through the plant stem with their ovipositor and parasitize larvae in the feeding tunnel (Melton & Browning 1986, Smith et al. 1987, Hawkins et al. 1987). Exactly how the parasite locates the host in the feeding tunnel is unknown. Possibly vibrations caused by larval feeding are detected by the searching parasite. In the laboratory, the natural physical location of acceptable hosts (i.e., larvae enclosed in a plant stem), must be duplicated for successful host finding. If fecund *A. pyralophagus* females are presented with acceptable and suitable hosts that are not enclosed in a stem or an artificial substitute, the parasites do not recognize the hosts and, thus, do not parasitize the hosts. In fact, acceptable, suitable hosts that are not found in the appropriate microhabitat context do not elicit any apparent host recognition or searching responses from *A. pyralophagus* (i.e., no antennation, locomotion or ovipositor probing). However, when these same host larvae are presented in tunneled grass stems, responsive females immediately begin locating and parasitizing the larvae through the stems. Host larvae placed in either paper or plastic drinking straws that adequately mimic the natural, cryptic, host microhabitat will elicit the same positive response from the parasites as do host larvae in grass stems. Successful parasitization can even be achieved by placing host larvae in the bottom of a Petri dish and covering them with filter paper or cloth. In general, parasites that enter the stem to attack their hosts do not require that the host be presented enclosed in the plant (stem, whorl, or leaf sheath) or an artificial plant mimic (drinking straw, corrugated cardboard) for successful parasitization in the laboratory, whereas parasites that drill through the plant

stem or emergence window must be presented with enclosed hosts for successful parasitization to occur.

Host Selection and Acceptance

After the parasite has found the host, the process of actually selecting an individual for oviposition begins. As with the previous processes, the host selection process is the result of evolution, which helps insure that the parasite progeny that are committed to the host have the best chance of surviving. In nature, parasites attack specific host stages (egg, larval, pupal) and attack either: a) is confined to a single host species (i.e., monophagous); b) is confined to a narrow range of host species (i.e., stenophagous); or c) includes a broad range of hosts (i.e., polyphagous), selecting and accepting any host that meets a broader set of criteria. Requisites for host acceptance may include host size, shape, texture, age, odor, behavior and previous parasitization status. The ovipositing female parasite must select hosts that are the correct life stage and age to support successful progeny development. For example, *Cotesia flavipes* will only accept 3rd- through 6th-instar *D. saccharalis* or *C. partellus* larvae as hosts; the range of acceptable instars corresponds to those instars found within tunnels in the plant stems. The ichneumonid *Xanthopimpla stemmator* Thunberg will accept *D. saccharalis* pupae as hosts, but will not accept *D. saccharalis* larvae as hosts even though both life stages occur in a similar cryptic microhabitat.

Host behavior also can be important to the acceptance process. The pupal parasite *X. stemmator* will readily accept *D. saccharalis* pupae enclosed in a stem, but very rarely accepts pupae that are exposed. Unlike *A. pyralophagus*, which does not recognize hosts that were not in the proper enclosed microhabitat, *X. stemmator* will recognize exposed pupae as hosts. However, *X. stemmator* is prevented from successful parasitization of exposed pupae because exposed pupae move when touched, which interferes with the lengthy process of oviposition. In contrast, pupae enclosed in a stem or a straw do not dislodge or interfere with the ovipositing parasite and oviposition is successful. Finally, some female parasites can determine the parasitization status of the host and can circumvent inter- and intraspecific competition by discriminate oviposition. *Stenobracon deesae* (Cameron), a larval ectoparasite of *Chilo* in India, inserts its ovipositor into the host prior to oviposition, which allows the parasite to distinguish between healthy and previously parasitized hosts, thus avoiding superparasitization (Narayanan & Chaudhuri 1955). Many trichogrammatid egg parasites are also able to discriminate between parasitized and unparasitized hosts, thus avoiding superparasitization (Metcalfe & Breniere 1969).

Host Suitability and Regulation

The previous sequence of processes of habitat selection, host finding, and host selection and acceptance serves to narrow the range of potential hosts that a parasite may encounter and parasitize. The sequential narrowing of potential hosts through the host selection process ensures that the host that is accepted is one that is physiologically suitable for the parasite. Physiological suitability of the host is an absolute necessity for successful development of the parasite progeny because of the intimate relationship between parasite progeny and hosts. A suitable host provides adequate shelter and nutrients for complete development of the parasite.

For laboratory rearing, the first choice of a host for rearing a given parasite is a natural host that has coevolved with the parasite. However, a coevolved host may not be in culture, or may not be reared easily enough to have sufficient host numbers for successful parasite rearing. When coevolved hosts are not available, many stemborer parasites are successfully reared on factitious hosts, which are hosts that can be reared in the laboratory, but are not known to be attacked by the parasite in nature. Such factitious hosts either are

Lepidoptera that are easily reared and readily available, such as the wax moth, *Galleria mellonella* L., or the actual, non-coevolved stemborer targeted for biological control. Old World parasites such as *C. flavipes* and *X. stemmator* are reared successfully on the factitious New World pyralid *D. saccharalis*, with which it has no coevolutionary history. In some cases, though, these surrogate hosts with no coevolutionary history may be completely acceptable to ovipositing females, but are not completely suitable for parasite development of the parasite progeny. For example, *C. flavipes* has no coevolutionary history with *E. loftini* but will accept it as a host. However, *C. flavipes* rarely develops in this particular host. Similarly, *C. flavipes* will readily oviposit in *B. fusca* larvae in the laboratory, but no *C. flavipes* progeny are produced. Partial suitability is also found in some stemborer/parasite relationships. *Cotesia flavipes* can complete development in the non-coevolved host *D. grandiosella*, but the majority of parasite larvae are encapsulated (Overholt & Smith 1990). Hosts that are acceptable for oviposition, but are not suitable or only partially suitable for parasite development, are often encountered in non-coevolved host/parasite relationships. Laboratory trials using factitious hosts should be sensitive to measuring the degree of host acceptability and host suitability.

Stemborer parasites can be sub-divided into two categories depending on the physical location in or on the host that the immature parasites develop: either internally within the host body or externally on the host cuticle. Those that develop internally in the host are considered endoparasites. Adult females of endoparasitic species typically deposit their eggs directly into the host's haemocoele. The eggs eclose and the parasite progeny develop to the mature larval stage inside the host, then emerge to pupate free from the host, or the progeny pupate within the host cadaver. In contrast, parasites that develop externally are ectoparasites. The adult female ectoparasite initially paralyzes the host and then oviposits directly on the host's integument or in close proximity to the host. The parasite progeny consume the host while attached externally and pupate near the host remains. Not all stemborer parasites fit neatly into these two categories. *Alabagrus stigma* (Brullé) and *Chelonus sonorensis* Cameron are endoparasitic until the final larval instar when the parasite larva feeds ectoparasitically. Certain tachinids larviposit their mobile, planidial larvae at the entrance to the host feeding tunnel; the parasite larvae must then locate the host by traversing the feeding tunnel. The mobile parasite larvae penetrate the host's integument and feed endoparasitically. A further exception is the tachinid *Palpozenillia*; eggs deposited near the tunneling borer must be ingested by the borer for parasitization to occur.

Host paralysis is common among the ectoparasitic Hymenoptera that attack stemborer larvae in the feeding tunnel. For ectoparasitic species, parasitism is a two-stage process, starting with host paralysis, followed by oviposition. First, the ovipositing female stings the host and injects a venom, which induces permanent paralysis. Subsequently, eggs are laid externally on the paralyzed host larva. In instances when the mobile host larva moves beyond the point of ovipositor contact before paralysis occurs, the ovipositing female lays her eggs in the larval tunnel. Immediately upon hatching from the egg, the mobile, planidial, first-instar parasite larva seeks the nearby paralyzed host and parasitizes it. Paralysis causes cessation of larval growth, and parasite progeny consume the host stage that was initially attacked.

Knowledge of these two modes of parasitization is useful in understanding the final process in successful parasitization, which is host regulation. The parasite must regulate certain host processes for the parasite's own advantage to insure the host is suitable and development of parasite progeny is complete. Parasitized hosts are different from their unparasitized counterparts both physiologically and ecologically. Changes in parasitized hosts caused by both the ovipositing female and her developing progeny include alterations

in growth rate, food consumption, development, morphology, behavior, respiration and biochemical and physiological activities (Vinson & Iwantsch 1980).

The successful development of endoparasitic species is influenced by the host's immune system and the ability of the parasites to evade this system. This area is the subject of recent intense interest; the wealth of information about immune responses is beyond the scope of this manual. However, for the purpose of understanding parasite success, some brief discussion is appropriate. The immune system of host insects is one of the primary means for the host to maintain homeostasis, by fighting off attacks from other organisms, whether the invaders be pathogens or parasites. In turn, a successful parasite must be able to evade the defensive response of the host immune system. Evasion can consist of two major classes: those evasions that are active responses by the parasite and those that are more passive, due to suppression or abrogation of the immune response by some factor from the parasite. Injection of an egg into a host by the female parasite can initiate the host's immune response. The injected egg may be recognized as a foreign body by the host, which activates the host immune response, especially the cellular response of encapsulation. Within the haemocoele of the host are circulating and fixed blood cells (haemocytes) that are the primary detectors and effectors of the immune response. In the case of eggs injected by the parasite, circulating haemocytes recognize the invader as foreign and attach to the surface of the invading egg(s). As more and more haemocytes attach to the surface of the invading egg, and to each other, the haemocytes thin and spread, eventually covering the surface of the egg(s). The complete covering of the invader, i.e., the encapsulation, in effect walls off the parasite progeny from the host, and eventually kills the enclosed parasite(s). Death of the encapsulated parasite progeny may be due to oxygen deprivation or production of toxins within the encapsulation.

Clearly many parasites are successful, and thus have evolved a mechanism for evading the host immune response. One type of host alteration that causes evasion of the immune response is due to teratocytes (Dahlman 1990), which are unusual cells produced by many braconid embryos. The role of teratocytes is unclear and the focus of much discussion (Strand & Wong 1991). Some studies suggest teratocytes affect the immune response of the hosts directly (Salt 1968, Strand et al. 1986), whereas other studies suggest teratocytes serve a trophic function (Sluss 1968). Regardless of the mechanism or role of teratocytes, they serve as a means of evasion of the host immune response.

Other means for evasion of the immune response are more passive. The eggs of some parasites have been shown to have surface features that either inhibit recognition by the host or otherwise protect against encapsulation (Salt 1968, Davies & Vinson 1986). Other parasites inhibit encapsulation with factors injected at the same time as parasite eggs by the female parasite, such as components from the venom gland of females (Rizki & Rizki 1984) and viruses (Stoltz et al. 1984). The viruses, known as polydnaviruses (reviewed in Fleming 1992) replicate and are stored in the calyx of the female parasite's ovaries. At the time of oviposition, viruses in the calyx fluid are injected along with parasite eggs. To date, polydnaviruses have been found exclusively in the Braconidae and Ichneumonidae. Among parasites of stemborers, polydnaviruses are known from the Banchinae, Campopleginae, Cheloninae and Microgastrinae (Fleming 1992).

Thus, numerous variations in the suppression of the immune response occur, but the effect is evasion of the host immune response to the benefit of the parasite and detriment of the host. Whether the host immune response is evaded actively or passively, it is imperative for successful maintenance of a parasite culture to have a host that can be regulated by the parasite. Likely, very different responses will be seen for coevolved host/parasite pairings than for use of factitious hosts in rearing, but this subject is ripe for future research.

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4

FORAGING STRATEGIES

Introduction

The series of processes necessary for successful parasitization, coupled with the general stemborer life history, provide a template for discerning how a particular parasite may utilize the host life stages. In this section, we consider the foraging strategies of parasites of stemborers. Traditionally, foraging strategies have concerned the behaviors and adaptations associated with finding food. However, we consider a parasite's foraging strategy to include how the parasite finds its hosts and how the parasite progeny utilize the host for nutrition and development. In addition to the information gleaned from the previous two sections, an understanding of the particular foraging strategy employed by the parasite will enhance biological control efforts directed toward stemborers.

A parasite foraging strategy can be defined as the set of behavioral and morphological adaptations that enable a parasite to exploit a particular host effectively. The strategy will include all aspects of the host/parasite association, including the method of attack, disposition of the host (cryptic or exposed), the cues employed to find the host, the host stage attacked, location of the parasite progeny on or in the host and the host stage from which the parasite progeny emerge. We have mentioned that a parasite's host range may be very broad (polyphagous), very narrow (monophagous), or somewhere in between (stenophagous). Regardless of the breadth of the host range, most parasites will exploit only one host life-history stage, such as eggs or larvae, or even only one subset of a life-history stage, such as early-instar larvae or mature larvae.

Although a particular parasite species may be very host-specific, there are usually numerous parasite species that will utilize the same host stage. The different parasite species that exploit a specific host stage in a similar manner comprise a guild (Ehler 1992, Miller 1980, Miller & Ehler 1990, Mills 1992, Root 1967). Therefore, in the case of stemborers, each life stage, i.e., egg, larva, pupa and adult, has a guild of natural enemies associated with it. For example, the egg stage of stemborers is parasitized and exploited by several species in the families Trichogrammatidae and Scelionidae, which comprise the egg parasite guild. Interestingly, there can be some overlap between guilds, especially for parasites with complex biologies that utilize more than one life stage. For example, members of the braconid subfamily Cheloninae parasitize the host egg, but consume and emerge from the host larva. We classify the Cheloninae in the egg-larval parasite guild because they attack the egg but exploit the larval stage.

Table 3 describes the foraging strategies of parasites of stemborers, arranged from egg parasites through pupal parasites. The specific foraging strategies are described more thoroughly below. For each foraging strategy, we have identified the method of attack, whether the host is exposed or cryptic, the types of cues thought to be used by the parasite to find the host, the host stage attacked, host stage from which the parasite emerges, whether the parasite is an endo- or ectoparasite and several examples of taxa that employ such a strategy. Note that within a parasite foraging guild, there can be several foraging strategies employed to utilize the host, depending on the specific age of the host attacked, or the behavioral or morphological adaptation used to attack the host. Thus, the sets of complex behavioral and morphological traits that a parasite has and uses to exploit a specific host stage serve to lessen the impact of interspecific competition.

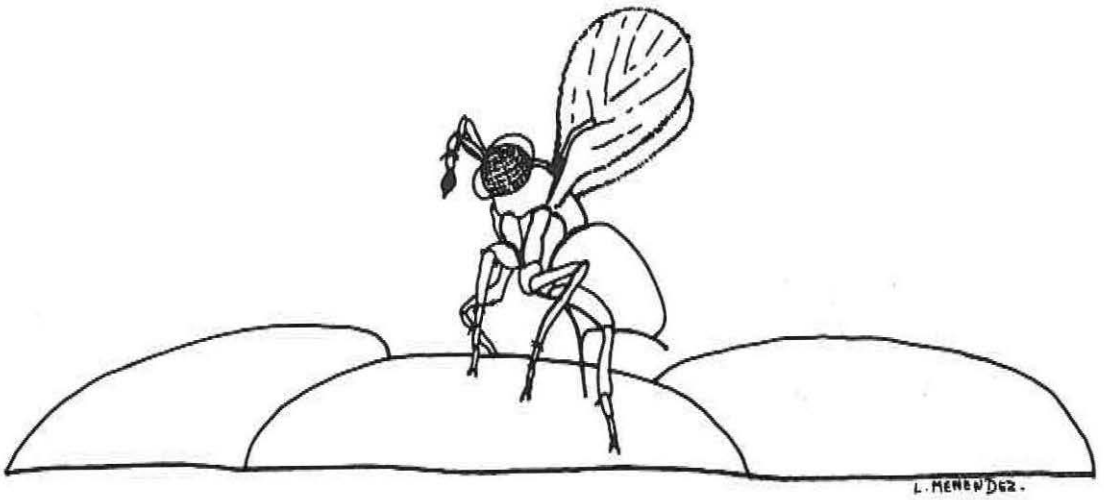
The particular adaptation and strategy employed by a parasite is constrained by characteristics of the host behavior and life history. The foraging strategy used also depends on the particular host stage attacked. Stemborer eggs are usually exposed, whereas larvae and pupae are primarily cryptic. Even among larval stages of stemborers, parasites will discriminate between early-instar larvae found in the leaf sheaths, later-instar larvae that tunnel in the plant stem, or mature larvae that construct the pupal chamber and associated moth exit window. In addition, as mentioned for the Cheloninae,

the host stage actually exploited for food by the parasite progeny may differ from the host stage attacked.

Egg Parasite Guild

Direct Attack

As mentioned in the section on stemborer life history, eggs of most stemborers are exposed, being deposited in the open on leaf surfaces or stems. Even the eggs of *Eoreuma, Eldana, Busseola,* and *Sesamia,* though deposited in crevices or leaf sheaths, are still exposed somewhat to egg parasites (Ingram 1958, van Leerdam et al. 1984, 1986, Browning & Melton 1987). The egg parasite guild uses a direct attack method to exploit this exposed host stage. The parasite may use one or several of a variety of cues to locate the host. It



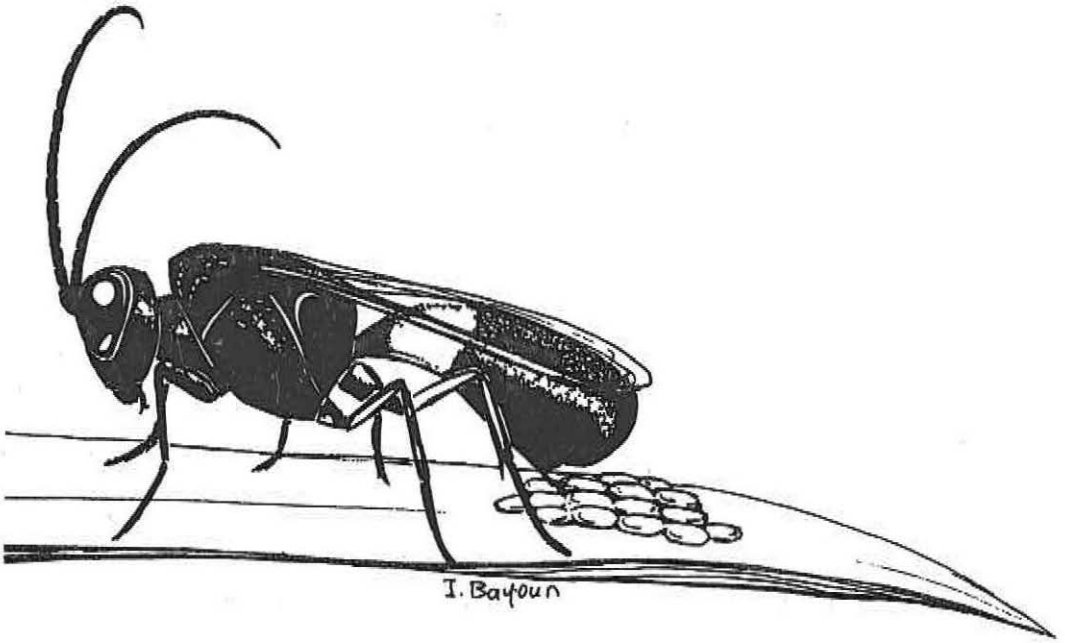
Trichogramma ovipositing in stemborer eggs (Egg guild, direct attack)

may use visual cues, such as the egg mass itself; or it may use chemical cues, such as a kairomone in the waxy layer covering the eggs or on the scales left by the ovipositing female moth, to find the area in which a female deposited eggs. Once the eggs are found, the parasite attacks the host directly, laying a single egg or multiple eggs within each host egg. The only major morphological adaptation is the small size of the parasite. If host eggs are deposited in a mass, the parasite likely marks those eggs that have been attacked and engages in area-restricted search behaviors that enhance finding subsequent unparasitized eggs within the egg mass. For parasites of *Eoreuma, Eldana, Busseola, Maliarpha* and *Sesamia,* whose eggs are laid in crevices and leaf folds, the parasite has direct access to those eggs that are at the periphery of the egg mass and, because of the small size of the parasite, they may also enter into the small crevices to parasitize other eggs within the egg mass. In our definition of the egg parasite guild, parasites attack and emerge from the host eggs. Examples of egg parasites include the trichogrammatid genera *Trichogramma* and *Trichogrammatoidea,* and the scelionid genus *Telenomus.*

Egg-Larval Parasite Guild

Direct Attack

This strategy is used by all parasites in the braconid subfamily Cheloninae and *Venturia ovivenans* (Zwart) (Hummelen 1974) in the ichneumonid subfamily Campopleginae. This attack method actually represents a composite of both the egg and larval guilds, because these parasites attack the host egg but exploit the larval stage. The exposed host eggs are found similarly to the process used by the egg parasite guild. In contrast to the very small trichogrammatids and scelionids, the Cheloninae and *V. ovivenans* are much larger than the host eggs being parasitized. This size differential between parasite and host provides the first clue for the complex life history. The Cheloninae and *V. ovivenans* are egg-larval parasites, ovipositing in the host egg, but the parasite progeny emerge from later-instar larvae that are tunneling in the plant stem. Parasites using this strategy are solitary endoparasites.

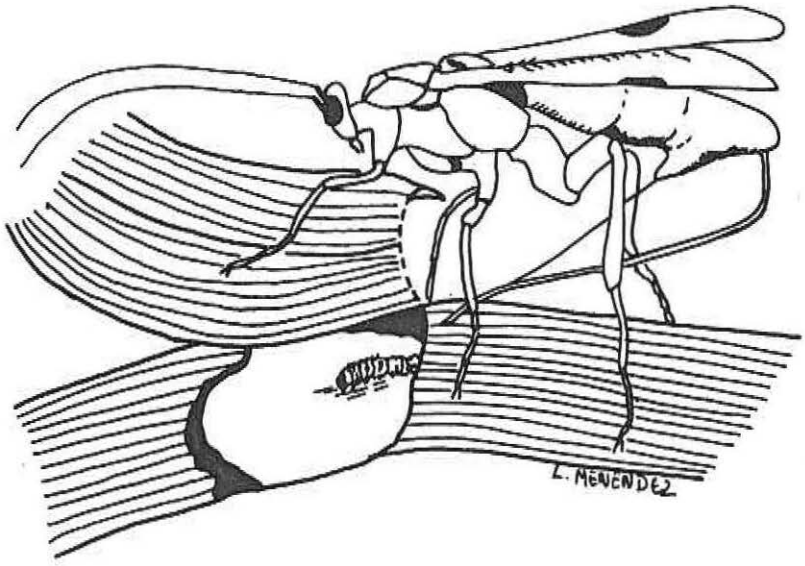


Chelonus ovipositing in stemborer eggs (Egg-larval guild, direct attack)

Larval Parasite Guild

Probe-and-Sting

Probe-and-sting parasites attack the two extreme ages of host larvae, either early-instar host larvae within the leaf sheath or mature host larvae that are excavating the pupal chamber. Parasites that use the probe-and-sting method to exploit early-instar larvae in the leaf sheath all use their ovipositor to probe and find the cryptic host. Two different variations are employed to attack small, early-instar hosts. The braconid *Macrocentrus* (Macrocentrinae) has a fairly small body size (< 5 mm), with an ovipositor that is as long as or longer than the body (5–7 mm). Because of its small size, *Macrocentrus* crawls into the



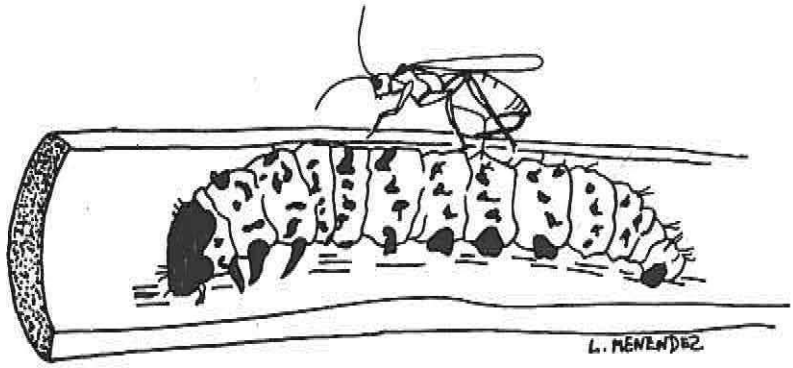
Alabagrus probing into the leaf sheath and ovipositing in early-instar stemborer larva (Larval guild, probe-and-sting)

narrow folds of the leaf sheath, thus gaining fairly close proximity to the early-instar host larvae. The braconid *Alabagrus* (Agathidinae) uses a slightly different method. *Alabagrus* has a much larger body (> 10 mm) than *Macrocentrus*, and is thus prevented from entering the narrow folds and crevices of the leaf sheaths. Instead, *Alabagrus* uses its very long ovipositor (approximately 15–20 mm), to probe into the leaf sheath crevices and parasitize the host. Note that the body size of the parasites to which we have alluded reflect sizes of species we have reared, and may not be indicative of other species in these genera. Regardless, these strategists must either have a long ovipositor or a small body-size to gain access to the early-instar host larvae that are feeding cryptically within the leaf sheath. Probe-and-sting parasites apparently use chemical cues provided by host frass or plant damage to locate the early-instar larvae feeding in the leaf sheaths. These parasites oviposit in the early-instar larvae and their progeny emerge from later-instar larvae that are tunneling in the plant stem. These probe-and-sting parasites are all endoparasites, but *Alabagrus* is solitary, whereas *Macrocentrus* is polyembryonic.

The other group of parasites that employs the probe-and-sting method attacks mature larvae. As the stemborer larva matures, it forms the pupal chamber by enlarging the terminus of the feeding tunnel, plugging the tunnel with frass, and constructing the moth exit window. The ichneumonids *Isotima* and *Mallochia* (Phygadeuontinae), and *Elasmus* (Elasmidae), probe through the exit window with the ovipositor and attack the mature larva enclosed within the pupal chamber. *Isotima, Mallochia* and *Elasmus* require the host to have made the moth exit window, which can be probed because of its thinness. *Isotima* and *Mallochia* are solitary ectoparasites, and *Elasmus* is a gregarious ectoparasite; their progeny consume the mature larvae and pupate within the stemborer pupal chamber.

Drill-and-Sting

Larvae of stemborers feed cryptically, being hidden either within the leaf sheath or within the tunnel bored into the plant stem. Parasites that employ the drill-and-sting strategy probably use a combination of chemical and physical cues, such as host frass and

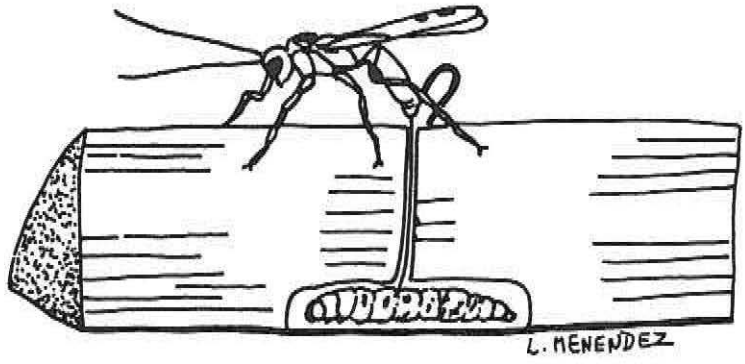


Allorhogas drilling through plant stem, paralyzing and ovipositing on stemborer larva (Larval guild, drill-and-sting)

the tunnel itself to find the larval host tunneling in the stem. Once the host position in the tunnel is located by the searching female parasite, she drills through the plant stem to attack the enclosed larvae. The adaptation employed by these parasites is a strengthened ovipositor that drills and penetrates the plant stem. Obviously, successful parasitization will occur in plants in which the stems are thin enough for drilling, or the host tunnel is near the stem surface and not beyond reach of the parasite ovipositor. Examples of parasites using this strategy are found in the braconid subfamilies Doryctinae, such as *Allorhogas, Heterospilus,* and *Rhaconotus,* and Braconinae, including *Bracon, Myosoma* and *Tropobracon.* These parasites are solitary or gregarious ectoparasites that paralyze the host before ovipositing on the host. Parasite progeny exsanguinate the paralyzed larvae and pupate near the host cadaver within the host tunnel in the plant stem.

Wait-and-Sting

Wait-and-sting parasites use a variation of the probe-and-sting method that is distinctive enough to be classified separately. Wait-and-sting parasites exploit larvae that are tunneling in the plant stem, but the parasites do not actively drill through the plant stem with their ovipositor to attack hosts. Stemborer tunnels have at least one exit to the outside

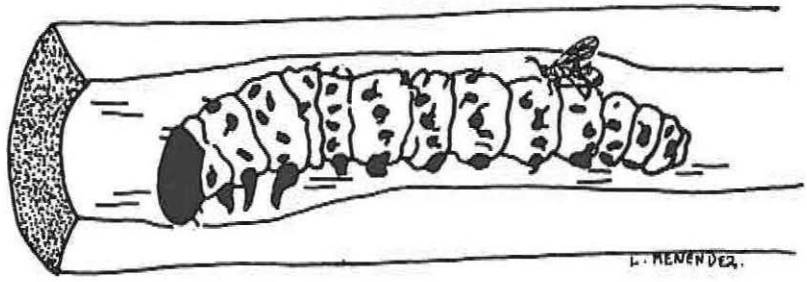


Stenobracon deesae probing stem, paralyzing and ovipositing on stemborer larva (Larval guild, wait-and-sting) (Redrawn after Narayanan & Venkatraman 1952)

of the plant, where many species deposit frass. Stemborers also construct other exits where the tunnel breaches the stem surface. Wait-and-sting parasites insert the ovipositor through one of the breaches, or wait with the ovipositor positioned at the tunnel entrance. As the host larva traverses the tunnel, either in the act of clearing the tunnel or due to other movement, the parasite is in a position to paralyze and oviposit on the host. In this case, the active part of searching is finding the breach in the tunnel or the tunnel entrance, then the parasite waits passively for the host to come in close proximity for parasitization. Examples of wait-and-sting parasites are the braconids *Digonogastra, Iphiaulax, Euvipio, Glyptomorpha* and *Stenobracon* (all Braconinae), which are solitary and gregarious ectoparasites. They attack later-stage larvae, which are paralyzed prior to oviposition.

Ingress-and-Sting

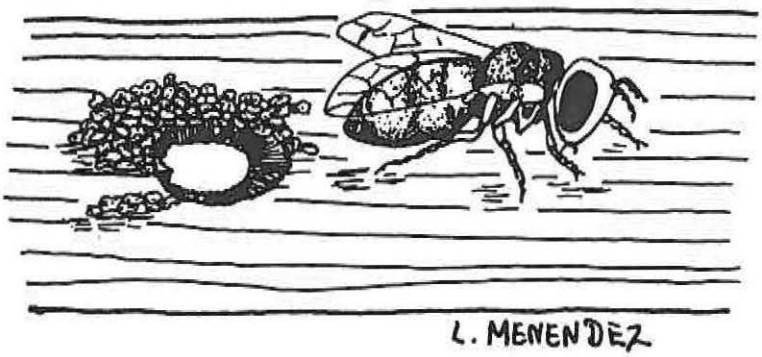
Stemborer tunnels are large in diameter, and many species maintain clean tunnels. Ingress-and-sting parasites are small enough to gain ingress through the host tunnel and attack the host larva feeding in the tunnel. These parasites use cues such as odor from host frass and the host tunnel itself to guide them to the immediate vicinity of the host. Once the chemical cue from the host frass attracts the parasite to the tunnel entrance, the parasite enters and traverses the host tunnel and attacks the host. Examples of ingress-and-sting parasites are the braconid genera *Cotesia* and *Apanteles* (Microgastrinae), and the bethylid *Goniozus*. The microgastrine braconids are solitary or gregarious endoparasites; the adults of many species are short-lived, surviving on the order of a few days. In contrast, the bethylid *Goniozus* is a long-lived gregarious ectoparasite. After depositing her eggs, the female *Goniozus* stays near the parasitized host and apparently provides some degree of parental care for her progeny (Clausen 1972, Conlong et al. 1984).



Cotesia inside feeding tunnel, ovipositing in stemborer larva (Larval guild, ingress-and-sting)

Planidial Ingress

Parasites of the family Tachinidae exploit stemborer larvae in the tunnel using two unique attack methods. In the first attack method, planidial ingress, the female uses cues from host frass or the host tunnel to indicate recent host activity and locate the immediate vicinity of the host, not the host *per se*. These cues stimulate the gravid female fly to larviposit mobile, planidial, first-instar maggots at the tunnel entrance and the maggots must then find the host by traversing the stemborer larval feeding tunnel. Once the host is found, the planidia penetrate the host integument and feed internally. Later-stage stemborer larvae are the targets of the planidial parasite larvae, and fly progeny emerge

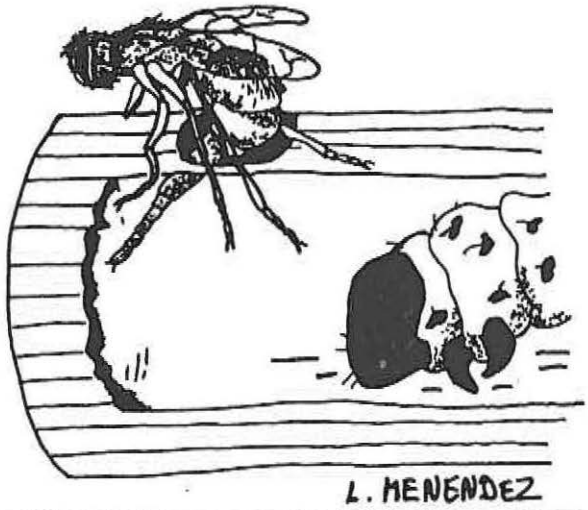


Lixophaga near host frass at tunnel breach, where larviposition occurs
(Larval guild, planidial ingress)

from either mature host larvae or, less commonly, host pupae. Examples of some tachinid genera that use this attack method include *Descampsina, Diatraeophaga, Lixophaga, Metagonistylum, Paratheresia* and *Sturmiopsis*. These genera may be either solitary or gregarious endoparasites. One immediate advantage of the planidial-ingress method is that the planidial larvae of some flies can find hosts that pack their tunnels with frass, such as the New World borer *Eoreuma*.

Bait-and-Wait

The second attack method used by tachinids, bait-and-wait, shows the least-direct host finding of all parasites of stemborers. In this case, the tachinid fly responds to cues associated with the host tunnel or host frass, and deposits her eggs either at the mouth of the tunnel or within the tunnel. The eggs are ingested by host larvae feeding in the tunnel.



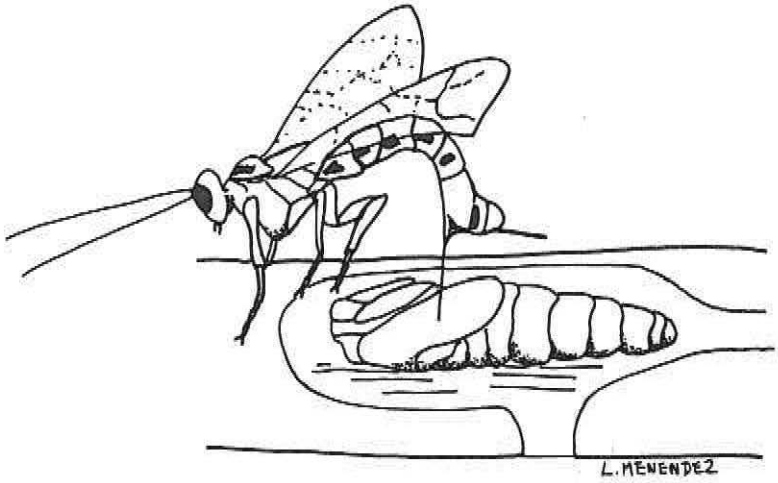
Palpozenillia with abdomen extended into feeding tunnel, ovipositing
(Larval guild, bait-and-wait)

Once ingested by the host larvae feeding in the tunnel, the parasite egg hatches and progeny then develop and emerge from mature host larvae and pupae. An example of a parasite using this method is the tachinid *Palpozenillia*. Progeny production is dependent upon the number of parasite eggs ingested, however the endoparasitic *Palpozenillia* is usually gregarious.

Pupal Parasite Guild

Drill-and-Sting

Like the larval drill-and-sting parasites, the attack method is similar for the pupal guild. Parasites using this method respond to cues resulting from plant damage or the pupal chamber. Parasitization is achieved by piercing the plant stem directly with the stout ovipositor and reaching the pupa within the chamber. The moth emergence window is not a requisite for successful host attack as it was for the probe-and-sting parasites. An example of a parasite employing this method is the ichneumonid *Xanthopimpla* (Pimplinae), which is a solitary endoparasite.



Xanthopimpla drilling through plant stem and ovipositing in stemborer pupa
(Pupal guild, drill-and-sting)

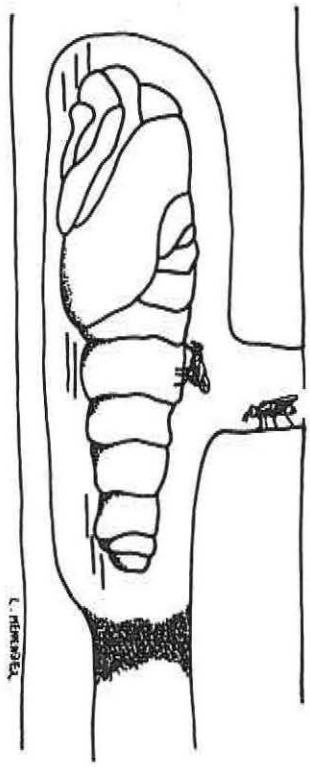
Ingress-and-Sting

As with the larval guild, there is a group of ingress-and-sting parasites within the pupal parasite guild. Unlike the larval parasites, however, pupal parasites using this method apparently do not enter through the larval feeding tunnel. As the host larvae mature and construct the pupal chamber, they tightly plug access to the tunnel with frass and detritus. However, the opportunity for attacking the host pupa for ingress-and-sting parasites is provided by the moth exit window, constructed by mature host larvae prior to pupation. Depending on the stemborer or the plant species, some exit windows are very fragile and become tattered as the plant dries, whereas others remain intact and sturdy during drying of the stem epidermis.For those species that have an "open window", the small pupal parasite can easily gain access into the pupal chamber and attack the enclosed pupa. For those hosts whose window remains intact, the parasite requires a more active means of

Table 3. Foraging strategies of parasites of tropical stemborers.

Attack Method	Host Disposition	Proximal Cues	Host Stage Attacked	Host Stage Emerged From	Endo/ Ectoparasite	Representative Taxa
EGG GUILD						
direct	exposed	host	egg	egg	endo	Scelionidae (*Telenomus*); Trichogrammatidae (*Trichogramma, Trichogrammatoidea*)
EGG-LARVAL GUILD						
direct	exposed	host	egg	larva in stem	endo	Braconidae, Cheloninae (*Chelonus, Phanerotoma*); Ichneumonidae, Campopleginae (*Venturia*)
LARVAL GUILD						
probe & sting	cryptic	frass, damage	larva in leaf sheath	larva in stem	endo	Braconidae, Agathidinae (*Alabagrus, Bassus*); Macrocentrinae (*Macrocentrus*)
drill & sting	cryptic	frass, tunnel	larva in stem	larva in stem	ecto	Braconidae, Braconinae (*Bracon, Habrobracon, Myosoma, Tropobracon*); Doryctinae (*Allorhogas, Heterospilus, Rhaconotus*)
wait & sting	cryptic	tunnel entrance, frass	larva in stem	larva in stem	ecto	Braconidae, Braconinae (*Digonogastra, Euvipio, Glyptomorpha, Iphiaulax, Stenobracon*)
ingress & sting	cryptic	tunnel entrance, frass	larva in stem	larva in stem	ecto endo	Bethylidae (*Goniozus*); Braconidae, Microgastrinae (*Apanteles, Cotesia*)
probe & sting	cryptic	damage, frass, moth exit window	mature larva in pupal chamber	mature larva	ecto	Ichneumonidae, Phygadeuontinae (*Ischnojoppa, Isotima, Mallochia*); Elasmidae (*Elasmus*)
planidial ingress	cryptic	tunnel entrance, frass	larva in stem	mature larva & pupa	endo	Tachinidae (*Descampsina, Diatraeophaga, Jaynesleskia, Lixophaga, Lydella, Metagonistylum, Palexorista, Paratheresia, Sturmiopsis, Zenillia*)
bait & wait	cryptic	tunnel, frass	larva in stem	mature larva & pupa	endo	Tachinidae (*Palpozenillia*)
PUPAL GUILD						
drill & sting	cryptic	pupal chamber, damage	pupa	pupa	endo	Ichneumonidae, Pimplinae (*Itoplectis, Pimpla, Xanthopimpla*)
ingress & sting	cryptic	damage, frass, moth exit window	pupa	pupa	endo	Chalcididae (*Brachymeria, Invreia, Psilochalcis, Spilochalcis*); Eulophidae (*Pediobius, Tetrastichus, Trichospilus*); Ichneumonidae, Ichneumoninae (*Dentichasmias, Ichneumon, Procerochasmias*)

gaining access through the sturdy exit window. In this case, several members of the pupal parasite guild use their functional mandibles to cut through the window and gain access to the enclosed host pupa. Examples of pupal ingress-and-sting parasites include the genera *Tetrastichus*, *Pediobius* and *Trichospilus*, which are all gregarious endoparasitic Eulophidae; the solitary endoparasitic ichneumonid *Dentichasmias* (Ichneumoninae); and the solitary endoparasitic *Psilochalcis* (= *Hyperchalcidia*) and *Invreia* (Chalcididae).



Pediobius entering stemborer pupal chamber through moth exit window
(Pupal guild, ingress-and-sting)

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5

KEY TO IDENTIFICATION OF STEMBORER PARASITES

Introduction

As the discussion has progressed, we have provided a framework for understanding stemborer parasites that incorporates biology, ecology and life-history. The information given has been in a context that allows the reader to generalize and extrapolate, with the ultimate objective to be able to predict the foraging strategy of the parasites discussed in detail as well as other species not discussed. We have provided basic information on the steps of successful parasitization and details on specific foraging strategies employed by stemborer parasites. We recognize that most field entomologists, especially those concerned with tropical stemborers, rarely have access to taxonomists with expertise in parasitic Hymenoptera or Diptera or have a large reference collection available. Therefore, before we move to the steps for rearing parasites, we will provide the reader with a means to identify parasites reared from stemborers with respect to the foraging strategies of the parasites.

In this section, a key is provided to the primary parasites of stemborers that are most likely to be encountered when collecting stemborers from the field. The objective of this key differs from most traditional taxonomic keys and, as a result, the key itself differs. Instead of being a true taxonomic key that is applicable to all genera of a family or subfamily, we limit the key to those taxa of parasites of stemborers that will be commonly encountered by the collector or biological control practitioner. In addition, we recognize the difficulty that many field entomologists — especially those with limited taxonomic training — have with traditional taxonomic keys. Therefore, for the following key, we: 1) limit its scope to a known group of parasites of stemborers; and 2) attempt to use biological and ecological information where possible to separate couplets in the key, thus minimizing the need for specialized training in morphology and taxonomy.

As a result of the limited scope of the key, its utility will be only within the context of collecting and rearing parasites for the intention of biological control of stemborers, and will not be applicable to the general collector or to a trained taxonomist interested in an entire taxon. The user of the key will need to know the life-stage of the stemborer collected, and from which stage of the host the parasite emerges, to use the key properly. By writing the key for an audience who has a specific purpose in mind and who only needs to identify a limited subset of parasitic taxa, we are able to exclude many taxa that may be difficult for the novice to separate taxonomically. In this way, we are able to make a key that requires a minimum amount of taxonomic or morphological expertise. Further, because we have designed the key with this specific audience and objective in mind, we hope that the key will be more "user-friendly", and will help, rather than deter, the field entomologist who would like to know what has been collected.

Hyperparasites, or parasites attacking parasites, representing the next trophic level, are omitted from the key. Thus the user must be sure the parasite is a primary parasite exploiting the stemborer before using the key. The reproductive status of the parasite, whether primary or hyperparasite, can usually be ascertained by careful observation of the life stage (host or primary parasite) from which the parasite emerges, or by dissection of the host remains.

Because the major purposes of the manual are to define parasite foraging strategies and assist in rearing stemborer parasites, the endpoints of the key couplets are parasite taxa that have similar foraging strategies and are reared similarly. In some cases, this will require identification to genus, as in the case of the diverse Braconinae. In other cases, the endpoint will be several families that are reared similarly, as for the Trichogrammatidae and Scelionidae. In each case, when a taxon is identified, the reader is directed to Table 4 for biological and ecological information and further direction to rearing instructions.

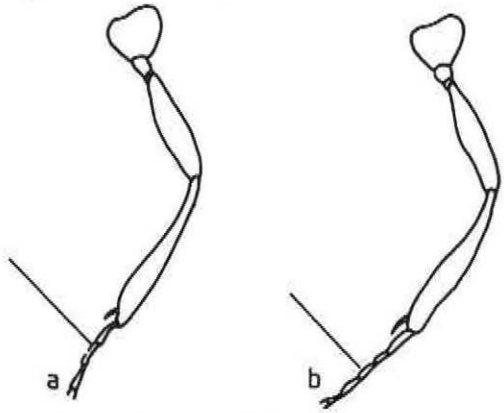
Key to Taxa of Parasites of Stemborers

1a Parasite adult(s) emerges from stemborer egg — **Egg Guild** 2

1b Parasite adult(s) or mature larva(e) emerges from stemborer larva or pupa — **Egg-larval,Larval or Pupal Guild** 3

2a Parasite adult has 3 segmented tarsi (fig. a) — **Trichogrammatidae** ..... *Trichogramma* spp., *Trichogrammatoidea* spp.

2b Parasite adult has 5 segmented tarsi (fig. b) — **Scelionidae** ..... *Telenomus* spp.



3a Parasite adult has one pair of wings — **Diptera** 4

3b Parasite adult has two pairs of wings — **Hymenoptera** 5

4a Gravid female with live maggots in uterus — **larvipositing Tachinidae** ..... *Lixophaga* spp., *Paratheresia* spp., *Metagonistylum* spp., *Jaynesleskia* spp., *Sturmiopsis* spp., *Zenillia* spp., *Descampsina* spp., *Diatraeophaga* spp., *Lydella* spp.

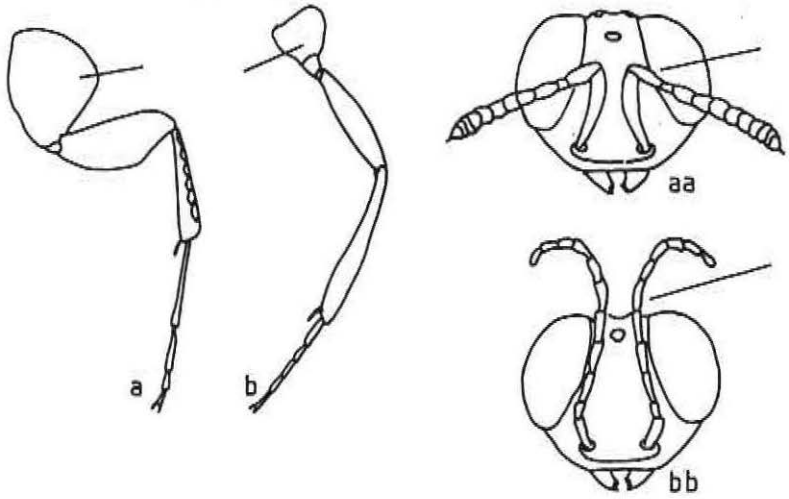
4b Gravid female with mature maggots remaining in the egg — **ovipositing Tachinidae** ..... *Palpozenillia* spp.

5a Parasite(s) emerges from stemborer larva — **Egg-larval or Larval Guild** 6

5b Parasite(s) emerges from stemborer pupa — **Pupal Guild** 25

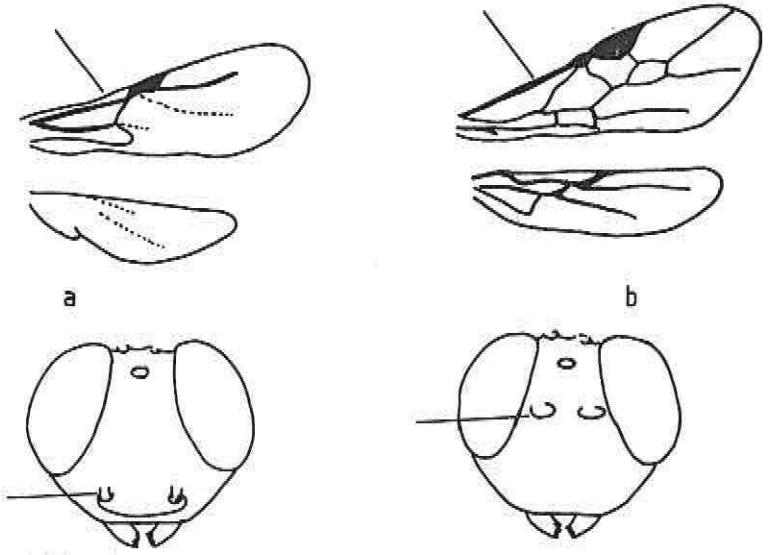
6a Hind coxa enlarged and disclike, outer surface of hind tibia with coarse dark bristles arranged in a diamond pattern. (fig. a), antennae elbowed (fig. aa) — **Elasmidae** ..... *Elasmus* spp.

6b Hind coxa not enlarged (fig. b), antennae filiform (fig. bb) 7



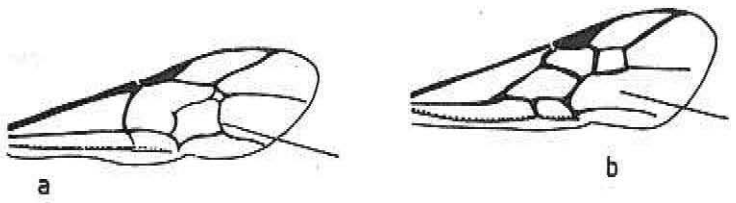
7a Costal cell present in fore wing (fig. a), hind wing without a closed cell. Antennae arising low on face (fig. aa) — **Bethylidae** ..... *Goniozus* spp.

7b Costal cell absent in fore wing (fig. b), hind wing with at least one closed cell. Antennae arising near middle of head or higher (fig. bb) 8



8a Fore wing with second recurrent vein present (fig. a) — **Ichneumonidae** 22

8b Fore wing lacking second recurrent vein (fig. b) — **Braconidae** 9



9a Parasite solitary 10

9b Parasite gregarious 17

10a Parasite larva(e) ectoparasitic 11

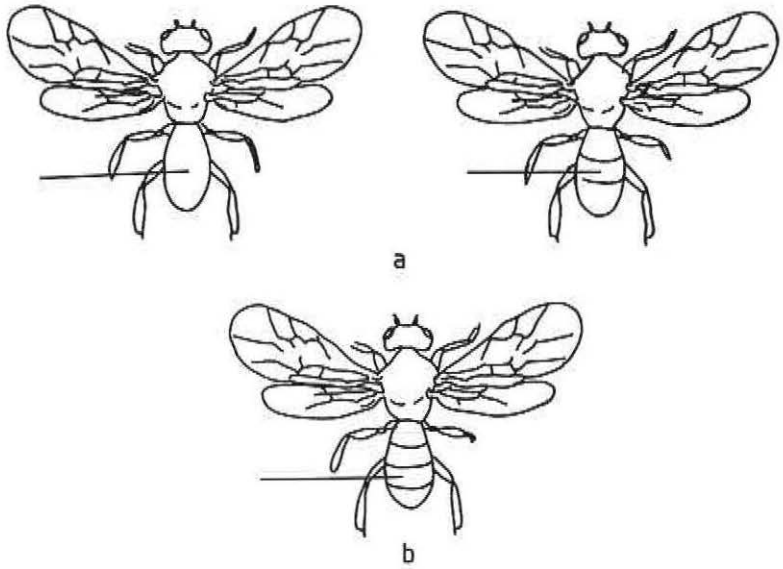
10b Parasite larva(e) endoparasitic 15

11a Parasite larva(e) feeds ectoparasitic during all instars 13

11b Parasite larva primarily endoparasitic, but feeds ectoparasitically in last instar 12

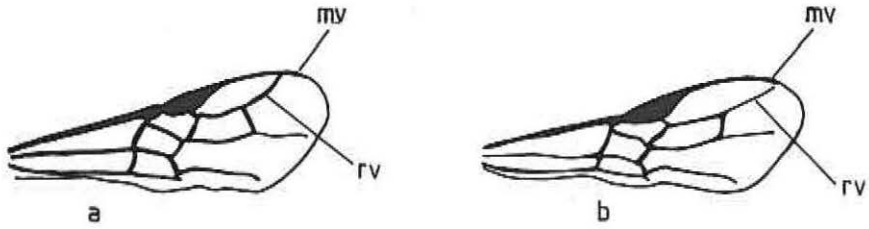
12a Abdomen 1 to 3 segmented in dorsal view (fig. a), in form of heavily sculptured carapace — **Cheloninae** ..... *Chelonus* spp., *Phanerotoma* spp.

12b Abdomen with more than 3 segments visible in dorsal view, not carapace-like; may be sculptured anteriorly, but smooth posteriorly (fig. b) — **Agathidinae** ..... *Alabagrus* spp.



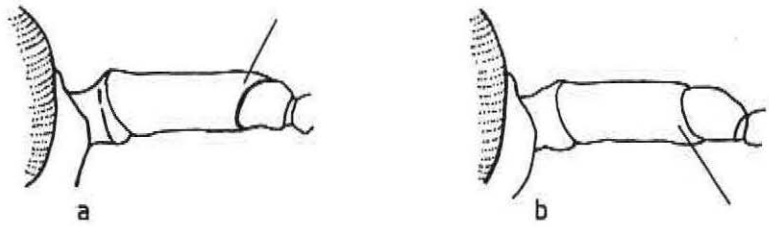
13a Metacarpal vein (mv) extends well beyond junction with radial vein (rv) in fore wing. Junction of mv and rv is well back from wing (fig. a). Native only to the Old World ..... *Stenobracon* spp., *Glyptomorpha* spp., *Euvipio* spp.

13b Metacarpal vein (mv) ends at or near junction with radial vein (rv) in forewing Junction of mv and rv occurs near wing tip (fig. b) 14



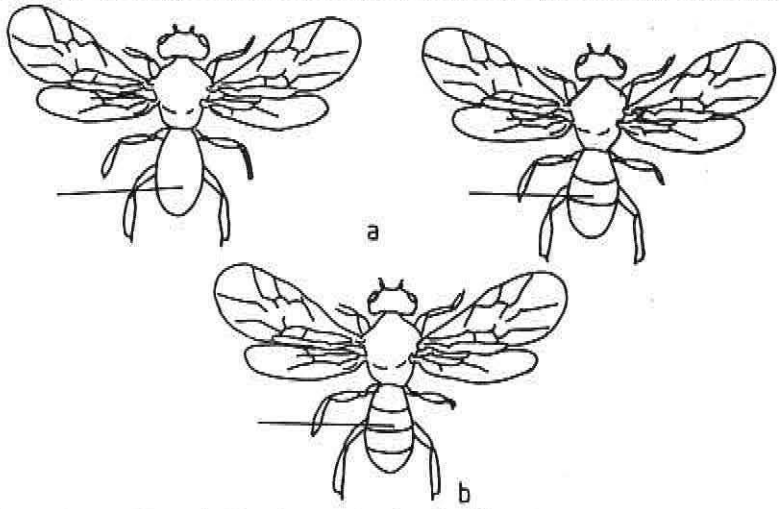
14a Antennal scape longer dorsally than ventrally in lateral view (fig. a) .... *Bracon* spp., *Myosoma* spp.

14b Antennal scape longer ventrally than dorsally in lateral view (fig. b). Native only to New World ..... *Digonogastra* spp.

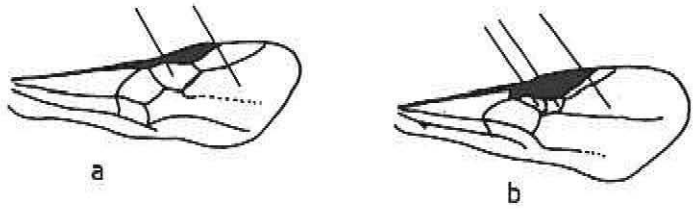


15a Abdomen with 1 to 3 segments in dorsal view (fig. a), in form of heavily sculptured carapace — **Cheloninae** ..... *Chelonus* spp., *Phanerotoma* spp.

15b Abdomen with more than 3 segments visible in dorsal view (fig. b), not carapace-like; may be sculptured anteriorly, but smooth posteriorly 16



16a Fore wing with only 2 submarginal cells (fig. a) 17
16b Fore wing with 3 submarginal cells (fig. b), — **Agathidinae** .....
..... *Alabagrus* spp., *Bassus* spp.

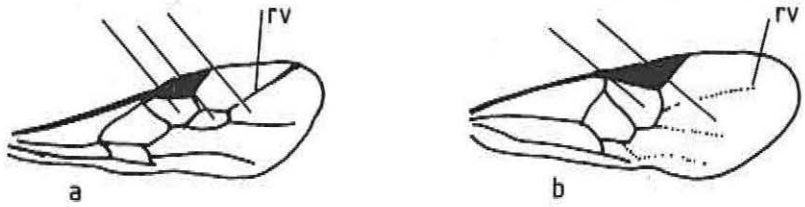


17a Radial vein of forewing weak, not reaching wing margin (fig. a) — **Microgastrinae**
..... *Apanteles* spp.
17b Radial vein of forewing distinct and reaching wing margin (fig. b) — **Orgilinae** .
..... *Orgilus* spp.

18a Parasite larvae feed endoparasitically 19
18b Parasite larvae feed ectoparasitically 20

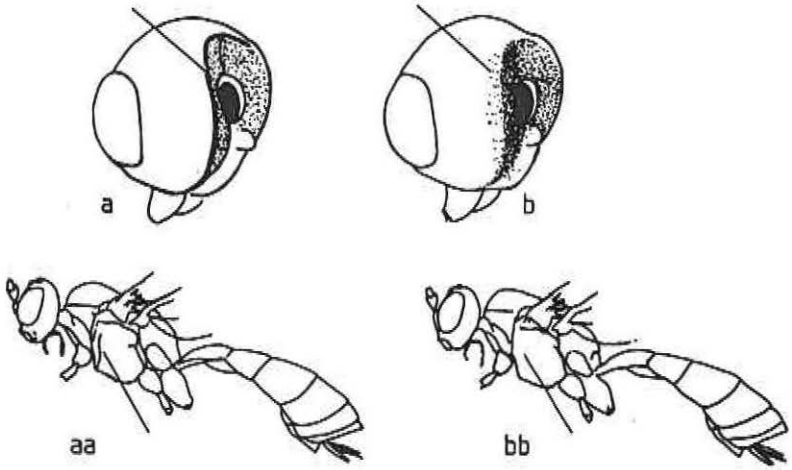
19a Radial vein (rv) of fore wing distinct throughout; with 3 submarginal cells (fig. a). Ovipositor equal to or greater than body length. — **Macrocentrinae** .....
..... *Macrocentrus* spp.

19b Radial vein (rv) of fore wing weak, not reaching wing tip; with only 2 submarginal cells (fig. b). Body mostly black. Ovipositor shorter than body length. — **Microgastrinae** ..... *Cotesia* spp., *Apanteles* spp.



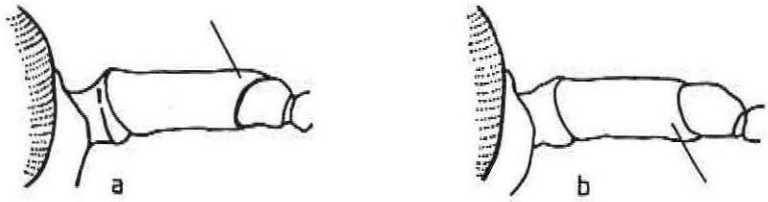
20a Occipital (fig. a) and epicnemial carinae (fig. aa) present — **Doryctinae** .....
..... *Allorhogas* spp., *Rhaconotus* spp., *Heterospilus* spp.

20b Occipital (fig. b) and epicnemial carinae (fig. bb) absent — **Braconinae** 21



21a Antennal scape longer dorsally than ventrally in lateral view (fig. a) .....
..... *Myosoma* spp., *Bracon* spp., *Tropobracon* spp., *Habrobracon* spp.

21b Antennal scape longer ventrally than dorsally in lateral view (fig. b) .....
..... *Digonogastra* spp., *Iphiaulax* spp.

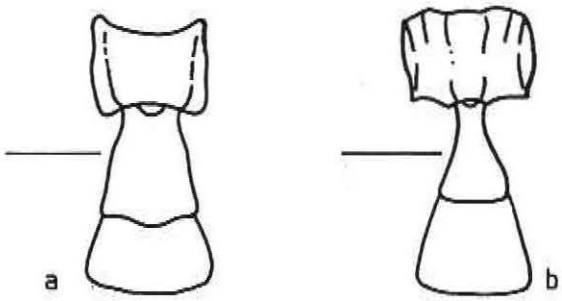


22a Parasite larva is ectoparasitic — **Phygadeuontinae** .....
..... *Isotima* spp., *Ischnojoppa* spp., *Mallochia* spp.

22b Parasite larvae endoparasitic 23

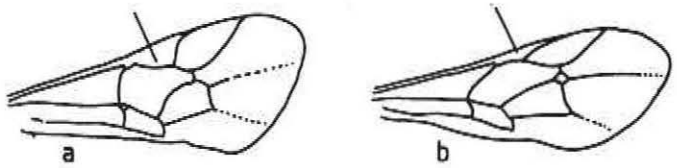
23a Metasomal segment 1 in dorsal view of nearly uniform width (fig. a) — **Banchinae**
..... *Syzeuctus* spp.

23b Metasomal segment 1 in dorsal view with anterior part slender and posterior part widened, (fig. b) 24



24a Stigma of fore wing short and widely triangular (fig. a), — **Cremastinae** .... *Cremastus* spp., *Temelucha* spp., *Pristomerus* spp.

24b Stigma of fore wing elongate (fig. b), — **Campopleginae** .... *Charops* spp., *Venturia* spp.

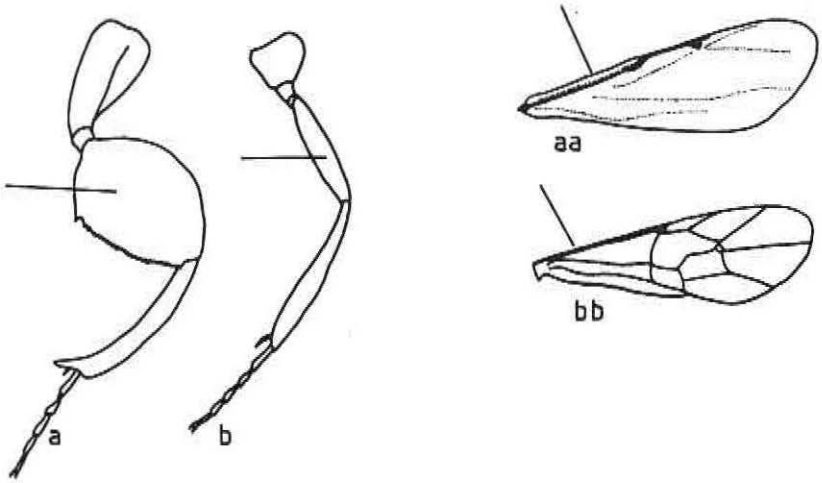


25a Parasites gregarious — **Eulophidae** .... *Pediobius* spp., *Tetrastichus* spp., *Trichospilus* spp.

25b Parasites solitary 26

26a Hind femur (Fm) enlarged and disclike (fig. a), costal cell present in forewing (fig. aa) — **Chalcididae** .... *Spilochalcis* spp., *Psilochalcis* spp., *Invreia* spp., *Brachymeria* spp.

26b Hind femur not enlarged (fig. b), costal cell absent in forewing (fig. bb) — **Ichneumonidae** 27



27a Metasomal segment 1 in dorsal view of uniform width (fig. a) — **Pimplinae** .... *Xanthopimpla* spp., *Pimpla* spp., *Itoplectis* spp.

27b Metasomal segment 1 in dorsal view with anterior part slender and widened apically (fig. b) — **Ichneumoninae** .... *Dentichasmias* spp., *Procerochasmias* spp., *Ichneumon* spp.

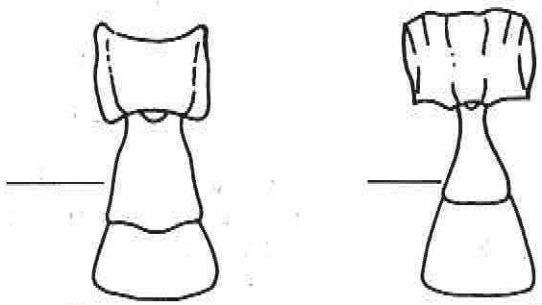


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Table 4. Taxa, guild and attack strategy employed by stemborer parasites.

Order	Family	Subfamily	Genus	Guild	Attack Method	Progeny Allocation	Larval Feeding Site
Hymenoptera	Bethylidae		*Goniozus*	larval	ingress & sting	gregarious	ectoparasitic
	Braconidae	Agathidinae	*Alabagrus*	larval	probe & sting	solitary	endoparasitic
			Bassus	larval	probe & sting	solitary	endoparasitic
		Braconinae	*Bracon*	larval	drill & sting	solitary/gregarious	ectoparasitic
			Digonogastra	larval	wait & sting	solitary/gregarious	ectoparasitic
			Euvipio	larval	wait & sting	solitary	ectoparasitic
			Glyptomorpha	larval	wait & sting	solitary	ectoparasitic
			Habrobracon	larval	drill & sting	gregarious	ectoparasitic
			Iphiaulax	larval	wait & sting	solitary/gregarious	ectoparasitic
			Myosoma	larval	drill & sting	gregarious	ectoparasitic
			Stenobracon	larval	wait & sting	solitary	ectoparasitic
			Tropobracon	larval	drill & sting	gregarious	ectoparasitic
		Cheloninae	*Chelonus*	egg-larval	direct attack	solitary	endoparasitic
			Phanerotoma	egg-larval	direct attack	solitary	endoparasitic
		Doryctinae	*Allorhogas*	larval	drill & sting	gregarious	ectoparasitic
			Heterospilus	larval	drill & sting	gregarious	ectoparasitic
			Rhaconotus	larval	drill & sting	gregarious	ectoparasitic
		Macrocentrinae	*Macrocentrus*	larval	probe & sting	gregarious	endoparasitic
		Microgastrinae	*Apanteles*	larval	ingress & sting	solitary/gregarious	endoparasitic
			Cotesia	larval	ingress & sting	gregarious	endoparasitic
	Chalcididae		*Brachymeria*	pupal	ingress & sting	solitary	endoparasitic
			Invreia	pupal	ingress & sting	solitary	endoparasitic
			Psilochalcis	pupal	ingress & sting	solitary	endoparasitic
			Spilochalcis	pupal	ingress & sting	solitary	endoparasitic
	Elasmidae		*Elasmus*	larval	probe & sting	gregarious	ectoparasitic
	Eulophidae		*Pediobius*	pupal	ingress & sting	gregarious	endoparasitic
			Tetrastichus	pupal	ingress & sting	gregarious	endoparasitic
			Trichospilus	pupal	ingress & sting	gregarious	endoparasitic

Table 4 continued.

Order	Family	Subfamily	Genus	Guild	Attack Method	Progeny Allocation	Larval Feeding Site
	Ichneumonidae	Banchinae	*Syzeuctus*	larval	unknown	solitary	endoparasitic
		Campopleginae	*Charops*	larval	unknown	solitary	endoparasitic
			Venturia	egg-larval	direct	solitary	endoparasitic
		Cremastinae	*Cremastus*	larval	unknown	solitary	endoparasitic
			Pristomerus	larval	unknown	solitary	endoparasitic
			Temelucha	larval	unknown	solitary	endoparasitic
		Ichneumoninae	*Dentichasmias*	pupal	ingress & sting	solitary	endoparasitic
			Ichneumon	pupal	ingress & sting	solitary	endoparasitic
			Procerochasmias	pupal	ingress & sting	solitary	endoparasitic
		Phygadeuontinae	*Ischnojoppa*	larval	probe & sting	solitary	ectoparasitic
			Isotima	larval	probe & sting	solitary	ectoparasitic
			Mallochia	larval	probe & sting	solitary	ectoparasitic
		Pimplinae	*Itoplectis*	pupal	drill & sting	solitary	endoparasitic
			Pimpla	pupal	drill & sting	solitary	endoparasitic
			Xanthopimpla	pupal	drill & sting	solitary	endoparasitic
	Scelionidae		*Telenomus*	egg	direct attack	solitary	endoparasitic
	Trichogrammatidae		*Trichogramma*	egg	direct attack	gregarious	endoparasitic
			Trichogrammatoidea	egg	direct attack	gregarious	endoparasitic
Diptera	Tachinidae		*Descampsina*	larval	planidial ingress	solitary/gregarious	endoparasitic
			Diatraeophaga	larval	planidial ingress	solitary/gregarious	endoparasitic
			Jaynesleskia	larval	planidial ingress	solitary	endoparasitic
			Leskiopalpus	larval	planidial ingress	solitary	endoparasitic
			Lixophaga	larval	planidial ingress	solitary/gregarious	endoparasitic
			Lydella	larval	planidial ingress	solitary	endoparasitic
			Metagonistylum	larval	planidial ingress	solitary/gregarious	endoparasitic
			Palexorista	larval	planidial ingress	solitary/gregarious	endoparasitic
			Palpozenillia	larval	bait & wait	solitary/gregarious	endoparasitic
			Paratheresia	larval	planidial ingress	solitary/gregarious	endoparasitic
			Sturmiopsis	larval	planidial ingress	solitary/gregarious	endoparasitic
			Zenillia	larval	planidial ingress	solitary/gregarious	endoparasitic

6

LABORATORY REARING

Introduction

Successful parasitization requires a sequence of distinct and consecutive processes. First the parasite must find the habitat that harbors the host. Next the host must be found, and the host must be acceptable for parasitism and suitable for parasite development. Laboratory rearing is usually concerned with the last three processes, host finding, host acceptance and host suitability. The initial step, selection of the correct habitat that harbors the host, is accomplished when host and parasite are placed in close proximity for parasitization during the laboratory rearing process. Thus, successful rearing of parasites of stemborers requires that an acceptable, suitable host be made available in a manner recognizable to the searching parasite. Presenting the correct host stage in the proper manner so that parasitization occurs requires knowledge of host life history, parasite biology and parasite foraging strategy.

Developing a successful rearing procedure for a specific parasite is greatly enhanced by being familiar with the general biology of stemborers, and their parasites and the general foraging strategies of these parasites. Information gleaned from observations made during field collection and parasite emergence in the laboratory provides such valuable clues for developing successful rearing techniques that we review these again. Written notes should include a tentative identification of stemborer and host plant, stemborer life stage when field collected and when parasite emerges, life stage of parasite that emerges from host, physical location of stemborer on plant, whether the parasite is solitary or gregarious, primary or hyperparasitic, and endo- or ectoparasite, parasite pupation site, sex of adults and duration of life stages. These biological and ecological observations are extremely valuable in helping discern the foraging strategy and taxonomic affinity of the parasite, and developing the special techniques necessary for laboratory rearing of each parasite.

Once the parasite is in culture, there are a few common difficulties that are often encountered in the rearing process, resulting in poor culture performance or even loss of the parasite culture. One of the most important aspects of maintaining a parasite culture is obtaining adequate mating. Dipteran parasites require fertilization for eggs to develop, whereas eggs of hymenopteran parasites will develop regardless of mating status. Thelytokous hymenopteran parasites (e.g., Agathidinae) develop by diploid parthenogenesis, and are almost always all females, so mating is not necessary. In the case of arrhenotokous hymenopteran species, however, mating is necessary to ensure production of females, as only fertilized eggs produce females. For these parasites, fertilized eggs become diploid females and unfertilized eggs become haploid males. For most species, the mated female can control whether an individual egg is fertilized or, for gregarious species, how many of the eggs are fertilized. Poor mating frequency is usually more of a problem with either solitary or polyembryonic parasite species rather than for gregarious species. Overmating can be as serious a problem, but with different results, as the spermatheca of the female can become packed, which can further skew the sex ratio. Usually the problems of inadequate and excessive mating for hymenopteran parasites can be avoided by regulating the numbers of males and females placed together, and the amount of time they are together. Aggressive males often disrupt mating pairs and prevent successful mating. The physical act of mating unsuccessfully numerous times can result in the female parasite shunning further male copulation, resulting in no sperm transfer and production of all males. Historically, dipteran parasites, for which mating is an absolute necessity for production of progeny, have been the most difficult to get to mate in the laboratory.

The second difficulty that is often encountered, to which we have alluded earlier, is the need to present the parasite an acceptable, suitable stemborer host in a recognizable form. Some parasites will accept hosts out of ecological context, i.e., in virtually any form or without odor or substrate cues; however, most parasites of stemborers require a host that is cryptically enclosed within a substrate. A major part of this manual is directed toward this problem, by recognizing the foraging strategy employed, and by placing parasites with similar strategies into appropriate taxonomic grouping.

Finally, some attempts at rearing parasites will use factitious or new-association hosts, with which the parasites have no coevolutionary history. Rearing coevolved hosts assumes that the parasite will already recognize, accept, and be able to regulate the host, and thus, this is not an issue. However, for factitious, new-association hosts, no such assumption can be made. Because there is no coevolutionary history, simply placing parasites and hosts together can result in failure, and no parasite progeny being produced. In the case of factitious hosts, it is absolutely essential to make detailed observations on the parasitization process. It is necessary to note whether the host is accepted, or if the host is accepted but no progeny are produced, possibly the host is not physiologically suitable for the particular parasite species or strain.

Egg Guild

Several genera in the hymenopteran families Trichogrammatidae and Scelionidae contain entomophagous species that exploit the eggs of stemborers as a food source. The trichogrammatid genera *Trichogramma* and *Trichogrammatoidea* and the scelionid genus *Telenomus* are primary, endoparasites of stemborer eggs. Taxonomy of *Trichogramma* and *Telenomus* is very difficult and has resulted in a confusion of specific names in these genera appearing in the literature. The only eulophid known to exploit stemborer eggs as a food source, *Tetrastichus schenobii* Ferriere, is unusual in that it preys upon the egg mass and neonate larvae of *Tryporyza* and is not parasitic in the strict sense (Pagden 1934).

Direct Attack

In nature, most stemborer eggs are deposited exposed on leaf surfaces, thus trichogrammatids and scelionids readily recognize and oviposit in host eggs deposited on most any substrate when parasite and host are confined in close proximity in the laboratory. Many *Trichogramma* species are highly polyphagous in the laboratory and many lepidopteran eggs are acceptable and suitable factitious hosts for laboratory rearing. One reason for the polyphagous nature of egg parasitoids may be that the host immune system is not well developed at the egg stage (Strand 1986). The direct host attack strategy and polyphagous nature of trichogrammatids and scelionids facilitate laboratory rearing. Adult *Telenomus* are 2–3 times as large as *Trichogramma* and appear to be more host specific. However, this observed host specificity may only be a manifestation of the restrictions that host size forces on acceptance and suitability. Host eggs that produce 4–5 *Trichogramma* adults will produce only one *Telenomus*, and host eggs that are too small to produce one *Telenomus* may produce one or more *Trichogramma*.

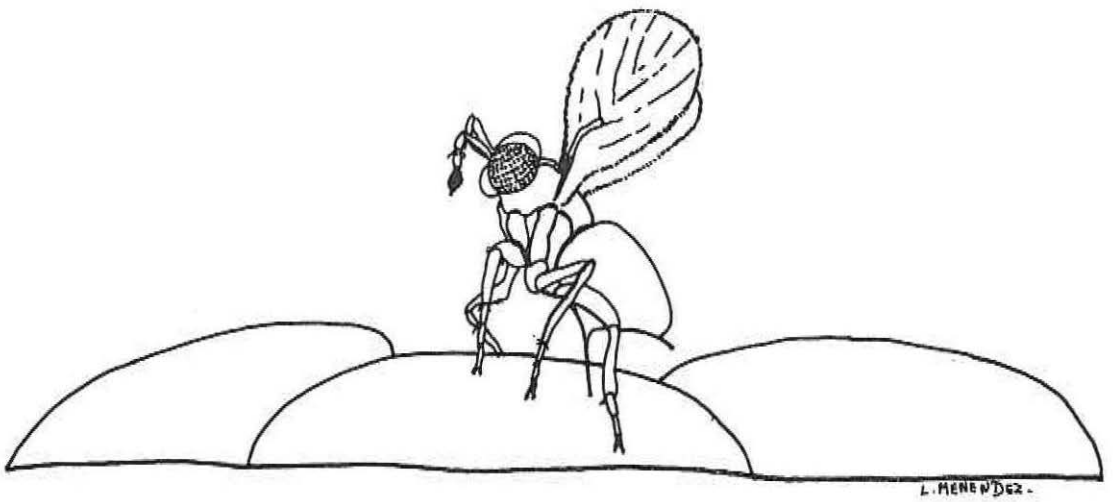
Usually more ingenuity is required to induce the stemborer female to oviposit than is required to induce the egg parasites to oviposit (more details are provided in the earlier section on Life History of Stemborers, Laboratory Rearing). Adult female *Diatraea* readily oviposit on smooth, waxy surfaces that mimic the lush, green leaves of host plants where they naturally oviposit. Commercially available waxed paper is a suitable substitute for the more restrictive green leaves. *Chilo partellus*, which in nature prefers to oviposit along the mid-ribs of green leaves, rather than the smoother leaf surface, will readily oviposit in

the creases of pleated waxed paper in the laboratory. *Eoreuma loftini*, on the other hand, does not oviposit readily on a smooth or exposed surface. To induce *E. loftini* to oviposit, re-creation of the natural oviposition substrate, i.e., crevices of dried plant material, must be reproduced (van Leerdam et al. 1984, 1986). An available substitute readily accepted as an ovipositional substrate is rough-surfaced paper toweling that is folded and sterilized. *Eldana saccharina* has a natural ovipositional behavior similar to *E. loftini*, preferring to oviposit in the crevices of dried host plant material (Atkinson 1979). As expected, folded paper toweling is the preferred ovipositional site in the laboratory (Atkinson 1978).

Female *Trichogramma* and *Telenomus* usually oviposit in all ages of stemborer eggs. However, eggs in the early stages of embryonic development appear to have greater acceptance and suitability. Hosts in the later stages of development, especially when the neonate larva is discernible through the egg chorion (the black head stage), usually produce fewer parasites. *Trichogramma* readily responds to increased host size by increasing the number of eggs the parasite lays in each host. Superparasitization is not a problem during culturing, unless too few unparasitized hosts are available for the number of searching female parasites. The initial female marks the host after parasitism and marked eggs are subsequently avoided by searching parasite females when host eggs are readily available.

Parasite eggs eclose in about 24 hours. Parasite larvae complete three instars and pupate. Growth of the third larval instar causes a darkening of the chorion of the parasitized egg, which is clearly evident by visual inspection; the parasitized eggs turn dark brown to black. This dark coloration is retained by the host egg chorion after the adult parasites emerge.

The first parasite to mature to the adult stage chews a round hole in the chorion of the host egg and emerges. Subsequent adults emerging from the egg use the same hole to exit. Males emerge first, remain on the egg mass and mate with the females when they emerge. Emergence of both sexes of parasites from single eggs or from the egg mass, coupled with immediate mating upon emergence, insures adequate mating frequency for production of females and continuous laboratory culturing. Females begin ovipositing within a few hours after mating.



Trichogramma ovipositing in stemborer eggs (Egg guild, direct attack)

For a general review of *Trichogramma* spp. and *Telenomus* spp. as biological control agents for stemborers, the reader is directed to Metcalfe and Breniere (1969). Recent reports by Rodriguez-del-Bosque and Smith (1991) and Rodriguez-del-Bosque et al. (1989) are included to document the level of stemborer egg parasitization on maize in the New World.

***Trichogramma* spp., *Telenomus* spp.**

Trichogramma spp. and *Telenomus* spp. can be reared using similar methodology. However, procedures must be modified to accommodate differences in the biologies between the two genera as well as differences in the biologies between species within genera. The excellent general, yet detailed, methodology for rearing *Trichogramma* spp., supplied by Morrison (1985), can be used for *Telenomus* spp. The following short summary on rearing egg parasites is presented as a general guide for developing a laboratory rearing procedure using available facilities. Trichogrammatids and scelionids can be reared for numerous generations in the laboratory by regularly supplying host eggs in small glass or plexiglass containers to ovipositing parasites. Container size can vary, but a 3.5 cm diameter x 30 cm long glass or plexiglass tube can be used to manipulate the parasites and hosts easily (Morrison 1970, 1985). Eggs that have been oviposited on a paper substrate are preferred to those oviposited on green leaf tissue, because green leaves distort upon desiccation and crumple easily when handled. The preoviposition period of egg parasites varies from 1–24 hours after adult emergence, thus host exposure to parasites should not be delayed. Fresh stemborer eggs, 24–48 hours old, should be exposed to ovipositing parasites for a 24-hour ovipositional period. Superparasitization is a problem only where the host parasite ratio is highly skewed and hosts are limited. Exposing hosts to ovipositing females for prolonged periods also can increase superparasitization by limiting the availability of unparasitized hosts. A ratio of approximately one female parasite per 10 host eggs for a 24-hour oviposition period circumvents superparasitization (Morrison 1985). When initiating cultures with field-collected parasites, a greater number of hosts per parasite should be supplied so that hosts are not limiting and full advantage can be taken of the parasite's reproductive potential.

At 28°C, the parasite egg will hatch in about 24 hours, followed by three larval instars requiring 1 day each for the first two instars and about 3 days for the third instar. Pupation requires an additional 2 days. The entire immature development requires about 7–10 days depending upon rearing temperature and parasite species. At the beginning of the third larval instar, dark melanin granules are deposited at the inner surface of the egg chorion, turning the host black. Darkening of the host egg not only indicates successful parasitization, but also can be used to mark this specific time in parasite development and serve as a benchmark for subsequent biological events. After the 24-hour exposure period for oviposition, the freshly parasitized eggs should be removed from the ovipositional container and held at >80% RH until adult emergence. Host larvae hatch from unparasitized eggs before parasite development is completed. Thus, if the stemborer larvae are cannibalistic, the exposed eggs must be examined regularly and host larvae removed to prevent consumption of the parasitized eggs. To facilitate handling the small parasites, one should transfer the parasitized eggs to the ovipositional container just prior to adult emergence, in order to continue the rearing cycle.

Adult longevity is variable, with the temporal distribution of oviposition and total fecundity dependent upon the parasite species (Metcalfe & Breniere 1969). Providing adults with a food source, such as a honey-water solution or a raisin, can increase longevity. Adults are susceptible to desiccation, and so the optimum relative humidities are those in excess of 80%. Adults are positively phototropic and negatively geotropic. This behavior can be exploited to facilitate adult movement (Morrison 1970). Trichogrammatids

and scelionids should be reared at ambient temperatures; extreme temperatures can affect survival and sex ratio, and therefore should be avoided.

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Egg-Larval Guild

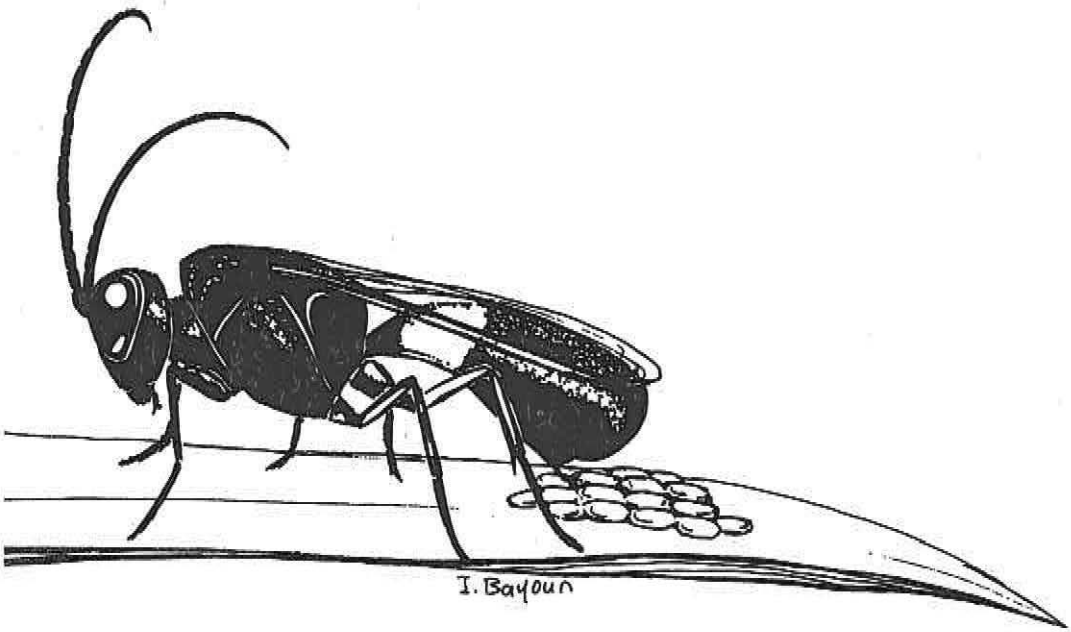
The egg-larval parasite guild is unusual in that the adult female parasite attacks the egg stage and the solitary, endoparasitic larva exploits for nutrition the stemborer larva tunneling in the stem. Thus the cues that dictate the behavior associated with habitat and host finding and host acceptance are provided by the egg stage of the host, whereas host suitability interactions are integral with the host larval stage. The egg-larval strategy is characteristic of the braconid subfamily Cheloninae, represented by the genera *Chelonus* and *Phanerotoma* attacking stemborers. The egg-larval strategy is also used by *Venturia ovivenans* Zwart to attack the New World stemborer, *Rupela albinella* (Cresson) in rice (Hummelen 1974). The egg-larval strategy employed by *V. ovivenans* appears to be unique among members of the subfamily Campopleginae, in which larval parasitization is characteristic.

The cues used by adult parasites in the egg-larval guild to locate and parasitize host eggs are apparently very similar to the cues used by foraging females in the egg guild. Host egg masses placed in close proximity to searching females are attractive and numerous eggs within the egg mass are accepted. After parasitization, the stemborer eggs hatch, and

the larvae must be fed until the third or a later instar when the mature parasite larva will emerge and pupate.

Direct Attack

The Cheloninae and *Venturia ovivenans* are solitary, internal, egg-larval parasites that have evolved a complex route to exploit the maturing stemborer larvae as a food source. Adult parasites oviposit in the stemborer egg, but development of the first-instar parasite larva



Chelonus ovipositing in stemborer eggs (Egg-larval guild, direct attack)

is arrested after hatching; after the stemborer egg hatches the parasite larva "hitches a ride" in the growing stemborer larva. When the stemborer larva has begun to mature and is tunneling into the stem, the parasite's growth quiescence is broken and the parasite larva begins to develop rapidly as it consumes the host larva. The last-instar parasite larva emerges from the host, feeds ectoparasitically, then spins a cocoon and pupates in the tunnel near the host cadaver. The emerging adult uses the host feeding tunnels for egress.

***Chelonus sonorensis* Cameron**

We have successfully reared *Chelonus sonorensis* in the laboratory using the coevolved host *E. loftini*. The rearing procedure was developed through an understanding of general chelonine biology and the more specific biology and rearing techniques reported for *Chelonus annulipes* Wesmael on the temperate maize stemborer *Ostrinia nubilalis* (Hübner) (Vance 1932, Wishart & Van Steenburgh 1934), and for *Chelonus texanus* Cresson on the noctuid *Spodoptera frugiperda* (J.E. Smith) (Luginbill 1928, Vickery 1929).

Upon emergence from the pupae, adult *C. sonorensis* are placed in a 250-ml glass container, supplied with streaked honey, and held at 24–27°C for 1–2 days for mating. Mating was rarely observed in the mating container. Apparently *C. sonorensis* do not always

mate readily because cultures often contain a preponderance of males. *Chelonus annulipes* copulates most readily in the end of a 10 cm glass vial held toward a strong light source (Vance 1932). This technique was not tried for *C. sonorensis*, but may prove valuable. Three-day to 6-day old *E. loftini* eggs laid on paper toweling are placed in a Petri dish and female *C. sonorensis* are introduced from the mating container. Females become active quickly and begin to move about the Petri dish. When they are within a few millimeters of the host eggs, they reduce locomotion and intensively palpate the eggs with their antennae. Females oviposit in numerous eggs within an egg mass. Several ovipositing females can be left with 8–10 egg masses for 8–10 hours without superparasitization. After the parasitization period, females are returned to the mating/holding cage, where they are kept with males until removed and supplied fresh eggs to parasitize.

Host eggs exposed to ovipositing females are kept on artificial diet until they hatch. Host larvae should be supplied with adequate food until the last-instar parasite larva emerges from the host larva. The parasite larva emerges from the host prior to maturity and feeds ectoparasitically during the ultimate larval instar. When the parasite larva initially emerges from the host, it is very white, but turns dark, often with a ruddy appearance, as it feeds externally on the cadaver. After the host is totally consumed, the matured parasite larva pupates. Do not disturb the mature larva during the period from emergence from the host until pupal formation is complete. Larvae disturbed during this development period do not successfully pupate (Vance 1932). Collect and hold *Chelonus* pupae at 24–27°C until adults emerge. *Chelonus sonorensis* life cycle from egg to adult requires about 35 days (Van Zwaluwenburg 1926).

The final step in successful parasitization of stemborer eggs by Cheloninae is host suitability. Age of the host egg is apparently critical for success by *C. annulipes* (Wishart & Van Steenburgh 1934) and *C. sonorensis*. Older eggs, containing a somewhat-developed larva, had the highest proportion of hosts that yielded *C. annulipes* (0.36), compared to newly laid eggs (0.27), and eggs ready to hatch (0.11). Thus, eggs that are approximately two-thirds through the developmental period appear to be the most suitable. Host maturity at parasite oviposition is an important aspect that needs attention during rearing of other chelonine parasites of stemborers.

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Larval Guild

The larval parasite guild exhibits the most diverse foraging strategies. These parasites have developed complex, yet ingenious strategies to exploit the large, mature stemborer larva as a food source. However, this diversity can be simplified by examining similarities in foraging strategies (Table 3). Initially lumping parasites into groups having a common

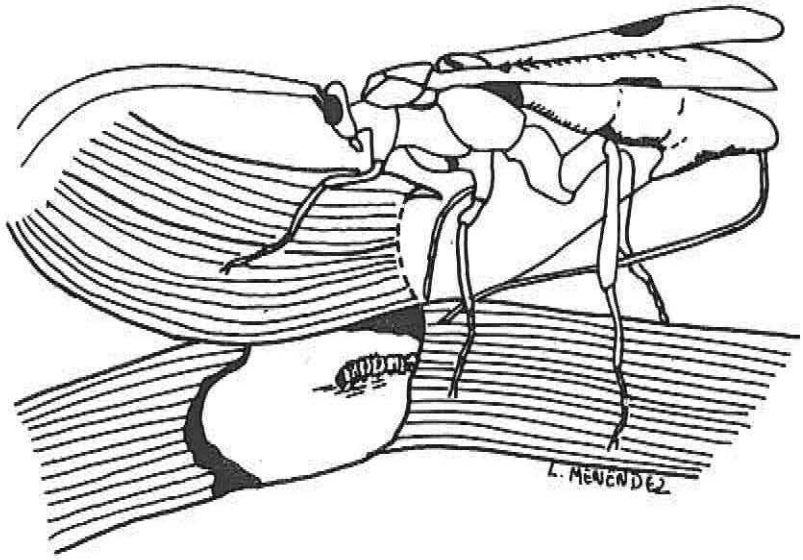
attack method (e.g. drill-and-sting, probe-and-sting) provides mechanistic groups. Further subdividing the attack methods by the particular life stage attacked simplifies the diverse array of strategies. As the parasites largely fit into natural taxonomic units, either as families or subfamilies, a common rearing procedure can be developed for each parasite genus, based on matching the method of attack with taxonomic affiliation. Specific parasite biologies and rearing procedures will follow these divisions.

Probe-and-Sting

Parasites employing the probe-and-sting strategy use the ovipositor for probing into crevices where the host larvae are feeding, and through frass or thin plant epidermal layers to attack host larvae, as opposed to drilling actively through thick layers of stem tissue with the ovipositor, as practiced by drill-and-sting parasites. Unlike drill-and-sting parasites, which may wait passively for stemborer larvae to contact the inserted ovipositor, after drilling into the host tunnel, probe-and-sting strategists continue to probe actively with the ovipositor for larvae until contact is made.

The probe-and-sting attack strategy is represented by genera in the Braconidae, Elasmidae and Ichneumonidae. Two braconid subfamilies, Macrocentrinae and Agathidinae, oviposit in the early larval instars feeding in the leaf sheaths, but utilize the mature stemborer larva as their food source. The best-known agathidine parasites of stemborers are large wasps with a long ovipositor that permits them to probe deeply into the cracks and crevices around the leaf sheaths as they search for early-instar hosts. The Macrocentrinae that attack stemborers are small-bodied with an ovipositor only slightly longer than the body. Unlike the agathidines, the macrocentrine parasite's small size does not prohibit access to the cryptic leaf-sheath mines of the early-instar stemborer larvae, thus the shorter ovipositor suffices. The Agathidinae are internal, solitary parasites and are represented by *Alabagrus stigma*. The Macrocentrinae are also internal parasites, but are polyembryonic, and are represented by *Macrocentrus prolificus* Wharton.

Mallochia pyralidis Wharton and *Isotima javensis* (Rohwer) are in the ichneumonid subfamily Phygadeuontinae. Many species in this large subfamily are primary ectoparasites



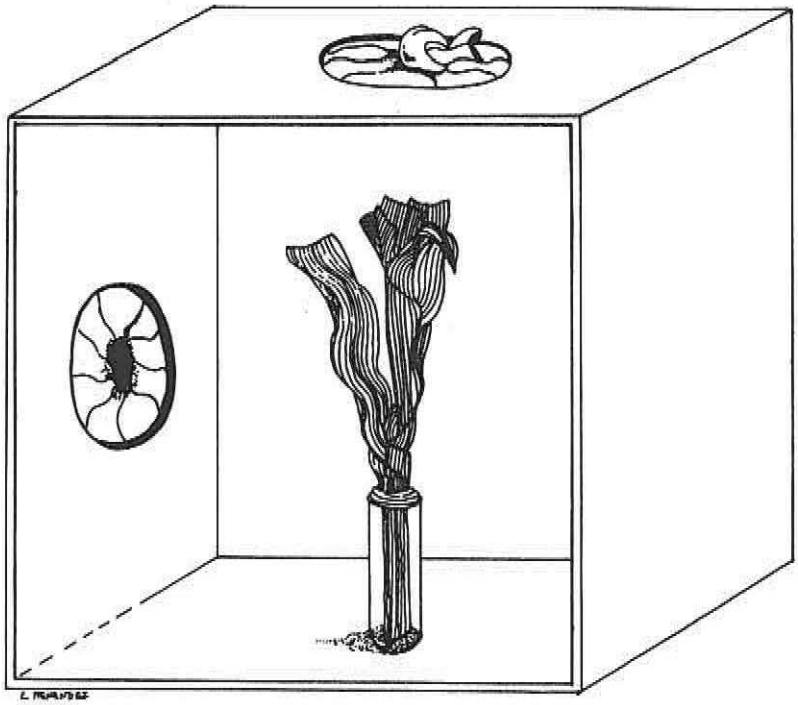
Alabagrus probing into the leaf sheath and ovipositing in early-instar stemborer larva (Larval guild, probe-and-sting)

of Lepidoptera larvae feeding in cryptic microhabitats, however few species utilize stemborers as hosts. *Mallochia pyralidis* and *I. javensis* utilize the probe-and-sting attack strategy as solitary, ectoparasites attacking mature larvae and prepupae of stemborers by probing with the ovipositor through the moth emergence window. The gregarious, larval ectoparasitic elasmid, *Elasmus zehntneri* Ferriére also utilizes the moth emergence window to locate and access its host, *Scirpophaga nivella* (F.). *Elasmus zehntneri* females probe through the moth emergence window with the ovipositor, paralyze the mature larval host and oviposit on or near the host.

***Alabagrus stigma* (Brullé) (=*Agathis stigmatera* Cresson)**

In the natural habitat, *A. stigma* attacks young stemborer larvae feeding in the leaf sheaths of gramineous plants. The elements of this natural setting that are essential for host recognition and successful parasitization must be reproduced in the laboratory. The physical microhabitat can be supplied by excising the green, leafy tops and at least one formed internode from maize, sorghum or sugarcane plants. Long leaves can be trimmed to extend 3 to 5 cm from the stem and the stem placed in a vial partially filled with water to maintain plant turgor. A cotton plug placed between the stem and vial lip prevents larvae from crawling into the vial and drowning. First- to third-instar *D. saccharalis* (those instars that naturally feed in the leaf sheaths) are placed on the leafy top and allowed time to move to the leaf sheaths and begin feeding before exposure to ovipositing adults. The infested leafy top and water supply are transferred to a large, clear plastic, sleeve cage (0.5 x 0.5 x 0.7 m) and secured in a normal upright position.

Adult female *A. stigma* that are greater than four days old are introduced into the sleeve cage containing the infested leafy top. The searching females are initially attracted to the



Sleeve cage showing excised plant stem with leaf sheaths for insertion of early-instar host larvae for exposure to *A. stigma* and *M. prolificus*

plant and are further attracted to the hosts by tissue damage from larval feeding and by larval frass. When the female contacts larval feeding perforations or frass, she probes into the damaged area for the feeding larvae with her highly flexible ovipositor. Upon contact with a host, the ovipositor is inserted into the larva and oviposition proceeds quickly.

Parasite eggs hatch in 3–5 days. Complete larval development requires about 20 days. Growth is slow initially, but the larvae feed voraciously and grow dramatically near maturity. When the stemborer larva is nearing maturity, the parasite larva is about half grown. At this time the parasite larva begins rapid growth, and upon reaching the last-instar larva pierces the host integument, exits, and feeds ectoparasitically until maturity. The mature parasite larva spins a whitish cocoon and pupates in the larval feeding tunnel. Pupation requires about 6 days.

Adults are almost always female with obligate, thelytokous reproduction. The few males that are produced are non-functional. Females require 3–4 days for preoviposition and live for 1–2 weeks, ovipositing throughout the adult life span.

After exposure to searching parasites, host larvae should be extricated from the leaf sheaths, isolated individually, and supplied food for continued growth. The earliest evidence of successful parasitization is when the parasite larva begins to feed ectoparasitically. Host larvae should not be exposed to ovipositing females for prolonged periods (> 24 hours), in order to circumvent superparasitization. Although searching females appear to avoid areas of the leafy top previously traversed by other females, they do not avoid previously parasitized hosts. The effects of superparasitization on rearing is not known, but the host can only support one parasite.

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***Macrocentrus prolificus* Wharton**

This polyembryonic endoparasite is reared very similarly to *A. stigma*. The host exposure scheme is identical to *A. stigma*, since the host age, microhabitat and cues for host location and acceptance apparently are the same. *Macrocentrus prolificus* adults are smaller than *A. stigma* and have a shorter ovipositor, but the small size is not as restrictive when the searching female enters the crevice between the leaf sheath and stem. For host exposure to ovipositing females, approximately 15 small (first- to third-instar) *D. saccharalis* larvae are placed at the base of each leaf sheath. About 5 larvae are allowed per ovipositing female. The *M. prolificus* female usually deposits only one egg per host.

The rate of parasite larval development is related to the host age when parasitization occurs. Larval developmental rate is slower when first-instar hosts are parasitized as opposed to third-instar host larvae. Evidence of successful parasitization is visible only when the mature parasite larvae emerge from the host to pupate. A single larval host produces up to 50 parasites, the actual number apparently is dependent upon host size. All individuals from a single egg are of the same sex because of polyembryonic reproduction. Occasionally, mixed-sex broods occur, having their genesis from more than one egg. Whether mixed sex broods are from a single or multiple oviposition by a single or multiple females is unknown. Pupation occurs communally in the stemborer larval feeding tunnel and requires about 12 days to complete. The developmental time from egg to adult emergence is generally 30–40 days, but is dependent upon the host larval stage parasitized, i.e., parasitized third-instar host larvae take less time to develop than parasitized second-instar larvae.

Pupae are harvested and broods isolated for emergence. Upon adult emergence, broods of both sexes are liberated into a large cage (0.5 x 0.5 x 0.5 m) and allowed about one

hour for mating. Newly emerged adults are negatively geotropic, positively phototropic and extremely active. Emergence containers must be tightly secured, especially at the top to prevent adults from wedging into crevices and dying or escaping. Females should not be liberated into cages with excessive numbers of males. Cultures of *M. prolificus* often produce a preponderance of males, thought to be caused by overmating that results in a packed female spermatheca, which hinders fertilization, or by excess males disrupting mating pairs and preventing successful copulation. Maintaining a 1:1 sex ratio for mating seems to be optimal. Adults are short-lived, living only 2–3 days at 25°C and ca. 80% relative humidity.

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***Mallochia pyralidis* Wharton**

The cue for succesful host-finding by *Mallochia pyralidis* is the moth emergence window. The searching female parasite locates the moth emergence window, probes through the window with her ovipositor, paralyzes the mature larva, then oviposits on or near the paralyzed larva. Thus the acceptable host stage is the mature *Eoreuma* larva that has constructed the moth exit window but has not pupated. Pupae are not acceptable hosts. Eggs hatch in two days and the first two larval instars are mobile and cannibalistic and feed at multiple sites on the host. This behaviour removes competing larvae and only one parasite is left by the third-instar, even though we found that 36% of the hosts receive multiple eggs in laboratory rearing. No explanation is available for the high rate of superparasitism observed in the laboratory colony. We did not believe hosts were limiting and suspected another factor was causing superparasitism. The latter two larval instars feed at single sites, completely utilizing the host. Larval development requires about a week. Pupation occurs next to the host cadaver and about 9 days are required until adult emergence. Reproduction is arrhenotokous and, although mating is frequently observed, the sex ratios in our colonies were approximately 3:7 (F:M). Rearing strategies to enhance mating and increase production of females have not been pursued. Adults are long-lived, averaging 47 days, with 90% of the eggs laid within the first 23 days.

Corrugated paper tunnels, that have been widened with forceps to approximately 1 cm, are used instead of living plants in the stem rearing procedure. Corrugated paper provides artificial tunnels to conceal hosts during exposure to ovipositing *Mallochia* females. Mature larvae are placed individually into tunnels, which are plugged with food, and are stapled to secure the larvae. Mature larvae cut the emergence window in the paper, which provides the appropriate proximal cue for host location, leading to oviposition.

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***Isotima javensis* (Rohwer)**

This solitary, ectoparasitic, phygadeuontine ichneumonid also requires the moth emergence window as the cue for host recognition and oviposition. After locating the moth emergence window, *I. javensis* females probe with the ovipositor through the window and paralyze the host larva prior to oviposition. Superparasitization is associated with

insufficient hosts, but like *M. pyralidis*, the first-stage larvae are aggressively cannibalistic and only one parasite larva survives.

Egg incubation requires 1–2 days, larval development 4.5–6.5 days, and pupal development 8–10 days at 25–35°C. However, at 35°C, larval and pupal survival is lessened. Total immature development requires 13–19 days. The larval stage of *I. javensis* diapauses in concert with its natural host, *Scirpophaga nivella* F., in the field. Diapause incidence is associated with the onset of winter, and is either triggered by the onset of host diapause or by environmental factors. The diapause appears facultative and should not be manifested in laboratory rearing unless photoperiod and temperature are not controlled. Adults live 8–10 days, and begin ovipositing within a few hours after copulation.

As with *M. pyralidis*, *I. javensis* has a very specific and very narrow temporal host parasitism window. Hosts are recognized and accepted only during the period between the time the mature larva constructs the moth exit window and the onset of pupation. Thus, the acceptable host stage approximates the prepupal stage, which is the stage when the mature stemborer larva has ceased feeding and excavation activity, has become truncated, and has turned a paler color. The longevity of *I. javensis* and *M. pyralidis* females helps ensure synchrony between searching parasite females and this narrow temporal window of host availability.

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***Elasmus zehntneri* Ferriére**

The host range of *Elasmus zehntneri* appears to be limited to mature larvae of *Scirpophaga nivella*. This parasite recognizes and accepts *S. nivella* as a host only after the moth emergence window is constructed by the mature larva (Cherian & Israel 1937). The mature host larva is visible through the window when the leaf sheath is removed. Female *E. zehntneri* probe through the thin covering of the moth emergence window with the ovipositor, paralyze the mature host larva, and deposit several eggs on or near the host. For laboratory rearing, thirty to forty host larvae that have constructed the moth emergence window in sugarcane stems are exposed to 60 female and 20 male *E. zehntneri* in 24 x 10 cm glass cylinders for 5 days. Eight days after exposure for parasitization, the *E. zehntneri* pupae can be removed and placed in containers for adult emergence.

Adults mate and females begin ovipositing within 1 day of emergence. Females deposit about 27 eggs per host, and superparasitism can result if hosts are limiting. Egg incubation requires 1 day, larval development 7–8 days and pupal development 5 days. Adult females live about 10 days when provided a 1:1 honey and water solution.

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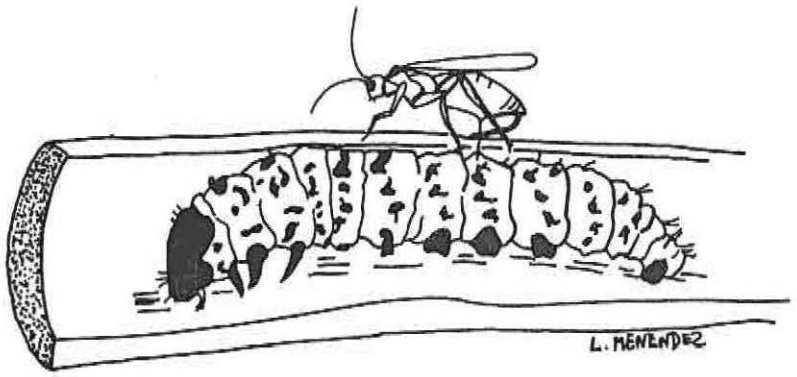
Drill-and-Sting

The drill-and-sting attack method in the larval guild is manifested in the braconid subfamily Braconinae, including the genera *Bracon*, *Habrobracon*, *Myosoma*, *Tropobracon*; and

the braconid subfamily Doryctinae, including the genera *Allorhogas*, *Heterospilus*, and *Rhaconotus*. Searching females parasitize host larvae tunneling in stems. The exact mechanism of initially locating their cryptic hosts in the stems is unknown,but searching females recognize that hosts are feeding or traversing certain areas of infested stems. When hosts are located, locomotion of the parasite ceases and females drill into the stem with the strong ovipositor. Once ovipositor contact with the larva is made, the female injects a venom that induces permanent paralysis. When drill-and-sting strategists attack stemborer larvae and do not make direct contact with the host as they drill into the feeding tunnel, they may wait passively for the stemborer larvae to traverse the tunnel and contact the ovipositor. Multiple eggs are subsequently deposited either on the host or near the host in the tunnel. The ectoparasitic parasite larvae consume the host and pupate communally near the host cadaver in the larval tunnel. Mating apparently occurs in the larval tunnel soon after adult parasite emergence.



Allorhogas drilling through plant stem, paralyzing and ovipositing on stemborer larva (Larval guild, drill-and-sting)

***Allorhogas pyralophagus* Marsh**

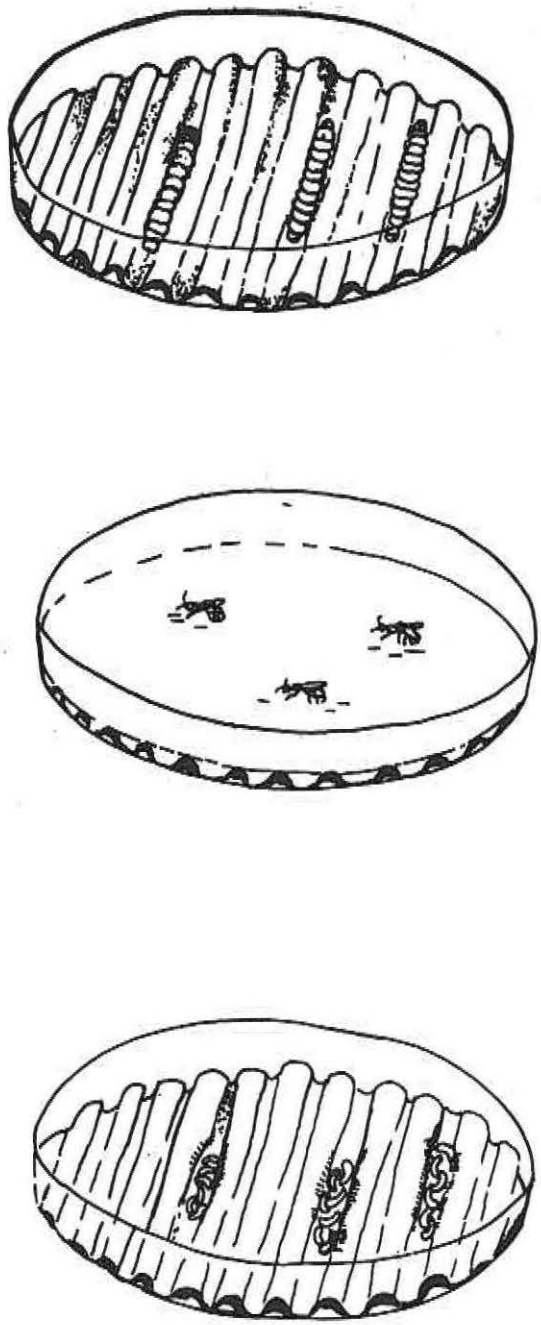
Initial laboratory rearing of *Allorhogas pyralophagus* utilized host larvae in small, 0.05 cm diameter, grass stems. Fourth-instar *E. loftini* or *D. saccharalis* larvae are allowed several hours to tunnel into 5 cm sections of grass stems. Ten infested grass stems are exposed to 10 mated females for 24 hours in 15-cm diameter Petri dishes. Following exposure, parasitized larvae are removed and held for parasite development. Parasite eggs are laid in loose clusters either on the paralyzed host or near the host in the feeding tunnel. After 2–3 days, eggs hatch and larvae feed gregariously on the host for 5–7 days. Mature parasite larvae pupate communally in a cocoon mass in the stemborer larval feeding tunnel near the host remains. After cocoon formation, pupae are harvested and placed in adult emergence cages (36 x 36 x 46 cm). Pupation requires about 1 week. Emergent adults are supplied with dilute honey on cotton balls and allowed 1 day for mating before transfer of females to oviposition units. Adult parasites survive 3–4 weeks in the laboratory at 26°C. Females oviposit throughout their life-span, but most oviposition is concentrated toward early adult life. Sex ratios are biased toward females in the laboratory culture. Brood size varies, normally ranging from 2–12 individuals.

Grass growth is usually seasonal, with drought and cold weather limiting the availability

of the correct stem size and freshness. In addition, succulent plant stems degrade rapidly after ablation and support growth of saprophytic and other undesirable microoganisms. Later laboratory rearing procedures substituted paper drinking straws and corrugated cardboard instead of plant stems as the substrate for enclosing host larvae for parasitization. Enclosing the host larvae in the paper substrate provided an artificial microhabitat that elicited the cues that were necessary to stimulate drilling with the ovipositor by the searching female parasite, but the microhabitat did not support growth of microbial contaminants. This change in rearing procedure did not appear to reduce parasite fertility, but it greatly enhanced rearing efficiency by providing a readily available substrate for the necessary host microhabitat, as well as increasing sanitation, by decreasing microbial growth.

Paper drinking straws (0.5 cm diameter) are cut to 5-cm lengths, a fourth-instar host larva is inserted in each piece and the ends are plugged with artificial diet or plant material to retain the host until paralyzed by the ovipositing female. Infested straws are exposed to females for 24 hours with a 1:1 ratio of parasites to hosts, either in Petri dishes or 0.5-l glass jars. The same procedure is followed for both grass stems and straws.

When paper drinking straws became difficult to procure (they were commercially replaced by plastic straws) we further changed the microhabitat to corrugated paper. The construction material for cardboard containers is corrugated paper sandwiched between two layers of heavy paper. To construct the corrugated paper ovipositional unit, the cardboard is first cut into circles that fit into a 9 cm diameter Petri dish (plastic or glass). Next, one layer of the outer paper is removed to expose the corrugations and the cardboard circle is placed, corrugations up, in the



Oviposition unit for drill-and-sting parasites. Larvae in corrugations (top), covered with filter paper for oviposition (centre), and paper removed

bottom of the Petri dish. Fourth- and fifth-instar larvae are placed in the troughs of the corrugated paper and a circular piece of filter paper is placed snugly over the corrugations accommodating the larvae and secured in place with tape. The corrugations separate the hosts to prevent cannibalism and provide an indentation to accommodate the larvae when covered by the filter paper.

Adult female parasites are transferred into the ovipositional unit to maintain a 1:1 host/parasite ratio. Searching female parasites readily find the host larvae, drill through the filter paper and parasitize the larvae. After 8–10 hours, parasite adults are transferred to another ovipositional unit to parasitize more hosts. The filter paper covering the larvae in the paper corrugations is removed and any mobile host larvae extracted. The remaining paralyzed larvae are retained in the unit for parasite development. The stage of parasite development can be viewed directly through the clear top of the Petri dish.

Parasite production can be increased dramatically by supplying the ovipositional units with an abundance of hosts and exposing them to numerous searching females. A 5:1 (or greater) parasite/host ratio exposed for just a few hours is adequate to obtain almost 100 percent paralysis of the host larvae and greater than 90 percent of exposed larvae parasitized. The paralyzed but unparasitized host larvae often serve as additional food for parasite larvae from adjacent superparasitized hosts. Ovipositional units can be stacked vertically to save space during the period when parasite development is being monitored. The unit can be placed directly into the mating cage just before adult emergence, which minimizes handling of mobile adult parasites.

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***Rhaconotus roslinensis* Lal**

Biology of *Rhaconotus roslinensis* and its rearing techniques are very similar to those of *A. pyralophagus*. *Rhaconotus roslinensis* can be reared using the same hosts and procedures; however, the biological nuances that exist between the two species are important for rearing, and so are discussed in some detail.

As with *A. pyralophagus*, host larvae must be presented in a cryptic manner to stimulate the ovipositing female to drill through the material containing the host and parasitize the host. *R. roslinensis* appears to be more limited than *A. pyralophagus* at penetrating plant tissues with its ovipositor. *Allorhogas pyralophagus* can easily penetrate thick paper and plastic drinking straws with its ovipositor to parasitize host larvae, whereas *R. roslinensis* is unable to penetrate tough or slick surfaces with her ovipositor, particularly a plastic

straw. However, numerous pin pricks in a plastic straw facilitate parasitization of hosts by *R. roslinensis*. The toughness of the material enclosing the host larva affects parasitization success and should be considered in rearing *R. roslinensis* and other drill-and-sting strategists such as *Habrobracon*, *Bracon*, *Tropobracon*, *Myosoma*, *Elasmus*, and *Heterospilus*, whose ability to penetrate plant tissues and other substrates with their ovipositor is unknown.

Adult parasite host-finding and parasitization behavior is similar to that of *A. pyralophagus*. Females drill into the stem and hosts are initially paralyzed before oviposition. Clutch size is independent of host size, but is not independent of host species. Clutch size of *R. roslinensis* averages 14 eggs per host on *Diatraea saccharalis* larvae, versus 5 eggs per host on *Eoreuma loftini*. Both hosts are factitious, acceptable and suitable, but *D. saccharalis* appears to be more acceptable and suitable, as shown by the increased oviposition and subsequent increased production of parasite progeny. At 26°C, total developmental time for all immature stages is about 19 days. Pupation is communal in the host tunnel near the cadaver. The preoviposition period for *R. roslinensis* is about 4 days, with an ovipositional period lasting 7–8 weeks. Again, as with *A. pyralophagus*, most eggs are laid early in adult life.

Caution is warranted when using artificial enclosures for parasitization of cryptic hosts. The continuous absence of important cues used by the searching female parasite for habitat-finding or close-range host-finding may preclude continuous selection for these important cues that occur in the natural habitat. A laboratory strain that is selected for certain artificial stimuli that are not present in the natural habitat could inhibit parasite colonization in the field.

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***Myosoma chinensis* (Szépligeti)**

Myosoma chinensis has numerous synonyms: *Microbracon chilonis*, *Amyosoma chilonis*, *Microbracon chinensis*, and *Bracon chinensis* (Quicke & Wharton 1989), which adds confusion to searches of the biological literature for this parasite. The two Old World species of *Myosoma* of importance as natural enemies of stemborers are *M. chinensis* and *M. nyanzaensis*. Both species are gregarious ectoparasites of the larvae of *Chilo* spp. tunneling in gramineous stems. *Myosoma chinensis* adults mate readily upon emergence, with a 2–11 day preoviposition period. Host larvae are readily attacked when they have tunneled in maize or sorghum stems. The female selects the location on the infested stem for drilling with her ovipositor, paralyzes the host upon ovipositor contact and lays 4–5 eggs on or near the paralyzed host. Oviposition can be lengthy, ranging from 30 minutes to one hour. Eggs hatch in approximately one day. Each female lays an average of 23 eggs during her lifetime.

Larval growth is rapid, requiring only 3 days from eclosion to cessation of feeding. The prepupal period lasts 3–4 days and duration of the pupal stage lasts 5–7 days. The entire life cycle requires about 13 days. The larvae feed gregariously and pupate communally in the host feeding tunnel. Adult females live up to 55 days, with an average longevity of 16.5 days. Males live an average of 14 days. Mating is with siblings from the gregarious cocoon mass, presumably within the host tunnel. Large numbers of *M. chinensis* are easily reared by sandwiching host larvae between pieces of tightly stretched muslin cloth and allowing mated females to parasitize larvae through the cloth. Using this technique, an average of

3–5 eggs are deposited on each host. Host larvae are exposed for 24 hours then removed and held for parasite pupation. Apparently, higher rates of parasitization were obtained when *M. chinensis* females were allowed to parasitize hosts communally. Females parasitizing hosts stimulate other females to parasitize. Isolated females often refused to oviposit (Subba Rao 1955).

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***Tropobracon schoenobii* Viereck**

This gregarious larval ectoparasite, also a drill-and-sting strategist, has been reared in the laboratory using the same hosts and preceding rearing technique described for *Myosoma chinensis*. Host larvae are placed between two layers of cloth stretched over the mouth of a 10–13 cm glass container enclosing the searching adult female parasites. The females paralyze and oviposit on the stemborer larvae through the cloth. Parasitized larvae are removed daily and isolated for continued parasite development. Care must be taken to collect externally laid eggs along with the paralyzed larvae. *Tropobracon schoenobii* also recognizes and parasitizes stemborer larvae that have tunneled in maize and rice stems.

Adult females are long-lived, and survive an average of about 43 days. However, the life cycle is relatively short; eggs hatch within 48 hours, larval development requires 4–6 days and pupal development 6–8 days.

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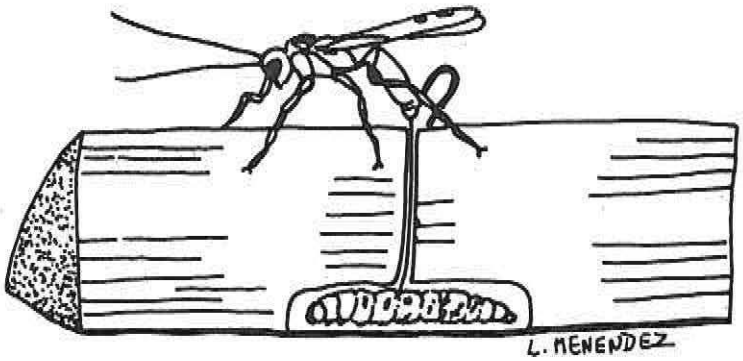
Wait-and-Sting

Parasite females employing the wait-and-sting host attack strategy are in the Braconidae, subfamily Braconinae, in the Old World genera *Euvipio, Glyptomorpha, Iphiaulax* and *Stenobracon*, and the New World genus *Digonogastra*. Wait-and-sting females contact and parasitize the host larva in the feeding tunnel with the ovipositor. The attack is very similar to probe-and-sting, except the wait-and-sting method is a more passive approach. This attack method differs from drill-and-sting in that the long, slender ovipositor of the wait-and-sting parasite is flexible and is used to probe for hosts in the larval feeding tunnels through passages created by larval feeding, whereas the more robust ovipositor of the drill-and-sting parasite is used for active drilling through plant tissue to contact host. For wait-and-sting parasites, ovipositor contact with the host is made by the searching females either waiting at the tunnel entrance for larvae to transport frass as a normal activity of tunnel cleaning, or probing in the breaches to the stem periphery created by the tunneling larvae. Tunneling behavior, such as clean tunnel maintenance or breaches to the outer wall is usually specific to stemborer genera or species. For example, *Eoreuma loftini* does not maintain a clear, clean tunnel. In fact, tunneling larvae usually pack the traversed excavations with frass and detritus. This stemborer also excavates complex transverse-horizontal tunnels that characteristically have numerous breaches to the stem periphery.



Stenobracon deesae probing stem, paralyzing and ovipositing on stemborer larva (Larval guild, wait-and-sting) (Redrawn after Narayanan & Venkatraman 1952)

In contrast, *Diatraea saccharalis* maintains a clean larval tunnel. Tunneling larvae transport frass and detritus to the tunnel entrance for deposition. If the tunnel entrance is just above a leaf sheath, a large accumulation of frass is often present. Regardless of where the parasite waits, adults detect the presence of the host larva near the breach, insert the ovipositor and sting the larva when it traverses the opening.

Successful rearing of parasites using this foraging strategy requires that acceptable, suitable hosts be presented to searching females in a cryptic manner, with avenues constructed for ovipositor access. Ovipositor access can be provided by making 0.5 to 1.0 mm diameter holes in the substrate enclosing the cryptic larva. The ovipositing female must be able to reach the host larva by unsheathing the ovipositor and introducing it through the substrate hole, thus the ovipositional apparatus must not place the host larva beyond ovipositor reach. Acceptable, suitable hosts are medium to large stemborer larvae that would normally be tunneling in the stem. Again, as with the other ectoparasites, oviposition is a two-stage process, i.e., paralyzation of the host larva followed by deposition of eggs on the host integument. Parasite larvae are both solitary and gregarious, feed ectoparasitically and pupate adjacent to the host cadaver.

***Stenobracon deesae* (Cameron), *S. nicevillei* Bingham**

Hosts are presented to searching females of this solitary, ectoparasite in plant stems cut into 7 to 8 cm lengths and split longitudinally. A groove, large enough to accommodate the host larvae, is excavated in the stem pith. The larva is placed in the groove and a piece of cellophane is affixed firmly over the bottom of the stem to imprison the larva in the groove. A small hole, 1.5 mm diameter, that leads from the stem periphery to the host larvae is drilled to accommodate the females' ovipositor. Fresh frass from the host larva attracts the female to the external opening where she inserts her ovipositor through the breach and parasitizes the stemborer larvae. The female initially paralyzes the host, then deposits an egg on the larval integument. The cellophane and the parasitized larva are removed, and the ovipositional apparatus can then be reused. Care must be taken to remove the parasite egg or small larva when the host is removed.

The parasite egg hatches in 1–2 days and the larva feeds externally on the host, completing 4 molts in 4–7 days. The larva pupates near the host cadaver. Pupation requires 10–16 days. Upon emergence, both sexes of adults are fed a sugar-water solution

and placed in a mating container in a well lighted area. Single pairs will mate in 15 x 5 cm glass vials. Females will begin ovipositing the day after emergence and adult females live 10–20 days.

Problems encountered in rearing *S. deesae* include superparasitization and a highly male-biased sex ratio. Although the ovipositing female usually discriminates against hosts previously parasitized, superparasitism occurs under laboratory conditions when hosts are scarce. When host density is four times the number of adult female parasites, only a few cases of superparasitism occur in a 48-hour exposure. In the laboratory, superparasitism results in a waste of eggs because early-instar parasite larvae are cannibalistic and only one larva matures from each host.

Approximately 90% of the *S. deesae* reared in the laboratory are males when reared on the factitious host *Corcyra cephalonica* Stainton (Narayanan & Venkatraman 1952). The male-dominated sex ratio in the laboratory is either due to poor mating frequency or the species of lepidopteran host. Six species of factitious hosts have been evaluated for rearing *S. deesae*, but only the "rice moth", *C. cephalonica*, was found to be suitable (Narayanan & Venkatraman 1952). The size and weight of this factitious host is about one-third that of the natural host, *Chilo partellus*, and more than one *C. cephalonica* is needed to rear a parasite. Narayanan and Venkatraman (1952) reported that the preponderance of males produced in the colony was due to the poor nutritional quality of the factitious host, *C. cephalonica*, and that the normal sex ratio was regained when *S. deesae* rearing was transferred from the factitious host to the natural host, *C. partellus*. In later rearing attempts, Sangwan (1973) supplemented the maturing *S. deesae* larval diet with additional paralyzed *C. cephalonica* hosts, which shifted the sex ratio from 65% males to 34% males. Apparently, supplying the developing female parasites adequate nutrition increased female survival.

In a natural *S. deesae* population, a preponderance of males (75%) was reported by Narayanan and Chaudhuri (1954). Sangwan (1973) reported a reversed sex ratio, where only 30% of a natural population was male. This difference in the proportion of males in a natural population might be explained by gleaning information from laboratory rearing. If the proportion of males in the population can be reversed from 65% to 35% by changing hosts or supplying additional hosts to increase nutrition, then this phenomenon could be manifested in the field when *S. deesae* is attacking several hosts. Saxena (1972) reported 10 lepidopteran hosts for *S. deesae*, with different levels of acceptance for each species.

A closely related parasite, *Stenobracon nicevillei*, has a biology and host range similar to *S. deesae*. The rearing procedure for *S. deesae* should suffice for *S. nicevillei*.

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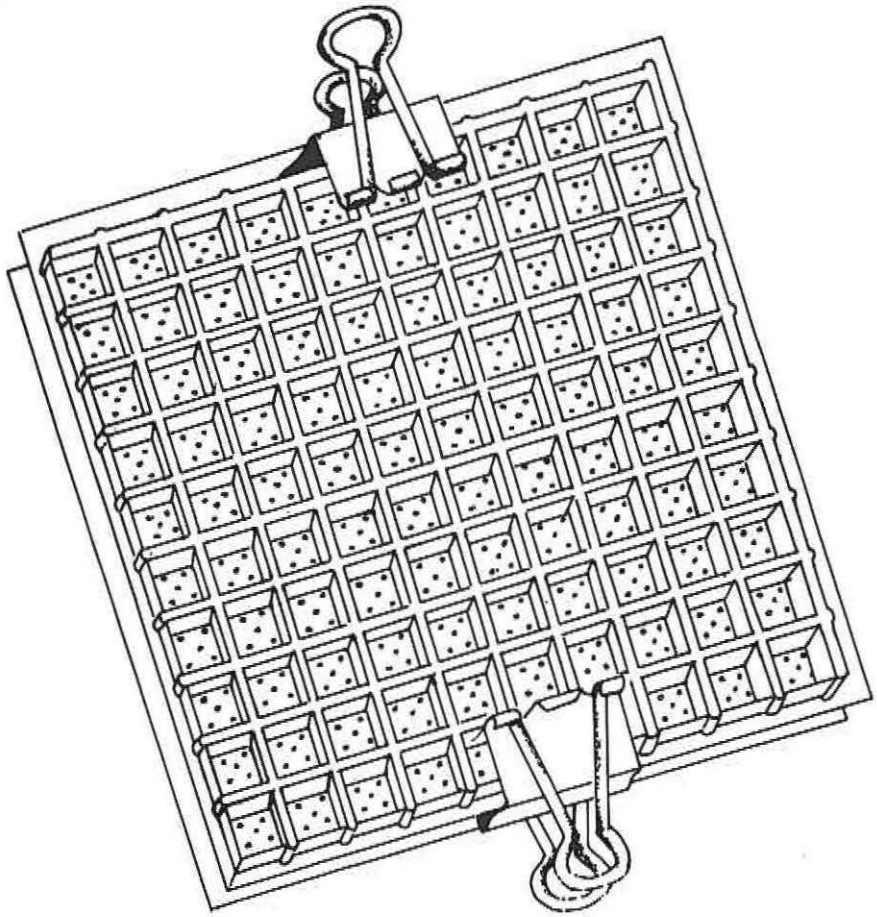
***Digonogastra kimballi* Kirkland**

Digonogastra Viereck is a New World genus that until recently was confused with the convergently similar Old World genus *Iphiaulax* Foerster. Two species of Neotropical *Digonogastra* attack stemborer larvae. *Digonogastra kimballi* Kirkland is a gregarious, larval ectoparasite, whereas *D. solitaria* Wharton and Quicke is a solitary, larval ectoparasite. The foraging strategies for *Digonogastra* and *Iphiaulax* should be almost identical and should share numerous similarities with other wait-and-sting attack strategists.

Host frass initiates oviposition in adult females of *D. kimballi* (Kirkland 1982). Females attack large host larvae by first paralyzing them and then ovipositing on the integument.



Ovipositional tray for exposing hosts to wait-and-sting parasites such as *Digonogastra*. Host larvae not depicted

Host recognition requires a cryptic host and an open passage for ovipositor insertion. *Digonogastra kimballi* can be reared on plant material using the technique for rearing *S. deesae*, or reared without host plant material, if the requirements of cryptic host and an avenue for ovipositor passage are not violated. An ovipositional tray constructed of plastic grid (each cubicle 0.75 x 13 x 18.5 cm) with a clear plastic bottom and removable clear plexiglass top is a functional substitute (Kirkland 1982). Holes (0.6 cm diameter) are drilled in the removable top to provide access to the enclosed host larvae by the parasite's ovipositor. *Diatraea grandiosella* larvae are placed individually into each cubicle without food. This design separates hosts and prevents cannibalism, yet constrains hosts to the cubicle for parasite access and provides an avenue for ovipositor insertion for host parasitization. During colony establishment, fresh host frass was smeared on the top of the ovipositional unit. After the adult parasite density had increased, using the frass did not increase parasitization.

Ovipositing females initially paralyze the host and then lay about 5 eggs on the host or on the nearby substrate. Parasite larvae pass through 5 molts in 4 days at 29°C. After the larvae have consumed the host, they pupate gregariously near the host cadaver. Pupation requires about 11 days. The removable top can be removed and the unit placed in an emergence container for adult emergence. Keeping the pupae in the ovipositional unit minimizes handling. About 16–21 days are required to complete the life cycle.

Adults require a 4–7 day preoviposition period. Most eggs are deposited in the first half of the ovipositional period, with a preponderance of male eggs deposited early and late in the ovipositional period. The sex ratio favors females during the third week of oviposition, and approximately 90% of the eggs are laid during the first 3 weeks of female life.

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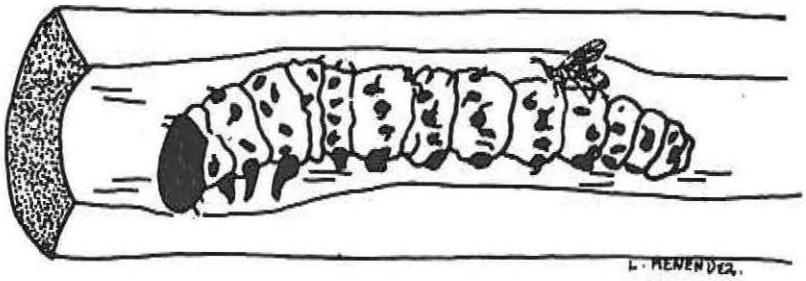
Ingress-and-Sting

Parasites using the ingress-and-sting strategy to parasitize stemborer larvae are small in size, which allows them easy access to larvae within open host tunnels. Examples of parasites using this strategy include the microgastrine braconids belonging to the genera *Cotesia* and *Apanteles*, and the bethylid *Goniozus*. Microgastrines in general have been found to be easy to rear in the laboratory. In our experience, we usually do not need to provide parasites with a plant substrate for successful parasitization. Further, even though the parasites in nature have to enter the host tunnel to parasitize the host larva, there is no need to replicate this microhabitat in the laboratory. Thus parasitization normally only requires that host and parasite be placed in close proximity.



Cotesia inside feeding tunnel, ovipositing in stemborer larva
(Larval guild, ingress-and-sting)

***Cotesia flavipes* Cameron, *C. chilonis* (Matsumura), *C. sesamiae* Cameron, *Apanteles diatraeae* Muesebeck, *Apanteles minator* Muesebeck**

Numerous rearing methods have been used successfully with *Cotesia* and *Apanteles* parasites of stemborers. We will report methods that work well for rearing *C. flavipes* using *D. saccharalis* as hosts, and then discuss some of the alternatives. As adult parasites emerge (usually in the morning hours), parasites are released into a 30 x 30 x 30 cm sleeve cage for approximately 1–2 h, to permit adequate time for mating. A bright light, either natural or artificial appears to stimulate mating. Prescribed numbers of female parasites (20–40) are aspirated into 0.93-l (1US quart) jars, that contain 20 host larvae and several pieces (10 sq cm) of artificial diet. The jar is fitted with a screen top lid, then the hosts and parasites are kept for 24 h at room temperature (approximately 24° C), a14L:10D photoperiod and > 50% relative humidity. After 25 h, the host larvae are removed from the jars and groups of 5–10 host larvae are placed into petri dishes containing artificial diet. Hosts are maintained on artificial diet until host pupae or parasite cocoon masses are noted. Parasite cocoon masses then are harvested and placed in vials with a fine mesh screen lid, and are kept in a high humidity (>70%) until emergence of parasite adults. Unfed adults live an average of 24 h, making necessary the immediate use of adults after emergence.

An alternative rearing method for *C. flavipes*, which we call "hand-stinging", may be preferable during initial laboratory colonization, as it assures that each host exposed is actually parasitized and provides visual evidence of host acceptance. Parasites are placed in a sleeve cage after emergence and allowed to mate for ca. 2 hours. Acceptable host larvae are held in soft forceps and offered individually to the parasites in the cage. Oviposition usually occurs within a few seconds when the host is placed close to the parasite; parasitism can be detected by closely watching the encounter between host and parasite. The parasite grasps the borer with her legs, curls the abdomen downward and forward, and inserts the ovipositor. At ovipositor insertion, the larvae reacts violently and then becomes quiescent but is not paralyzed. The process of oviposition is quite rapid, lasting only about 3–5 seconds. Once a host is parasitized it is removed from the cage, placed on diet, and an additional host is offered. This can be continued for as long as the parasites show interest in oviposition. Additional exposures can be made on subsequent days until the parasites are dead.

C. flavipes is easily reared on third- through sixth-instar larvae of the coevolved host *Chilo partellus* or the factitious host *Diatraea saccharalis*. Parasites accept exposed larvae, but do not recognize the larvae until they are within very close proximity. First- and second-

instar larvae usually are not accepted as hosts. Parasites required approximately 14 days to complete egg and larval development, with an additional 6.5 days for pupal development. No difference was found for either the production of parasite progeny or sex ratio as a function of host instars when 3rd- through 6th-instar larvae of the factitious host *D. saccharalis* was used. The number of progeny ranged between 46 and 62 per host, with sex ratios ranging from 5.2:1 to 8.3:1 (F:M). Increasing the number of parasites in the exposure jars beyond a 1:1 parasite:host ratio does not cause a concomitant increase in parasitization. About 5–15% of the *D. saccharalis* hosts encapsulated early-instar *C. flavipes* larvae.

As would be expected for closely related parasites, the rearing procedures and life-history parameters for all microgastrine parasites of stemborers are similar. Sathe and Nikam (1984) reported that 25°C was the optimal rearing temperature for *C. flavipes*, due to the combination of short developmental time and maximal survival. Kajita and Drake (1969) found *Cotesia* (=*Apanteles*) *chilonis* reared at 25°C required 4 days for egg development, 8 days for larval development, and 5 days for pupal development. At 30°C, egg and larval development was shortened by one day each. Developmental times for *Cotesia flavipes* are almost identical to those of *C. chilonis*. Davis (1944) reported developmental times for *Apanteles diatraeae* of 4–8 days for egg stage, 10–25 days for the three larval stages, and 7–10 days for pupation, with a wide range of adult longevity, ranging from 1–21 days.

Kajita and Drake (1969) found differences in the clutch size as a function of temperature for both *C. chilonis* and *C. flavipes*. For *C. chilonis*, they reported an average of 31 progeny per host at 25°C, with only 26 progeny per host at 30°C, whereas for *C. flavipes*, they found 37 progeny per host at 25°C versus 60 progeny per host at 30°C. The 31 progeny they observed for *C. flavipes* at 25°C using *C. suppressalis* was far below the 53 progeny per host we reported at 24°C using *D. saccharalis* (Wiedenmann et al. 1992), whereas their results at 30°C were nearly identical to our results at 24°C. Davis reported *A. diatraeae* had clutches that ranged from 15 to 146 individuals. Unlike our results (Wiedenmann et al. 1992) on the lack of difference in clutch size as a function of host instar, Mohyuddin (1971) found that *C. flavipes* reared on its aboriginal host, *Chilo partellus*, did produce more progeny when later-instar larvae were parasitized. Whether the difference between our results and those results is due to using factitious hosts versus aboriginal, coevolved hosts, or due to differences in experimental methods is not known. Ullyett (1935) found that the number of parasite progeny per host by *C. sesamiae* using *Busseola fusca* (Fuller) as a host ranged from 60–100. Although our *C. flavipes* adults lived only 24 h, other workers have found that the addition of plant juices or honey will increase survival of *C. flavipes*, *C. chilonis* and *Cotesia sesamiae* up to 4–7 days. Mohyuddin (1971) reported that 90% humidity increased survival of immature parasite stages. However, Kajita and Drake (1964) reported that increased humidity caused decreased adult survival of *C. flavipes*, but increased survival of *C. chilonis*.

Other interesting results were that the number of prickings (stings) by *C. flavipes* was shown by Varma and Bindra (1974) to increase the number of parasite progeny produced using *C. partellus* as a host, whereas Beg and Inayatullah (1980) found the opposite, that the number of progeny decreased with multiple stings on *C. partellus*. Because of this discrepancy, and the fact that numerous parasite progeny are produced with a single sting, it may be advisable not to try to parasitize the host multiple times.

Beg and Inayatullah (1980) also found that only certain stemborers were suitable for development of *C. flavipes*. The stemborers *C. partellus* and *C. infuscatellus* Snellen were accepted and suitable for parasite development, whereas *Tryporyza incertulas* (Walker) and *Ostrinia kasmirica* (Moore) were stung but did not support parasite development. This is similar to our observation that *C. flavipes* readily accepted *Eoreuma loftini* as a host, but the host was unsuitable for parasite development. Varma and Bindra (1974) and Wiedenmann et al. (1992) found that they never had 100% parasitization when more than one host was

exposed to multiple *C. flavipes* females, and concluded that females normally only parasitized one host in their rearing protocol. Although the physical details of the Varma and Bindra (1974) rearing protocol were not reported, their finding parallels our conclusions that the proportion of hosts parasitized by *C. flavipes* females reaches an upper limit of less than 1.0 at higher host or parasite densities. Because of this result, we normally use the ratios of 20 host larvae to 20 or 40 parasites in the rearing jars.

We have reared *C. chilonis*, *C. flavipes*, *A. diatraeae* and *A. minator* successfully in the laboratory using the methodology reported for *C. flavipes*. We also have had some degree of success with *C. sesamiae* using *Chilo partellus* as the host. However, production of *C. sesamiae* progeny gradually declined until the colony was lost when *D. saccharalis* was used as host. Poor progeny production was probably due to the factitious host (*D. saccharalis*) not being a suitable host, and not a result of rearing technique. The addition of grass stems for host larvae frass production greatly enhanced parasitization of *D. saccharalis* larvae by *A. diatraeae*. This is the only microgastrine we have reared that appears to require the presence of frass, especially frass from grass stems, for successful parasitization.

As a note of precaution, the three species of *Cotesia* discussed in this section are closely related and quite difficult to separate morphologically. Whenever more than one culture of *Cotesia* spp. (or more than one culture of other morphologically similar species) is being maintained by a biological control program, efforts should be made to separate both spatially and temporally the rearing as much as possible. This will minimize the risk that individuals from one culture will invade and contaminate another culture. If the invading species (or strain) is more aggressive than individuals in the invaded culture, the invaders may rapidly and completely take over the colony, and the person in charge of rearing may never know that the culture has been lost.

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***Goniozus natalensis* Gordh, *G. procerae* Risbec**

Goniozus natalensis and *G. procerae* are long-lived gregarious ectoparasites from the Old World, where they have been recorded from several stemborer species including *Eldana saccharina*, *Coniesta* (=*Acigona*) *ignefusalis*, and *C. partellus*. As a parasite of stemborers,

Goniozus is unique in several ways. This genus is the only taxon of the Bethylidae of importance in biological control of stemborers. *Goniozus* also has unique behavior, in that after parasitizing the host larva, the female remains in the stemborer tunnel and provides some maternal care for her progeny.

Details on rearing *Goniozus* are taken in part from Conlong et al. (1984) and Ndoye (1980). Newly-emerged adults were collected daily and sexes placed together in a glass 0.5-l jar for 4 h to ensure mating. For exposure, four fifth-instar host larvae were placed in artificially bored sections of sugarcane and placed with two *Goniozus* females. The female stung the host larva, which paralyzed it, then laid her eggs on the dorsal and lateral surfaces of the host. As the parasite larvae emerged from the eggs, they attached themselves to the host and fed externally on the host. The larval stage averaged two weeks at 25°C. Female *Goniozus* remained in the burrow until the parasite larvae pupated. An average of eight parasites developed per host larva. Emergent parasite adults had sex ratios averaging 5:1 (F:M), with males emerging first. Males were reported to bite open other cocoons and mate with females before they emerge. After leaving her developed progeny from one parasitization, females search for another host. Adults were reported to live 15–30 days, which permitted them to parasitize up to three larvae. Ndoye (1980) reported developmental times for *Goniozus procerae* using *C. ignefusalis* as a host. In that report, the egg stage lasted 4–5 days, larval stages approximately one week, and pupal stages approximately 4–5 days. Interestingly, Ndoye reported an 8–9 day preoviposition period, which was not reported for *G. natalensis*. We have also had success rearing *G. natalensis* using *D. saccharalis* as a host.

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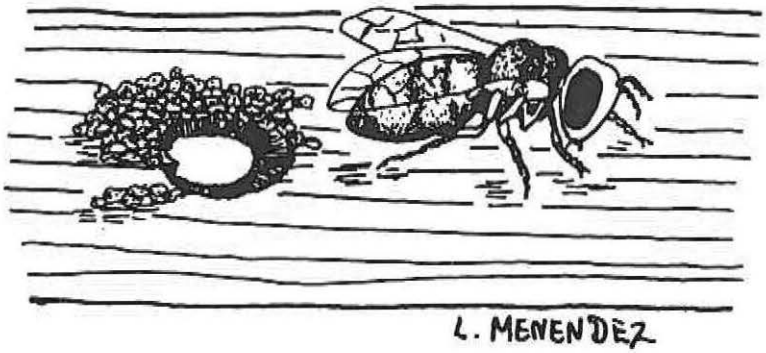
Planidial Ingress

Numerous tachinid flies attack tropical stemborers around the world, perhaps most notably the genera *Descampsina, Diatraeophaga, Jaynesleskia, Lixophaga, Metagonistylum, Paratheresia* and *Sturmiopsis*. The tachinid genus *Palpozenillia* uses a different attack method, which will be discussed in the next section. The two unique biological characteristics of the tachinid attack strategy are the life-stage of progeny that are deposited by the gravid female and that the host-finding method is a two-stage process. Tachinids can be either oviparous, larviparous or ovolarviparous. Regardless of the specific ovipositional biology, these tachinids have a long gestation period, during which the fly eggs mature within the uterus. Most of the flies mentioned above are larviparous, although Bartlett (1941) claimed that *Metagonistylum minense* Townsend eggs do not hatch within the uterus, but rather hatch only after exposure to air or disruption of the uterus. Host finding is unique among tachinid parasites of stemborers using the planidial-ingress attack strategy. Female flies are attracted to host frass to larviposit, but it is their mobile progeny that find the host itself. Planidial maggots are deposited at the entrance to or within the host tunnel. Planidia are negatively phototropic, which guides them to the proximity of the host larvae feeding in the enclosed tunnel. Maggots then penetrate the cuticle of the host, usually the



Lixophaga near host frass at tunnel breach, where larviposition occurs
(Larval guild, planidial ingress)

intersegmental membrane, with their mouth hooks. Maggots initially spend some time living freely inside the host body, but then attach themselves to a tracheal branch or main trunk for the remainder of larval development.

Rearing methods for tachinids are fairly well documented for several species, such as *Lixophaga* and *Sturmiopsis*, and these will be used as general rearing models for the following discussion; major deviations in technique or life history will be noted separately. Excellent and very complete references to tachinid rearing can be found in Bennett (1969), Carnegie and Leslie (1979), and Nagarkatti and Rao (1975); methods described below were partly gleaned from these references and our own experiences using *D. saccharalis* and *E. loftini* as hosts.

***Lixophaga diatraeae* Townsend**

Adult flies, which are positively phototropic, emerge from puparia and are transferred to 25 x 25 x 35 cm mating cages. Cage sides can be covered with cheesecloth or nylon mesh. Adults are provided with cotton pads soaked in either distilled water, dilute sugar water, or dilute honey solution. Solutions should be changed daily to avoid fermentation. For food, adults can be provided with either split raisins, sugar cubes, raw sugar, or split jellybean candies. We also provide adult flies with a fructose-egg diet, which is a mixture made up of agar, distilled water, 42% fructose syrup and dried whole egg.

Lixophaga mates readily (unlike many other tachinids), requiring no manipulation of lighting conditions or special cages. After 7–12 days, or when a female dies, the abdomen is opened and the uterus is removed and placed in a dilute (2% NaCl) saline solution. After the uterus is removed and ruptured, eggs and larvae (maggots) can be separated. According to Bennett (1969), *Lixophaga* usually contains fewer than 100 maggots. Maggots are transferred individually to host larvae (third- through sixth-instar) with the use of a fine brush, which contains only one or a few bristles. One to three maggots can be transferred to each host larva. Host larvae then can be removed to artificial diet and reared until presence of fly puparia is noted. The larval stage requires 7–10 days and the pupal stage requires another 9–12 days, depending on rearing conditions. Puparia are collected, placed in individual 10 mm diameter vials plugged with cotton, and held in a high humidity until fly emergence. We position the vial with the cotton plug down, because the emerging flies are positively phototropic, and this positioning minimizes the emergent flies getting trapped between the vial wall and cotton plug, rendering them useless. The

complete developmental time from mating to adult is approximately 25–33 days. Adults normally live a few weeks.

***Sturmiopsis inferens* Townsend, *S. parasitica* Curran**

Rearing procedures for the two species *S. inferens* and *S. parasitica* are largely similar to the procedures for *L. diatraeae*. Newly emerged *S. inferens* females are isolated individually with 2–3 older male flies in a glass vial. Newly emerged *S. parasitica* females are isolated individually with one older male. The vial is shaken vigorously in bright sunlight, then brought into the shade. Using this method, mating begins within 5 minutes, and lasts 3–15 minutes. Females mate only once, whereas males commonly mate with 4–5 females. Adult flies live 3–4 weeks. According to Nagarkatti and Rao (1975), mated females have negligible mortality if provided a moistened sponge, sugar cubes and cotton swabs soaked in honey.

Gestation of *S. parasitica* takes 18 days at 26°C (Nagarkatti & Rao 1975). Females are dissected into a 2% sodium chloride solution. Each female contains 500 to 900 maggots. Freshly hatched maggots are transferred to distilled water and stored for 3–4 days at 1.5°C (Nagarkatti & Rao 1975), or for 4–5 days at 4°C (Carnegie & Leslie 1979) with minimal mortality, but died within 2 days if kept at room temperature. Maggots being transferred to host larvae are dipped briefly in a 2% solution of 0.05% sodium hypochlorite to protect from fungal infection. One to three maggots are transferred per host larva. Survival of parasites is enhanced by placing the maggot just posterior to the host head capsule. Larval periods require 12–14 days at 26°C, followed by a pupal period of another 12–19 days. Mature fly larvae emerge either from host larvae or pupae.

Variations in the above-mentioned methods and biologies exist. Carnegie and Leslie (1979) reported that *Descampsina sesamiae* Mesnil would not mate, even using the method of shaking the vial and exposing it to bright light. Unlike the failure with *Descampsina* and the finicky nature of *Sturmiopsis* and *Diatraeophaga* (Nandagopal et al. 1980), *Metagonistylum minense* requires no special cages or lighting conditions for successful mating, and even artificial light is adequate (Bartlett 1941, Carnegie & Leslie 1979). Unlike the long developmental periods of *Sturmiopsis* and *Lixophaga*, *M. minense* takes only 16–20 days to develop (Bartlett 1941). This species also produces more progeny than *Lixophaga*, with a range of 300–700 eggs, the number varying with size of the female parasite. Scaramuzza (1939) reported a method for rearing *Paratheresia* (=*Theresia*), in which the female fly is not sacrificed to harvest maggots. The gravid female fly is placed into a glass vial, the interior of which had been wetted. The introduced female adheres to the wall of the vial and, in the process of freeing herself, liberates maggots. By repeating the process several times daily, a considerable number of maggots can be collected.

Suitable host ranges for tachinids vary greatly. According to Bennett (1969), *Diatraea saccharalis*, *D. impersonatella* Walker and *D. lineolata* are suitable New World stemborer hosts for *L. diatraeae*, although in the laboratory it can also be reared on numerous Old World borers of the genera *Chilo*, *Bissetia*, *Sesamia* and *Scirpophaga*, as well as other non-stemborer Lepidoptera species. *Diatraea saccharalis*, *D. impersonatella*, *D. busckella* Dyar & Heinrich, *D. rosa* Heinrich and *Scirpophaga nivella* are suitable hosts for *M. minense*, although it can also be reared rarely on *Diatraea centrella* (Möschler) and *D. lineolata*. The host range for *P. claripalpis* is broadest among the tachinids using the planidial-ingress host attack method, including *Eoreuma loftini* and 16 species of *Diatraea*. Nagarkatti and Rao (1975) found that suitable hosts for *S. parasitica* were *Sesamia inferens* Walker, *Chilo auricilius* Dudgeon, *C. partellus*, *C. indicus* Kapur and *C. infuscatellus*. Bennett (1969) reported that *Sesamia inferens*, *S. calamistis* Hampson and *C. infuscatellus* (Hampson) were suitable hosts for *Sturmiopsis inferens*. Carnegie and Leslie (1979) showed that *Eldana saccharina* was not

a suitable host for *Sturmiopsis inferens*, and both *E. saccharina* and *S. calamistis* were not suitable for *M. minense*.

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Bait-and-Wait

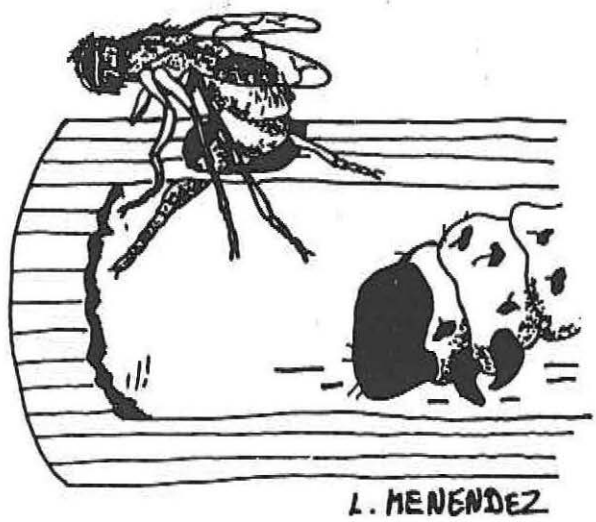
For this attack strategy, the adult fly is separated both spatially and temporally from the host. Unlike the Tachinidae that use the planidial-ingress method for host finding, the bait-and-wait strategists use a completely passive host-finding approach. Instead of the parasite finding the host, in this case, the host finds the parasite. This strategy is exemplified by the New World tachinid genus *Palpozenillia*. The female parasite apparently finds the host tunnel by detecting frass, then extends the ovipositor into the host tunnel, where the eggs are deposited (Simmonds 1958). As the host larvae traverse the tunnel and feed, they ingest the parasite eggs, which then hatch in the gut.

***Palpozenillia palpalis* (Aldrich)**

Palpozenillia has a fairly broad host range that includes numerous species of *Diatraea* as well as *Castnia licoides* Boisduvall (Castniidae) (Bennett 1969). Rearing *Palpozenillia* is easily accomplished once the biology of the parasite is recognized and understood. Simmonds (1958) used cages 1.85 m high and 1 m in diameter for mating, and reported that the cages needed to be covered with dark green cloth, as no mating occurred if the cage was covered in white cloth. Adult flies were fed sugar water or cane juice, and the cage was kept humid. The preoviposition period is 10–14 days. Because of the necessity for egg ingestion by the host, the methods detailed for hand-parasitizing hosts for planidial-ingress tachinids are not appropriate. Instead, gravid *Palpozenillia* females (> 10–14 days old) are dissected to remove eggs (600–800 per female). Some eggs are usable immediately, because they contain fully formed larvae with conspicuous mouth hooks; those eggs with partially developed larvae are kept damp for 1 to 2 days, or until they mature and the conspicuous mouth hooks are present. Two or more eggs are placed onto the surface of either a piece of artificial diet or sugar cane, then a narrow (3–5 mm) glass tube is pressed into the diet or cane, which then encloses both the diet and the eggs. A host larva is inserted into the tube, head-first, facing the eggs and diet, and the tube is plugged with cotton behind the

larva. As the borer larva feeds, it ingests the parasite eggs, which subsequently hatch in the borer gut.

First-instar parasite larvae feed initially within the gut, then enter the host fat body. During the third (ultimate) instar, feeding by the larval parasite increases as it consumes the remainder of the host. Mature parasite larvae emerge from the host and form puparia. Simmonds (1958) found the time from ingestion of egg to formation of puparium required 9 days using *Diatraea centrella* (=*canella*) as the host. This developmental period is very different from the life history data from other references he cites, such as a report that the first-instar stage took 20 days using *Castnia* as host, and a total of 72 days required for egg-to-adult development. He also reports that, using *D. centrella* as host development took 25 days, of which 12 days were spent in the pupal stage.



Palpozenillia with abdomen extended into feeding tunnel, ovipositing (Larval guild, bait-and-wait)

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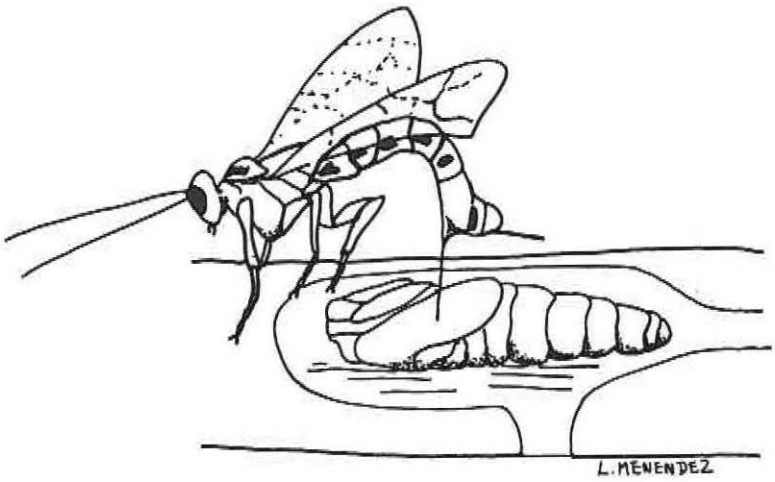
Pupal Guild

Parasites attacking pupae exhibit both the drill-and-sting and the ingress-and-sting attack methods. The ingress-and-sting approach has the most taxonomic diversity in the pupal guild and includes several genera of the Eulophidae, Ichneumonidae and Chalcididae. The Eulophid genera *Tetrastichus*, *Pediobius* and *Trichospilus* are gregarious endoparasites with fairly diverse host ranges. Some species in these genera also are facultatively hyperparasitic. The ichneumonid *Dentichasmias busseolae* Heinrich is a solitary endoparasite that also has a wide host range, which encompasses several stemborer genera. The biology of the solitary, endoparasitic chalcid, *Psilochalcis* (= *Hyperchalcidia*) *soudanensis* Steffan, is poorly known.

Drill-and-Sting

The ichneumonid genus *Xanthopimpla* is an example of parasites in the pupal guild that use the drill-and-sting attack method. Adult females locate the pupal chamber in the stem and actively drill through the plant rind and attack the pupa. The female initially punctures the pupa several times with her ovipositor and feeds on liquid expelled from

the pupa. In contrast to the drill-and-sting parasites of the larval guild, *Xanthopimpla* does not paralyze the host prior to oviposition and is not ectoparasitic. A single egg is laid internally in the host and the subsequent larval stage develops internally. Pupation occurs in the host pupal chamber. Presumably the adult utilizes the moth exit window to egress.



Xanthopimpla drilling through plant stem and ovipositing in stemborer pupa
(Pupal guild, drill-and-sting)

***Xanthopimpla stemmator* (Thunberg), *X. citrina* (Holmgren)**

Xanthopimpla stemmator is easily reared in the laboratory using *D. saccharalis* as a host. All ages of pupae are acceptable to the ovipositing female, but pupae in the first half of the developmental period are most suitable. Pupa must be cryptic, and successful rearing requires *Xanthopimpla* females drilling through a substrate for host recognition and oviposition. Host pupae can be placed in hollowed-out plant stems, paper straws or wrapped tightly in tissue for exposure. Hosts prepared for oviposition can be exposed daily to ovipositing females in 0.93-l (1 U.S. quart) glass jars. Females may superparasitize a host in the laboratory, but either early-instar parasite larval cannibalism or the host immune defenses results in only one survivor. After exposure to ovipositing *Xanthopimpla* females, host pupae should be removed from the cryptic microhabitat and placed in a holding container. Unparasitized pupae will produce moths prior to the emergence of parasite adults. Eggs hatch in one day and the larva molts 4 times in 5–7 days. Pupation requires 11–12 days; thus, the total developmental period lasts 17–20 days.

The adult sex ratio ranges from 1:1 to a preponderance of females. Females live 30–60 days and males 20–40 days when sugar-water solutions are provided. *Xanthopimpla* is very active during daylight hours. Copulation commences upon emergence and reoccurs every several days, with a preoviposition period of 2–4 days after initial mating. Females do not appear to be very fecund and parasitize only few hosts per day. However, the long female life span provides a steady parasite population increase when hosts are readily supplied for parasitization.

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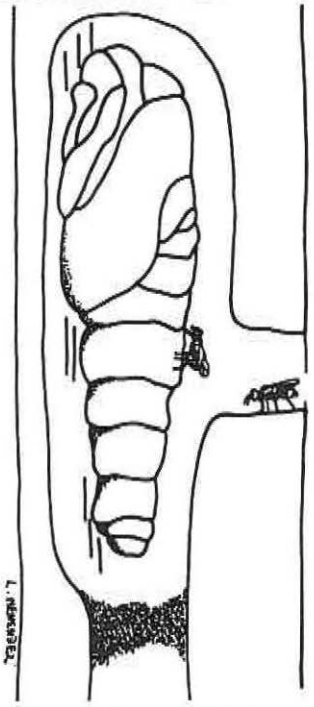
Ingress-and-Sting

These pupal endoparasites gain access through the moth exit window and directly attack the host pupa. The gregarious eulophids *Tetrastichus*, *Pediobius* and *Trichospilus*, are quite small and, upon gaining access, can easily traverse the excavations of most stemborers. The integrity of the moth emergence window appears to be the physical restraint that limits these eulophids access to the pupa in the natural microhabitat. The intact moth emergence window prevents *Pediobius furvus* Gahan from reaching the acceptable and suitable factitious host *Eoreuma loftini* (Pfannenstiel et al. 1992), whereas *P. furvus* successfully enters the tattered moth emergence window of *Diatraea grandiosella* and parasitizes the enclosed pupae (Overholt & Smith 1989, 1990). In contrast, the chalcidid *Psilochalcis soudanensis* has functional mandibles and cuts a hole in the moth exit window of its hosts (Mohyuddin & Greathead 1970). Also, access to the pupal chamber by the ichneumonid *Dentichasmias busseolae* Heinrich is not restrained by the construction of the moth emergence window of *Chilo partellus* (Mohyuddin 1972).

Rearing the gregarious eulophids does not require hosts to be cryptic or associated with tunnels, as the adult females readily parasitize naked, exposed pupae. Conversely, *Dentichasmias busseolae* only oviposits in borer pupae located within grass stems, which requires reconstruction of the natural ovipositional microhabitat to provide the cues necessary for successful host location and subsequent host acceptance.



Pediobius entering stemborer pupal chamber through moth exit window (Pupal guild, ingress-and-sting)

***Pediobius furvus* Gahan, *Tetrastichus ayyari* Rowher, *T. inferens* Yoshimoto, *T. israeli* Mani & Kurian, *Trichospilus diatraeae* Cherian & Margabandhu**

These gregarious, endoparasitic eulophids are all easily reared by exposing *Diatraea* or *Eoreuma* host pupae to ovipositing female parasites in small containers. Generally, pupae in any stage of development are acceptable hosts, but pupae in the first half of their development are the most suitable hosts. Multiple eggs are deposited internally and hatch in one day. Larvae feed internally for 8–10 days and pupate within the host pupa. Pupation requires about 10 days and, thus, the entire life cycle requires about 20 days. Pupae should be exposed to ovipositing females for only one day, then removed, and new pupae added. Emerging adults cut holes in the pupal cuticle, and mate immediately. Both

sexes are produced in a host; the number of adults produced per host generally depends upon the size of the host, with large pupae producing up to 370 *P. furvus* adults. Females begin ovipositing within a few hours of emergence. Providing sugar-water for adults doubles the longevity from 4 days to 8 days for *P. furvus*. *Tetrastichus* spp. live more than 20 days. Adults live 2–3 times longer under cool temperatures and can be held in refrigeration at about 10°C when hosts are not available. At 10°C we can completely maintain colonies and slow down rapid population increase of *Trichospilus diatraeae* to save labor in colony maintenance. These eulophids are much like the trichogrammatids and will utilize many acceptable and suitable factitious hosts in the laboratory. However, field collections do not reflect the polyphagy observed in the laboratory, and apparently polyphagy is an artifact of laboratory conditions.

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***Dentichasmias busseolae* Heinrich**

All ingress-and-sting parasites attack exposed hosts after entry is gained to the larval tunnel or pupal chamber. Thus, rearing parasites with this attack method is generally very simple and only requires placement of the host in close proximity to the ovipositing female. Re-creation of a natural microhabitat to provide chemical and physical cues in addition to those provided by the host is usually not necessary.

Dentichasmias busseolae is an exception to this generalization and successful rearing requires re-creation of the microhabitat and the cues necessary for host location. To provide the natural oviposition microhabitat necessary for successful parasitization, mature host larvae are inserted into short tunnels precut in plant stems. Several mature larvae can be implanted in tunnels precut in several internodes of large diameter stems to provide a multiple-oviposition microhabitat. The mature larva tunnels very little before constructing the pupal chamber and the moth emergence window for pupation in the internode. After the moth emergence windows are constructed, infested stems are exposed to searching *D. busseolae* females. When we reared *D. busseolae* on the factitious

host *D. saccharalis*, the moth emergence windows were purposely tattered to enhance parasite access. After exposure of 1–2 days, host pupae are harvested and retained for parasite emergence. Adult parasite emergence is enhanced by keeping parasitized host pupae in a humid environment.

A single egg is deposited internally, the larva feeds for 14 days and pupates within the host pupa. Seventeen to 20 days are required for development of the immature stages. Maintaining a high humidity and providing sugar-water increases adult longevity.

Dentichasmias busseolae appears to have a much narrower host range than *Tetrastichus*, *Pediobius* and *Trichospilus*. Natural hosts of *D. busseolae* in Africa appear limited to *Chilo partellus*, *Chilo* sp. and *Coniesta ignefusalis*, although *Busseola fusca*, *Sesamia calamistis* and *Eldana saccharina* are acceptable and suitable hosts under certain laboratory conditions (Mohyuddin 1970). New World factitious hosts that are acceptable in the laboratory include *Diatraea saccharalis*, *D. grandiosella* and *Eoreuma loftini*. *D. busseolae* females will parasitize these stemborer pupae when provided in sugarcane or maize stems as described above. The proportion of the hosts parasitized is unknown; however immature development is marginal and the sex ratio is skewed to males. Laboratory colonies of *D. busseolae* reared on these factitious hosts progressively degenerate with each generation and have not been maintained for more than three generations.

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7

INSIGHTS AND APPLICATIONS

With an understanding of the host life history, the steps of successful parasitization, the different methods of parasitization associated with foraging strategies, a key for tentatively identifying the stemborer parasite, and rearing methods associated with each of the parasite guilds and foraging strategies, we have sufficient information to begin pursuing biological control of stemborers. Understanding the stemborer life history provides a background, from which one can construct ecological life-tables of borer populations and measure and quantify naturally occurring mortality for each of the life stages. The section on successful parasitization puts into context the hierarchical series of steps that have to occur for a parasite to exploit the stemborer host, whether the parasite is co-existing with the host in nature, being reared in the laboratory, or being colonized in a biological control project. Recognition of the hierarchy will permit the aware observer an entry point for understanding how the host-parasite association may have evolved and the requisites for the process to be emulated in the context of a biological control intervention.

The section on foraging strategies is the heart of this manual. Recognition of foraging strategies provides the important template for predicting the specific guild or method of parasitization an unidentified parasite species may employ. Developing a scenario of the parasite guild and a foraging strategy of a specific parasite opens the door for pursuing biological control of stemborers. Identification of the foraging strategy used by a specific taxon of parasites will simplify both rearing efforts and field-colonization strategies. The foraging strategy is the capstone in the working model of the crop-host-parasite association: the limitations imposed by crop agronomics, the biology and ecology of the stemborer host and parasite complex, the necessity of following the hierarchical steps to successful parasitization and how the parasite exploits the host. Understanding the foraging strategy within the entire ecological context also allows the best possibility of an accurate post mortem evaluation of an unsuccessful biological control intervention, such that another attempt may be successful, and that the final conclusion is not that biological control doesn't work, but that the specific biological control attempt didn't work because of some error.

Placing the parasites into guilds and assigning foraging strategies points out the commonalities in the way hosts are exploited. A quick look at Table 4 shows that most members of a subfamily employ the same foraging strategy. However, there are exceptions. The subfamily Braconinae contains both wait-and-sting and drill-and-sting strategists, and the Tachinidae contain both planidial ingress and bait-and-wait strategists. Another problem occurs with the ichneumonid subfamilies Banchinae, Campopleginae and Cremastinae. With the exception of *Venturia* in the Campopleginae, the attack methods of parasites in these groups are either unknown, speculated, or unconfirmed. Clearly, more work and careful observations must be made on these ichneumonids, to clarify the exact foraging strategy employed. Recognition that the foraging strategies largely follow taxonomic affinities provides an entry point into the use of non-coevolved new-association natural enemies for biological control. For example, the Old World borer *Scirpophaga* is attacked by the extant doryctine braconid *Rhaconotus roslinensis;* use of Table 4 shows the biological control practitioner that the New World doryctine parasite *Allorhogas pyralophagus* employs the same strategy and may warrant investigation as an alternative natural enemy for colonization against *Scirpophaga* or other related borer pests.

As we mentioned in the introduction, the borer *Elasmopalpus lignosellus* has a different life-style than all other stemborers discussed in the text, and its parasites are treated separately in Appendix I. Despite its differences, *E. lignosellus* has associated with it parasites that can be fit into the same template of guilds and foraging strategies as the parasites of all the other stemborers. Also, even though we do not treat parasites of *Ostrinia* in the text, we expect that parasites of *Ostrinia* will fit into the same template, as well. As a result, we

feel that the biological control practitioner can derive the basis for recognizing foraging strategies of parasites of *Ostrinia* and, therefore, can use the same processes for initiating a biological control program against the various species of *Ostrinia*.

It is also important to recognize that the foraging strategy that is used by the parasite species most successful in exploiting the host may be at least partly a consequence of the morphology of the crop plant with which the parasite and host evolved: the drill-and-sting strategy may work very well in a plant with a small-diameter stem, such as rice, whereas it may be largely ineffective in a crop with a large-diameter stem, such as sugarcane. This suggests that breeding programs for specific morphological characteristics of the crop plant may have an impact upon the success of a biological control intervention. In contrast, some parasites employ a strategy that is not limited by plant characteristics, but by the behavior of the stemborer. The microgastrine braconids that use an ingress-and-sting strategy have averted the limitations imposed by large stem size, by exploiting the hosts by entering into the tunnels excavated by the borers. The success of *Cotesia flavipes* against borers in large-stemmed sugarcane points to the lack of importance of stem diameter for the success of ingress-and-sting strategists. However, the stemborer must leave an open tunnel for this strategy to work; acceptable and suitable hosts that pack their tunnels tightly block parasite ingress and cannot be exploited by *C. flavipes* or other ingress-and-sting parasites in the larval guild.

The key presented allows field entomologists to identify, usually to subfamily or genus, the parasite reared from a field-collected egg, larval or pupal stage of a stemborer. Identification of a parasite to genus will provide the best clues for rearing in the laboratory, provided the biology of the taxon is known. However, placement of the natural enemy into the correct family and subfamily, which should be accomplished with minimal difficulty, can often be even more informative than identification to genus. Placement of a parasite into a subfamily provides a wide base of biological information, such as its foraging strategy, which will allow the reader to derive broad implications necessary for rearing.For example, identification of an unknown parasite to the ichneumonid subfamily Pimplinae, coupled with the information in Table 4, reveals that the parasite should be a true pupal parasite and, thus, the foraging strategy and laboratory rearing methods can be deduced. As another example, recognition that an unknown parasite is an agathidine braconid tells the collector that the parasite attacks early-instar larvae that are cryptically enclosed in leaf sheaths, but the older larvae tunneling in the stem are exploited for nutrition. Thus, searching agathidine females probably will not accept and attack larvae that are exposed and out of a proper ecological context.

The section on rearing is not intended to be a how-to manual, or a step-by-step, follow-the-instruction approach to rearing. Instead, we attempt to point out details that may enhance successful rearing, while keeping a wider perspective on rearing, so the reader can make inferences and apply insights to rearing other species, or the same species using other methods. We cannot overemphasize the importance to successful rearing of observation and collecting biological information, from host collection in the field through parasite emergence in the laboratory, as well as adult parasite behavior. Age of the host when collected can provide key information on the host stage attacked. Coupling the acceptable host information with the possible attack methods, we can then devise an appropriate method for laboratory rearing of the parasite.

We hope to leave the reader with a new philosophical approach to biological control of stemborers. We hope that the reader will no longer have in mind a narrow approach, or will only try the one method that may have worked previously, when planning a biological control intervention. Rather, we hope the biological control practitioner will recognize the broader perspective, i.e., that life history processes, foraging strategies and taxonomy are

all interconnected and that the tritrophic crop-pest-parasite system needs to be viewed from this perspective. Such a perspective offers not only the best chance of a successful intervention against a specific borer pest, but also a chance to understand why the success occurred, so it can be replicated elsewhere.

Appendix I

***Elasmopalpus lignosellus* (Zeller)**

Elasmopalpus lignosellus, an important stemborer of the New World tropics and subtropics, is excluded from the main text and is treated separately because its life history deviates too broadly from the other stemborers presented. Most stemborers inhabit the aerial portions of gramineous plants, whereas *E. lignosellus* is commonly considered a soil inhabitant. The eggs of *E. lignosellus* are laid in the soil near the base of the plant and are well hidden from casual observation (Smith et al. 1981). Eggs are opaque when first deposited and turn red as hatching approaches. Upon emergence from the egg, the reddish-colored first-instar larva crawls across the soil surface and locates the host plant. All larval stages construct silken feeding tubes attached to the plant at the feeding site on or below the soil surface. As the larva grows, additional, larger feeding tubes are constructed resulting in numerous feeding tubes attached to the base of the host plant. Feeding tubes are not visible unless the plant is carefully removed from the soil. Larval feeding is usually confined to the plant stem near the soil surface. However, when seedling plants and ratoons or tillers are attacked, the larva often exhibits the common stemboring habit of tunneling into the stem. In these instances the feeding tube is extended into the plant stem, and the larva tunnels upward, usually destroying the apical meristem. Boring into the stem causes the characteristic deadheart of the small ratoons of sugarcane (Bennett 1962) and kills plant seedlings. The tunneling habit is restricted to the small ratoons and seedlings.

The later-instar larvae are bluish-green in color and are very active when removed from the feeding tube. Disturbed larvae wriggle and thrash violently, resulting in the name "jumping borer" in the Caribbean Islands. The mature larva constructs a sock-shaped pupation chamber in the soil at a greater depth than where larval feeding occurs. The pupal chamber is constructed of silk, but is heavier walled and more substantial than are the larval feeding tubes. Pupation occurs at the bottom of the sock-shaped chamber and passage to the soil surface by the newly emergent adult is through the neck of the sock. Pupation behavior of *E. lignosellus* is very similar to behavior of the other stemborers, i.e., an enlarged site for the pupa to reside and a pathway is constructed for moth egress.

Elasmopalpus lignosellus oviposits, feeds and pupates in the soil rather than aerially on the host plant like the other tropical stemborers (Table 1). However, the silken feeding tunnel enclosing the larva and the pupation chamber in the soil constructed by *E. lignosellus* are functionally the same as the bored stem enclosing the larva and the excavated pupal chamber in the plant stem, which is characteristic of other tropical stemborers. The cryptic nature of the larval and pupal stages coupled with the familial taxonomic affinities, would lead to the conclusion that the parasites comprising the foraging guilds of *E. lignosellus* and other tropical stemborers (Table 1) should be similar. Hymenopteran parasite genera that attack both *E. lignosellus* (Johnson & Smith 1981, Smith & Barfield 1982) and other tropical stemborers (Table 2) include *Chelonus* in the egg-larval guild; *Alabagrus* (=*Agathis*), *Bracon*, *Chelonus*, *Habrobracon*, *Illidops* (=*Apanteles*), *Macrocentrus*, *Orgilus* and *Pristomerus* in the larval guild; and *Invreia* in the pupal guild. The foraging strategies for the parasite genera shared in common are essentially the same. Although each parasite species within a genus will have a characteristic host range, members of the genus will have a common foraging strategy. For example, *Alabagrus* and *Macrocentrus* females will probe and sting the early-instar larvae whether the larva is feeding cryptically in the plant leafsheaths or is feeding cryptically in a silken tunnel in the soil at the plant base. *Chelonus* will seek out and oviposit in the host eggs wherever laid, and exploit the larval stage for food and shelter regardless of the stemborer attacked. *Bracon* and *Habrobracon* will drill and sting the cryptic larva whether the larva is enclosed in plant tissue or a silken tunnel.

The egg parasite guild for *E. lignosellus* apparently is absent (Johnson & Smith 1981). Apparently ovipositing in the soil has successfully circumvented exploitation by the egg parasite guild found in other stemborers (Table 4). However, *Chelonus*, even though considered an egg-larval-guild parasite, successfully finds *E. lignosellus* eggs near the soil surface. The larval parasite guild is fairly rich, containing about 20 species of Hymenoptera and Diptera (Smith & Barfield 1982). Genera of *E. lignosellus* parasites not in common with those in Table 2 include the larval parasites *Horismenus* and *Stomatomyia*. *Horismenus* is a gregarious, larval endoparasitic eulophid that may use an ingress-and-sting-attack strategy. *Stomatomyia* is a solitary, endoparasitic tachinid that oviposits on the integument of the later-instar larvae. Thus for successful attack by *Stomatomyia*, the later-instar *E. lignosellus* larvae must be exposed for direct oviposition, because *Stomatomyia* adults do not actively seek the larval host in the silken tunnels nor do they use the attack strategies of planidial-ingress or bait-and-wait utilized by the other tachinid stemborers. *Stomatomyia* is most successful in attacking *E. lignosellus* larvae when the host is exposed when traveling on the soil surface between plants (Johnson & Smith 1981).

The pupal parasite guild for *E. lignosellus* is not rich, containing only the three species in the genus *Invreia* (Hymenoptera: Chalcididae) and the bombyliid (Diptera) *Geron aridus* Painter. The biology of *G. aridus* is unusual, in that the parasite is actually a larval-pupal parasite, and is a facultative hyperparasite, either using *E. lignosellus* or the primary parasite attacking *E. lignosellus* as the host (Johnson & Smith 1981). *Invreia* locates *E. lignosellus* by first finding the surface opening of the pupal chamber, then traversing the neck to the distal end that contains the pupa. If the pupa is not formed, *Invreia* will wait until pupation is completed and attains the acceptable host stage before ovipositing. This behavior of *Invreia* is similar to other ingress-and-sting parasites of the pupal guild that locate the moth emergence window and traverse the excavation to the host pupa for parasitization.

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8

GLOSSARY

arrhenotoky — A parthenogenetic form of reproduction, in which females are produced from fertilized eggs (biparental), whereas males are produced from unfertilized eggs. Also called haplodiploidy. Most parasitic Hymenoptera use this form of reproduction.

ectoparasite — A parasite that deposits its egg on the outside of the host cuticle, and the parasite larva develops and feeds externally on the host.

endoparasite — A parasite that deposits its egg inside the host and the parasite larva develops and feeds internally within the host. Some endoparasitic species may feed internally through the first few instars, but emerge from the host and feed externally in the ultimate larval stage.

encapsulation — An immune response by the host to the injection of a parasite egg. The parasite egg or larva is enveloped by circulating haemocytes, which then wall off the enclosed parasite from the host haemocoele, serving to kill the parasite, either by oxygen or nutritional deprivation.

exsanguination — Complete consumption by a parasite of the fluids of the host's body.

factitious host — An acceptable, suitable host that has not coevolved with a given parasite species. May also be considered a new-association host.

facultative hyperparasite — An opportunistic parasite species that is usually a primary parasite, but which may be hyperparasitic when the primary host has been previously parasitized.

gregarious parasite — A parasite species in which more than one parasite progeny emerges from the host, and normally more than one egg was deposited in the host. Polyembryonic species (see below) are a special case, because the multiple progeny emerge from an individual parasite egg.

guild — A functional grouping of taxa of organisms that exploit a common resource in different ways. A parasite guild exploits a given host stage, but each member may use slightly different foraging strategies for that exploitation.

host feeding — The process by which an adult parasite uses the puncture wound made by insertion of the ovipositor to feed and gain nutrition from the host.

hyperparasite — A parasite that attacks a primary parasite already parasitizing a host. Hyperparasites can be facultative (see above) or obligate (see below). A hyperparasite can be distinguished from a primary parasite by dissection of the host from which the parasite emerges, and looking for a second meconium. Also called a secondary parasite.

kairomone — An external chemical message sent by one organism, that has adaptive value to the receiving organism.

larviparous — A parasite that deposits larvae, rather than eggs. The larvae are usually deposited either away from or outside the host, and then the planidial larvae find, attach to, then enter the host. See planidial-ingress strategy.

meconium The accumulated larval waste products that are voided by the ultimate larval instar just prior to pupation. Each parasite voids one meconium, which allows distinguishing primary parasites from hyperparasites, or multiple parasitism of a single host.

monophagous A parasite species that utilizes only one host species, or perhaps sibling species of hosts. Contrast with stenophagous and polyphagous.

multiple parasitism More than one species attacking and depositing progeny in or on a host (interspecific competition). In contrast to hyperparasitism, in multiple parasitism the host is attacked, not the primary parasite. Differs from superparasitism (intraspecific competition), in which the host is attacked by more than one parasite, but only of one species.

new association A non-coevolved host-parasite association. The host and parasite share no coevolutionary history. See also factitious host (above).

obligate hyperparasite A hyperparasite that must attack a primary parasite species for successful development. Differs from a facultative hyperparasite, which can develop in either the primary parasite species or the herbivore.

oviparous A parasite species that deposits its progeny in the form of eggs.

parasite An animal that feeds in or on another living animal (host) for all or at least part of its immature life cycle, consuming all or part of its tissues, and eventually killing it. Most parasites require only one host for immature development. Also referred to as a parasitoid.

parasitism The act of a parasite attacking and ovipositing (parasitizing) in or on a host.

parasitization The result of parasitism, which includes also the fate of the immature parasite and the attacked host.

parthenogenesis Development of the egg without fertilization. Arrhenotokous (haplo-diploid) parasites produce males (haploid) by parthenogenesis. Thelytokous species produce females (diploid) by diploid parthenogenesis, and males are unknown or rare and non-functional.

planidial larva The deposited, mobile, parasite larvae that find hosts near the area in which they were deposited by an adult parasite.

polydnavirus Particles found in some parasitic Braconidae and Ichneumonidae that are involved in the abrogation of the host immune system as a response to a challenge from a foreign object, such as injection of a parasite egg.

polyembryony Development of more than one individual parasite from only a single egg. Usually evident by production of > 1 parasite, and all of one gender or a highly skewed sex ratio. Found primarily among Braconidae and Encyrtidae (parasitic on stemborers), as well as Platygastridae and Dryinidae (not parasitic on stemborers).

polyphagous A parasite species whose host range is very broad, encompassing many host species or host species from diverse taxa. Contrast with monophagous and stenophagous.

predator An animal that attacks and feeds on other animals (prey) that are usually smaller or less powerful than itself. The prey animal is usually killed and either partly or entirely consumed. Most predators attack and consume many prey.

primary parasite A parasite that attacks a herbivorous host, and that host is not another parasite. Contrast with secondary parasite or hyperparasite.

proovigenic A parasite female that has a full complement of eggs at her adult emergence. No other eggs are developed during the lifetime of the adult. Because all nutrients allocated to the eggs are derived from the larval parasite stage, the number of parasite progeny is a function of the amount of energy obtained from the host.

secondary parasite Also known as a hyperparasite (see above). Contrast with primary parasite.

solitary parasite A parasite that deposits only one egg per host, or (in the case of superparasitism) more than one egg was deposited in the host but only one parasite progeny is capable of being produced by the host.

stenophagous A parasite whose host range is restricted to a narrow group of host species. Hosts may be within one narrow taxon, or may be few species within several related taxa. Contrast with polyphagous host range (above), which is much broader, and monophagous (above), which is restricted to only one, or very closely related, host species.

superparasitism Parasitization of a host that results in more progeny of a single species being deposited in the host than can mature in that host (intraspecific competition). Superparasitism is often associated with rearing under artificially high parasite densities or crowded conditions.

synomone Information sent from one organism that is received by an organism of another species, and which has adaptive benefits for both sender and receiver.

synovigenic A parasite female that continues to develop eggs through her adult lifespan, or at least over some part of her life. May emerge as an adult with immature ovaries. Uses energy obtained as an adult for allocation to progeny.

teratocyte Unusual cells produced by many braconids. At hatching, teratocytes circulate through host hemolymph and may affect host immune response.

thelytoky Diploid parthenogenesis, in which females are produced from unfertilized eggs. Males are either unknown, or are very rare. Progeny are uniparental.

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ISBN 92 9064 056 1

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