CACTOBLASTIS CACTORUM (LEPIDOPTERA: PYRALIDAE) IN NORTH AMERICA: A WORKSHOP OF ASSESSMENT AND PLANNING

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ABSTRACT

The cactus moth, *Cactoblastis cactorum* Berg (Lepidoptera: Pyralidae), has been an important biological control agent of introduced and weedy prickly pear cacti (*Opuntia* spp., Cactaceae) in many parts of the world. *Cactoblastis*, a native of Argentina, was introduced into the Caribbean in 1957 to control weedy, but native species of prickly pear infesting rangeland. It has spread through the Caribbean and in 1989 was first found in Florida. It has now spread as far north as coastal Georgia. There is a continuous distribution of acceptable host species of *Opuntia* from southern Florida across the southern United States to the Pacific Coast. Mexico is a center of endemism and has many species of *Opuntia*. Prickly pear cacti constitute a highly important and uniquely desert-adapted subsistence food and cash crop in Mexico. Prickly pears have other valuable uses, such as in the production of cochineal dye and in desert landscaping. Because *Cactoblastis* readily attacks many novel hosts within *Opuntia*, it will likely have serious impacts on the ecology of desert environments and on the agricultural and horticultural uses of prickly pears. Further, if *Cactoblastis* does result in significant damage, it is likely to serve as another source of criticism of classical biological control. *Cactoblastis cactorum in North America, A Workshop of Assessment and Planning*, was held in Tampa, Florida in September 2000. Major subject areas covered include the biology and economic importance of *Opuntia*, the biology, biological control history, and current status of *Cactoblastis*, and potential methods of controlling *Cactoblastis* in North America. This paper summarizes findings of the workshop and provides an introduction to the workshop proceedings.

Key Words: biological control, cactus moth, chemical control, F_1 sterility, *Opuntia*

RESUMEN

La palomilla del cactus, *Cactoblastis cactorum* Berg (Lepidoptera: Pyralidae), ha sido un agente de control biológico importante contra varias especies de cactus exóticos e invasivos pertenecientes al género *Opuntia* (Cactaceae) en varias partes del mundo. Esta especie, originaria de Argentina, fue importada al Caribe en 1957 para controlar especies nativas de cactus que estaban infestando las áreas de forraje para ganado. La especie expandió su distribución a través del Caribe y en 1989 fue detectada por primera vez en Florida. Hoy en dia, su distribución hacia el norte alcanza el área costera del estado de Georgia. Desafortunadamente, existe una distribución continua de hospederos del género *Opuntia* desde Florida a través de los estados del sur de los Estados Unidos hasta llegar la costa del Oceano Pacifico. Méjico es un centro de endemismo donde existen varias especies endémicas de *Opuntia*. Estas especies constituyen una fuente importante de alimento y forraje en Méjico y son utilizadas en la manufactura de tintes y como vegetación en la jardinización de áreas semidesérticas. Debido a que *C. cactorum* ataca muchas especies dentro del género *Opuntia* su distribución tendrá consecuencias negativas en la frágil ecología de las areas desérticas y en los usos agrícolas y hortícolas de estas plantas. Asimismo, si el daño causado por *C. cactorum* es excesivo, esto servirá como otro punto para criticar al area de control biológico clásico. Un taller de trabajo titulado *Cactoblastis cactorum* en Norte America: un taller de planeamiento y evaluación fue llevado a cabo en Tampa, FL en Septiembre, 2000. Los temas que se discutieron incluyen: (a) la biología e importancia económica de *Opuntia*, (b) la biología, historia de control biológico y estatus actual de *C. cactorum* y (c) posibles métodos de control para esta especie en Norte America. Este artículo resume las conclusions del taller y sirve como introducción para los otros artículos que se presentan.

Prickly pear cacti are members of the platyopuntia group of *Opuntia* (Cactaceae). There are about 200 members in the genus, and they have a distribution, primarily in more arid areas and in well-drained soils, from the southern plains of Canada to South America; the genus is especially well-represented in Mexico. Opuntias are dominant components of the natural environment in drier climates of the New World where they are native. They are highly important as nurse plants for other plant species and as food and habitat for a variety of birds, reptiles, mammals, insects, and other animals (Russell & Felker 1985). Native Americans have used prickly pear stems (cla-

dodes) and fruits as important dietary components for probably thousands of years. Prickly pear cacti comprise an important cultivated food crop in Mexico (see papers by Badii & Flores, Soberon et al., and Vigueras G. & Portillo in this proceedings) and, to a lesser degree, in the United States. They are also an important forage for domesticated livestock. Prickly pear cacti have other commercial uses as well, such as for the production of cochineal dye by *Dactylopius* spp. and as an important landscaping plant in arid areas. Because of their various beneficial attributes, especially for fruit production, forage and fodder, dye production, and as an ornamental plant, prickly pear cacti have been purposefully distributed by humans throughout many drier areas of the world where cacti are not native, including Europe, Asia, Africa, and Australia. Opuntias were being spread worldwide as a source of fruit and cochineal dye as early as the 16th century (Rowley 1997). Transport and colonization is facilitated by the fact that most opuntias are adapted to vegetative reproduction; cut stems can survive for months in transit and then readily establish roots when provided with soil and water. Unfortunately, some opuntias are capable of becoming invasive weeds and have done so in many areas where they have become naturalized. Because of their fierce spines and dense growth, they can produce impenetrable thickets that displace native plant and animal communities or make land unproductive for livestock grazing and other human uses.

One of the great early successes in the biological control of weeds was the liberation of millions of hectares of Australian farmland, rangeland, and natural habitat from the scourge of a complex of alien and highly invasive species of prickly pear cacti. Students of biological control are familiar with the classic "before and after" pictures (e.g., DeBach 1974). The biological control agent, still effective after over 70 years, is the cactus moth, *Cactoblastis cactorum* Berg (Lepidoptera: Pyralidae), a native of Argentina and neighboring areas.

In many successful cases of biological control, natural enemies that have proven their effectiveness are introduced elsewhere in the world where the same pests are creating problems; this is the case with *Cactoblastis* (Zimmermann et al. 2000, reprinted in this proceedings). Most of the redistribution of *Cactoblastis* has been to areas where the cactus family is not native, and some of these programs have resulted in successes similar to what occurred in Australia. In 1956, the decision was made to release *Cactoblastis* onto the island of Nevis, in the Caribbean (part of the Leeward Islands group of the West Indies). On Nevis, a complex of *native* prickly pears, dominated by *Opuntia triacantha* (Willdenow), were considered to be undesirable pests in over-grazed rangeland where they out-competed grasses and caused serious injury to livestock and handlers (Simmonds & Bennett 1966). Three species of natural enemies, including *Cactoblastis*, were shipped from South Africa and released on Nevis in early 1957. *Cactoblastis* was apparently the only natural enemy to establish; it rapidly spread, resulting in the collapse of prickly pear plants, and the biological control program was considered "outstandingly successful" (Simmonds & Bennett 1966). Based upon this success, *Cactoblastis* was introduced onto Montserrat and Antigua in 1960, where it also became established and resulted in substantial reduction of prickly pear populations (Simmonds & Bennett 1966). Simmonds & Bennett (1966) also reported that *Cactoblastis* had spread either naturally or by unofficial human transport to St. Kitts and the U.S. Virgin Islands. Since this period, *Cactoblastis* has spread, either naturally or with intentional or unintentional human involvement, through many regions of the Caribbean, including to Puerto Rico, the Dominican Republic, the Bahamas, and Cuba, where it now attacks both weedy and non-weedy native *Opuntia* spp. (see Zimmermann et al. 2000).

In 1989, *Cactoblastis* was first identified from mainland North America, namely, southern Florida (Habeck & Bennett 1990). How it arrived in Florida is unclear. It is unlikely but possible that it was intentionally and illegally introduced. It may have arrived through natural dispersal by flight, possibly storm-aided. Another possibility is that it was unintentionally introduced, such as by a hobbyist cactus grower traveling from the Caribbean. Perhaps the most compelling possibility was proposed by Pemberton (1995), who suggested that it may have been unintentionally introduced through commerce. Pemberton (1995) documents that 300,000 *Opuntia* plants, originating from the Dominican Republic and destined for nursery sales, annually arrived in Miami during the 1980s. He also documents 13 interceptions of *Cactoblastis* at Miami ports from 1981-1986, including larvae found in stems originating from the Dominican Republic (Pemberton 1995).

Since its original discovery in southern Florida, *Cactoblastis* has moved northwards through natural dispersal (see Stiling & Moon, this proceedings) and now is present and causing noticeable damage in coastal areas of Georgia. Natural spread westward has been slower, but it was reported at our workshop that infested nursery stock had been found in the garden department of a large chain store in Pensacola in western Florida (N. Coile, Florida Department of Agriculture and Consumer Services) suggesting that dispersal through Florida and neighboring states may likely be facilitated through the nursery industry or by unintentional casual transport by home gardeners. Where it is established in Florida and Georgia, *Cactoblastis* is relatively com-

mon and noticeable to the general public, especially in regard to the collapse of specimen plants in the home landscape.

Workshop Rationale and Planning

My first awareness of the establishment of *Cactoblastis* on continental North America was from the paper by Pemberton (1995). As both a biological control scientist and a hobby cactus grower, the Pemberton paper was of significant professional and personal interest. That level of interest was raised substantially in 1999, when hobbyist cactus growers in Florida began to appeal to "cacti_etc", the largest international listserver devoted to the discussion of cacti and other succulent plants, for information on how to control this new "pest" that was damaging landscape opuntias. At this point it was clear that *Cactoblastis* would be an increasingly important issue with the general public.

Because there is a continuous distribution of prickly pear cacti from southern Florida through the Gulf Coast states, into the southern Midwest and Southwest (Benson 1982), and thereby into Mexico, there is the likelihood that *Cactoblastis* will spread throughout *Opuntia* habitat in climatically favorable regions of North America. Based upon its known impact on several species of *Opuntia*, both overseas and in their native habitat (e.g. Nevis), we must assume that there may be potentially substantial impact on both ecologically-important wild *Opuntia* populations as well as on agriculturally and horticulturally important opuntias in the southern United States and throughout Mexico. As *Cactoblastis* was originally intentionally introduced into the Caribbean Basin as a biological control agent, I was concerned that the science and practice of biological control could be held accountable, especially in light of recent critical commentary regarding non-target effects of classical biological control (for example, see Follett and Duan 1999, Strong and Pemberton 2000). For these reasons, I contacted several scientists familiar with the situation to determine if a workshop to explore the issues was advisable; the response was unanimously favorable, and an organizing committee was formed (see Acknowledgments).

It was our intent that this be a true workshop, necessarily limited in size to facilitate discussion and therefore open by invitation only, with each participant serving one or more specific roles. Further, it was our intent that a diversity of interests be represented including biological control, botany, conservation biology, ecology, entomology, and horticulture, and that there be representation from Mexico. The participants and their roles are presented in Table 1. The workshop was organized in such a way as to include formal presentations as well as discussion periods. The workshop agenda (Table 2) was organized to address several objectives, summarized by the following questions:

- How far is *Cactoblastis* likely to expand its range?
- What might be the impact on natural stands of *Opuntia* spp. and the other species of plants and animals that depend on opuntias as a resource? What will be the impacts on localized endemic *Opuntia* spp.?
- What will be the impacts on agricultural and horticultural uses of prickly pear?
- If the biological and economic impacts of *Cactoblastis* are substantial, what are possible means of control?
- How will this situation likely affect the science and application of classical biological control?

The workshop was conducted September 20-21, 2000, in Tampa, FL.

Workshop Results

At the conclusion of the workshop four working groups were formed to address research needs, education and outreach, risk assessment and regulatory issues, and international collaboration; the activities of these working groups is ongoing. A white paper detailing the findings and recommendations of the workshop is in preparation; therefore, full details will not be presented here. However, for the sake of completeness of this proceedings, the discussions held at the workshop are summarized below, in the context of the questions posed (above) to address the workshop objectives. For more information, references are provided to the appropriate papers published in this proceedings and elsewhere.

How far is *Cactoblastis* likely to expand its range?

Within 10 years of its first recorded appearance in southern Florida, *Cactoblastis* was known to be established in coastal Georgia (Stiling 2000), a distance of about 650 km. Its natural westward spread has been slower, but there is high potential for rapid spread over large distances by human transport as witnessed by infested nursery stock found at Pensacola.

Opuntia stricta Haworth, a favorable host for *Cactoblastis*, is common throughout Florida and extends westward through the Gulf states to southern Texas and into adjacent Mexico. The species diversity of *Opuntia* increases significantly in Texas, and even more so in Mexico. Soberon et al. (this proceedings) present bioclimatological mapping for the possible spread of *Cactoblastis* through Mexico. Based upon climate and favorable hosts, they conclude that the most likely route of invasion is through Texas. Once in Mexico, the potential area of infestation is sub-

TABLE 1. PARTICIPANTS AT THE *CACTOBLASTIS CACTORUM* WORKSHOP, SEPTEMBER 19-21, 2000, TAMPA, FL.

Name, Title; Area of Interest	Affiliation	Role*
Mohammad H. Badii, Research Professor; biological control	Department of Biology, Univ. of Nuevo Leon, Mexico	IP, P
Duke Benadom, President, Cactus and Succulent Society of America; horticultural applications of cacti	Simi Valley, CA	S
Kenneth A. Bloem, Co-Director, Center for Biological Control; biological control, genetic control	USDA, APHIS, National Biological Control Institute, and Florida A&M Univ., Tallahassee	E, OC, P, S, W
James E. Carpenter, Research Entomologist; genetic control	USDA, ARS, Tifton, GA	P, S
Nancy Coile, Curator of the Herbarium and Botany Administrator; plant conservation	Division of Plant Industry, FL Dept. of Agriculture and Consumer Services, Gainesville	IP
James Cuda, Assist. Professor; biological control of weeds	Dept. of Entomology and Nematology, Univ. FL, Gainesville	E, OC, W
Jordan Golubov, Ecologist; natural resource and conservation biology	Comisión Nacional Para el Conocimiento y Uso de la Biodiversidad (CONABIO), Tlalpan, Mexico	P, S
Doria Gordon, State Ecologist and Courtesy Assoc. Professor; plant conservation	Florida Chapter, Nature Conservancy, and Dept. of Botany, Univ. FL, Gainesville	IP
Marjorie Hoy, Professor; biological control	Dept. of Entomology and Nematology, Univ. FL, Gainesville	S
Mary Irish, Horticulturist and author; landscaping in arid areas	Scottsdale, AZ	P, S
Norman Leppla, Professor; biological control	Dept. of Entomology and Nematology, Univ. FL, Gainesville	OC, S
Daniel L. Mahr, Professor; biological control; Research Chair, Cactus and Succulent Soc. America	Dept. of Entomology, Univ. WI, Madison	E, OC, P, S, W
Lance Osborne, Professor; pest management of nursery and landscape plants	Central FL Res. and Ed. Center, Univ. FL, Apopka	P, S
Robert W. Pemberton, Research Entomologist; biological control	USDA, ARS, Fort Lauderdale, FL	P, S, W
Donald Pinkava, Director of the Herbarium; systematics and biology of the Cactaceae	Dept. of Plant Biology, AZ State Univ., Tempe	P, S
Jackie Poole, Endangered Species Botanist; plant conservation	TX Dept. of Parks and Wildlife, Austin	IP
Mayra Perez-Sandi y Cuen, MacArthur Fellow; conservation, environmental and agricultural protection	San Diego, Churubusco, Coyocan, Mexico	P, S
Peter Stiling, Associate Professor; ecologist	Dept. of Biology, Univ. of South FL, Tampa	E, OC, P, S, W
Jon Rebman, Curator of Botany; biology of desert plants; systematics of Cactaceae	San Diego Natural History Museum, CA	P, S
Ana Lilia Vigueras G., Entomologist; plant protection	Dept. of Botany and Zoology, Univ. of Guadalajara, Mexico	P, S
Helmuth Zimmermann, Research Scientist; biological control	Agricult. Res. Council, Plant Protection Res. Centre, Pretoria, South Africa	P, S

*Roles: E = proceedings editor; IP = invited participant; OC = organizing committee; P = proceedings author; S = speaker or discussion facilitator; W = white paper author.

TABLE 2. AGENDA OF THE *CACTOBLASTIS CACTORUM* WORKSHOP, SEPTEMBER 19-21, 2000, TAMPA, FL.

Session	Presentation or Panel	Speakers
A. Field trip to view damage.		
B. Introduction to the Workshop	1. Introduction and welcome	K. Bloem
	2. Objectives and charge to participants	D. Mahr
	3. The role of the Cactus and Succulent Society of America	D. Benadom
C. The Plant. Biology, Economic Importance, and Conservation Status of *Opuntia*	4. The biology of *Opuntia*	D. Pinkava, J. Rebman
	5. Commercial uses of prickly pear: the nursery and landscape industries	M. Irish
	6. Commercial uses of prickly pear and the impact of *Cactoblastis* in Mexico	J. Golubov, J. Soberon, A. L. Vigueras G.
D. The Insect. Biology and Status of *Cactoblastis cactorum*	7. Biological control of *Opuntia*: a world summary	H. Zimmermann
	8. *Cactoblastis* in the Caribbean: history and impact—open discussion	Participants
	9. Biology, host range, distribution, and impact of *Cactoblastis* in Florida	P. Stiling
E. Panel Discussions	10. Potential impact of *Cactoblastis* on *Opuntia* and its environment	M. Irish, J. Rebman, P. Stiling, A. L. Vigueras G.
	11. Potential impacts of *Cactoblastis* on the practice of biological control	K. Bloem, M. Hoy, D. Mahr, H. Zimmermann
F. *Cactoblastis* Management Strategies	12. Host range testing and risk assessment in biological control—past and future	M. Hoy
	13. Potential for biological control of *Cactoblastis*	R. Pemberton
	14. Insecticidal controls	L. Osborne
	15. F_1 sterility: applications for research and management	J. Carpenter, K. Bloem
	16. Discussion session: should we embark on classical biological control of *Cactoblastis*?	Moderator: K. Bloem
	17. The proposed FAO *Cactoblastis* awareness program in Mexico	M. Perez-Sandi y Cuen
G. A Plan for *Cactoblastis*	18. Where to from here? A working session	Facilitator: N. Leppla
	19. Concluding comments	D. Mahr

stantial (see maps in Soberon et al., this proceedings). Similar predictive bioclimatic modeling has not been conducted for the U.S. Although *Opuntia* is native to most contiguous U.S. states (with the exception of the far Northeast), the northern distribution of *Cactoblastis* will likely be restricted by winter minimum temperatures. Further, its success in the hottest and most arid areas of the desert Southwest may be restricted by climatic conditions.

A recommendation of the workshop is that bioclimatic modeling be conducted to determine areas of the U.S. most likely to be successfully colonized by *Cactoblastis*.

What might be the impact of *Cactoblastis* on natural stands of *Opuntia* spp. and the other species of plants and animals that depend on opuntias as a resource? What will be the impacts on localized endemic *Opuntia* spp.?

Host plant testing of *Cactoblastis* has been minimal and information is primarily from observations of species attacked in its native habitat or from areas of biological control programs. Novel hosts are readily attacked, but not all prickly pears are susceptible. It does not generally utilize chollas (the cylindropuntia group of *Opuntia*) but is known to occasionally infest *O. imbricata* (Haworth) De Candolle in South Africa. *O. imbricata* is an abundant native arborescent cholla in the southwestern U.S., from Colorado in the north southward to central Mexico (Benson 1982) (see Soberon et al. 2000, and this proceedings, for a review of host information).

In many arid areas opuntias are dominant components of the plant community. They provide food and moisture for herbivores, and shade, shelter, and nesting sites for a variety of vertebrates and invertebrates. Although it is thought that the ecological roles played by opuntias in natural environments are very important, there is relatively little quantitative data on the subject (but see references in Soberon et al. 2000, reprinted in this proceedings). Therefore, it is difficult to predict the potential impact of *Cactoblastis* on the total biotic environment.

Some species of *Opuntia* are localized endemics that could be severely affected by *Cactoblastis*. Studies of the impact on and protection of one such species in the Florida Keys, *O. corallicola* Small, are presented in this proceedings by Stiling and Moon. There are at least six taxa of *Opuntia* in Texas that have very localized distributions and therefore would be especially vulnerable to *Cactoblastis* parasitism (J. Poole, pers. comm.).

One recommendation of the workshop is that documentation be developed on localized endemic and/or threatened species of *Opuntia* in the United States and Mexico. Another recommendation is that studies be conducted to determine the importance of the ecological roles of prickly pears in natural environments. These baseline studies must be conducted prior to further expansion of the range of *Cactoblastis*.

What will be the impacts of *Cactoblastis* on agricultural and horticultural uses of prickly pear?

Papers by Vigueras G. and Portillo, and Soberon et al. (this proceedings) fully document the extent of the prickly pear industry in Mexico. Over 30 species of *Opuntia* are used in Mexico for human food or livestock feed. Over 3,000,000 ha are harvested; of this, over 200,000 ha are cultivated on family farms or commercial plantations, with the remainder of production originating from natural stands. The average income generated by prickly pear products in Mexico averaged about $50 million/yr annually through the 1990s. Although some of the commercially-used Mexican opuntias are known to be susceptible to *Cactoblastis*, most uncultivated but utilized species have not been tested.

In addition to the likely loss of an important food crop, there would be sociological consequences resulting from *Cactoblastis* damage. There are nearly 30,000 producers of prickly pear for fruit and vegetable use. In some areas, this is the only viable agricultural crop and revenues are important. Further, because prickly pear is such an important subsistence crop in many areas, loss of this food source would have substantial dietary impact on local residents.

There is a prickly pear food industry in the U.S. as well, but we were unable to gather information on its extent or value. However, we assume that the U.S. industry would also be affected by *Cactoblastis*.

Irish (this proceedings) documents the importance of prickly pear cacti as landscape plants in the arid Southwest. Arizona nurseries alone maintain an inventory of over a half million plants with a retail value approaching $10 million. It is not known what the impact of *Cactoblastis* may be on some of the commonly cultivated species, but the impact on the nursery industry and the ornamental landscape could be significant.

One recommendation from the workshop is that extensive host testing be conducted. Species tested should include those that are used for agricultural and horticultural purposes, those that are dominant components of natural ecosystems, and localized endemics that could be seriously affected by the introduction of *Cactoblastis*.

If the biological and economic impacts of *Cactoblastis* are substantial, what are possible means of control?

Cactoblastis is not the only insect pest of cultivated and wild *Opuntia*. Badii and Flores (this proceedings) summarize other insects that sometimes must be controlled in prickly pear cultiva-

tion. Both mechanical and chemical controls are employed. Because Mexican growers are already familiar with certain insecticide products, appropriate choices could be evaluated for use against *Cactoblastis*. Leibee and Osborne (this proceedings) summarize additional information on potential insecticides for use against the cactus moth. However, chemical control will not be a practical or an environmentally responsible practice for protecting the millions of hectares of natural *Opuntia* vegetation. Further, it may be difficult to provide adequate pesticide safety training to subsistence growers and users of prickly pear.

Carpenter and colleagues (papers in this proceedings) report on the potential usage of F_1 sterility to eradicate localized infestations and manage the spread of *Cactoblastis* and suggest potential uses of this technology for research purposes. F_1 sterility has the advantage of being species-specific and therefore environmentally friendly, and research on its potential use in reducing the rate of spread of *Cactoblastis* needs to be accelerated. However, F_1 sterility is not self-sustaining and, for practical and economic reasons, unlikely to be used over the millions of square kilometers likely to be ultimately infested with *Cactoblastis*.

Biological control of *Cactoblastis* would, on the surface, seem to be an ironic but logical solution to this problem; papers by Pemberton and Cordo (this proceedings) thoroughly examine this possibility. Several natural enemies of *Cactoblastis* are known, but a thorough search through its large native range has not been conducted. Most of the known natural enemies are generalists and therefore pose potential risk to several native pyralid moths that use *Opuntia* throughout North America. It is possible that these native pyralids may be regulating certain *Opuntia* spp. sufficiently to preclude them from becoming weedy pests, and introduced *Cactoblastis* natural enemies could conceivably upset any such relationships.

However, biological control is the only self-perpetuating control option as well as the only practical approach that might be useful in protecting opuntias in their vast native habitats; if biological controls are not available, we are resigned to accept the alternative environmental impacts that will result. Therefore, when considering arguments against the use of oligophagous natural enemies, it is imperative to also consider the consequences of not using them.

Education is an important component of pest management. Mexican scientists have submitted a proposal to FAO for funding a project on multiple aspects of dealing with *Cactoblastis*. One of the proposed components is educational, which will include printed media and radio and television programming for the general public, and also target cactus societies, cactus farmers, agricultural authorities, extension personnel, and the conservation community (Perez-Sandi y Cuen, this proceedings). No similar coordinated educational activity is underway in the U.S. Indeed, before being invited to the workshop, the environmental and horticultural communities in the U.S. Southwest were unaware of the impending threat of *Cactoblastis*.

The workshop resulted in the following recommendations regarding potential control methods.

Insecticidal controls must be explored. In addition to efficacy, studies must also be conducted on phytotoxicity (some insecticide solvents are known to be phytotoxic to cacti) and residual persistence that could be hazardous to consumers of treated fruits or stems. Application methods and timing must also be researched.

Research on F_1 sterility and its application to slowing the rate of spread of *Cactoblastis* must be accelerated.

Research must be conducted to determine the presence of specialized natural enemies of *Cactoblastis*, and to evaluate their potential for use in a classical biological control program. Also, research should be conducted on the possible environmental implications of releasing generalist natural enemies, should specialists not be found. Research must also be conducted to firmly establish the importance of opuntias in fragile arid environments; only with such information can the costs and benefits of classical biological control be fully evaluated.

It is imperative that an educational program be initiated immediately. Target audiences should include agricultural inspectors, extension personnel, the nursery industry, cactus and succulent societies, conservation groups, and the general public. Key target states should include Florida, Georgia, Alabama, Mississippi, Louisiana, Arkansas, Oklahoma, Texas, New Mexico, Colorado, Utah, Nevada, Arizona, and California.

How will the *Cactoblastis* situation likely affect the science and application of classical biological control?

This is a complex question without easy answers. The extent of the impact of *Cactoblastis* on biological control will likely ultimately depend on the extent of its impact on opuntias. Since Howarth's (1991) review article on the environmental impacts of biological control, there has been increased scrutiny of the science in general as well as specific projects. An easy explanation for the release of *Cactoblastis* onto Nevis is that the world was a different place 40 years ago, and societal priorities were more on protecting our food supply than on preserving biodiversity. Today, both ecologists and biological control researchers understand the need for selecting specialized natural enemies in biological control programs. What is less obvious is how to make de-

cisions when a pest is having a major impact in agricultural or natural environments, and the only natural enemies available are not strictly monophagous. In today's world, it is unlikely that *Cactoblastis* would be released onto Nevis, regardless of the degree of weediness of the native opuntias. However, given the potentially serious degradation of natural environments that could be caused by *Cactoblastis*, it is less obvious whether or not to use oligophagous natural enemies for classical biological control of the cactus moth. It is unproductive to condemn historical events that were perfectly acceptable within societal views of the day. But today it is incumbent upon the discipline of biological control to fully consider environmental (i.e., non-target) outcomes of a project. What we do not have is an adequate decision-making mechanism to weigh the risks vs. the benefits of both environmental and socioeconomic impacts of biological control projects that necessitate the use of natural enemies that are not strictly monophagous. This is very important because relatively few natural enemies of insects or weeds are strictly monophagous. The workshop participants agreed that an appropriate approach to *Cactoblastis* is to consider the use of biological control, but to do so in a fully informed context. This will require a concerted research program as outlined above. Such a project would be greatly facilitated by a decision-making process that currently is not provided by the U.S. Department of Agriculture. Further, research on the classical biological control of *Cactoblastis* should be conducted as a project of international cooperation, with collaboration between the United States, Mexico, and other affected countries.

A note on the sequence of papers in this proceedings will be helpful. The first two papers deal exclusively with the host plant, *Opuntia*: Rebman and Pinkava give a thorough summary of the biology and systematics of the group and Irish discusses the uses of prickly pear cacti as landscaping plants and as a nursery crop in the southwestern United States. The next four papers deal with the uses of prickly pears in Mexico and the potential threat of *Cactoblastis* to natural populations and cultivated plantings: Soberon and colleagues review the importance of *Opuntia* and provide results of research models to predict invasion by *Cactoblastis* to and spread within Mexico; Vigueras G. and Portillo provide specific information on opuntia uses; Perez-Sandi y Cuen outlines a Mexican proposal to deal with the impacts of *Cactoblastis*; and Badii and Flores discuss other pests of prickly pear and the chemical and nonchemical means used to control cactus pests in Mexico. The following six papers deal with aspects of research on *Cactoblastis*: Stiling and Moon discuss work on protecting rare Florida cacti; Leibee and Osborne suggest areas of chemical control research; Pemberton and Cordo present two papers on biological control; and Carpenter and colleagues discuss the application of F_1 sterility. The final paper is a reprint of the overview of *Cactoblastis* and its impacts in North America by Zimmermann and colleagues.

In summary, *Cactoblastis* has the potential to be devastating to fragile arid environments in the United States and Mexico by the destruction of its *Opuntia* hosts. Localized endemics may be especially impacted. Further, *Cactoblastis* may have severe socioeconomic implications in rural Mexico where opuntias are both a subsistence food and a unique desert-adapted cash crop. Although the destruction of landscape and nursery plants in the arid Southwest may be less traumatic than the loss of food, we are still facing potential losses to *Cactoblastis* of many millions of dollars annually. Workshop participants are hopeful that cooperative state, national, and international programs can be launched to be proactive in addressing this problem.

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OPUNTIA CACTI OF NORTH AMERICA—AN OVERVIEW

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ABSTRACT

The Cactaceae are a diversified group of New World plants with a wide array of evolutionary and ecological strategies that has given them the ability to adapt to many different habitats. The family is both interesting and challenging because of its varied morphology, adaptations to the environment, and reproductive systems. Of the groups within the cactus family, the opuntias are one of the most successful and widespread, but they exhibit many taxonomic difficulties and are, therefore, not well understood.

Key Words: Cactaceae, taxonomy, diversity, adaptation, reproductive strategies

RESUMEN

Las cactáceas son un grupo de plantas muy diversificado con una impresionante colección de estrategias evolutivas y ecológicas que les ha dado la habilidad de adaptarse a muchos hábitats diferentes en el nuevo mundo. Esta familia es interesante y desafiante debido a su variación morfológica, diversas adaptaciones al medio ambiente, y a sus sistemas de reproducción. Dentro de los grupos de la familia de las cactáceas, las opuntias son de los más exitosos y ampliamente distribuidas, pero presentan muchas dificultades taxonómicas y por lo tanto no son del todo entendidas.

The Cactaceae are an exciting and challenging group of plants because of their varied morphology and succulence, their showy flowers, their adaptations to the environment, and their reproductive strategies. The family has ca. 1600 species in ca. 115 genera (Barthlott & Hunt 1993). Cacti occur naturally from just south of the Arctic Circle in Canada to the tip of Patagonia in South America. Native cacti are restricted to the New World, except for one species, *Rhipsalis baccifera* (Miller) W. T. Stearn or mistletoe cactus of tropical Americas, which prehistorically migrated to Africa, Madagascar and Ceylon (Barthlott 1983). The sticky small fruits of *R. baccifera* were presumably carried across the Atlantic Ocean by birds.

Cacti grow at altitudes from below sea level (e.g., at Death Valley, CA) to over 4,500 m in the Andes; and in climates having no measurable rainfall to more than 500 cm of annual precipitation. Cacti vary in size from that of a large marble to as tall as 20+ m and weighing several tons.

There are three centers of cactus diversity: (1) central Mexico, from where the North American cacti have evolved, 2) the Andean region, and 3) Brazil. The dispersal of species radiating from these three centers has overlapped very little, except for human introductions. There is a subcenter extending from northern South America, northward through the Antilles and West Indies to Florida. The origin of all cacti is probably in South America, perhaps 90-100 million years ago (Gibson & Nobel 1986). However, there are no fossil records known beyond the desert packrat (*Neotoma* sp.) middens of the Pleistocene (McCarten 1981).

TAXONOMY

The discovery of betalains in cacti helped taxonomists understand the phylogenetic position of the Cactaceae. Betalains are reddish pigments found in a small, related group of families in the order Caryophyllales (Carnations order). Other flowering plants have similarly colored pigments called anthocyanins, which are synthesized via a different chemical pathway. Betalains get their name from red beets (the genus *Beta* in the Chenopodiaceae), which are red in color due to the presence of the betalain, betanin. Certain betalains are responsible for the red to purple prickly-pear pads, particularly when under stress as in *Opuntia macrocentra* Engelmann. The Cactaceae were once classified near the carrot family (Apiaceae), but now the family is placed in a very different order, the Caryophyllales, along with the only other betalain-producing angiosperm families, Achatocarpaceae, Aizoaceae, Amaranthaceae, Basellaceae, Chenopodiaceae, Didieriaceae, Nyctaginaceae, Phytolaccaceae, and Portulacaceae (Cronquist 1988).

Barthlott (1988) presented a phylogeny of the Cactaceae. There are three subfamilies of cacti—the phylogenetically basal Pereskioideae, the

Opuntioideae (the subfamily we are specifically interested in for this symposium), and the most derived and speciose Cactoideae, comprising some 80% of all cacti. The greatest diversity of cacti is in South America.

The Opuntioideae differ from all other cacti in having glochids (small, barbed, and deciduous spines) and seeds that are completely enwrapped by a funicular stalk, which becomes hard and bony. The largest genus in this subfamily is *Opuntia*, and in its very broad sense numbers perhaps 200 species (Barthlott & Hunt 1993).

The opuntias (representatives of the subfamily Opuntioideae) of the United States total 5 genera, 61 species, 18-20 additional varieties and many interspecific hybrids (Pinkava, ined.). The true chollas (*Cylindropuntia*, Fig. 1) have cylindric stem segments and completely deciduous spine sheaths. *Cylindropuntia* has 20 species, six additional varieties and at least nine named interspecific hybrids in the United States. The club-chollas (*Grusonia*, Fig. 2) are low mat- or clump-formers with cylindric to spheric stem segments having spines with only the tips being sheathed. In the United States, there are eight species and one interspecific hybrid of club-chollas. The prickly-pears (*Opuntia sensu stricto*, Fig. 3) have mostly flattened stem segments and are completely without spine sheaths. There are 31 species, 12-14 additional varieties and at least seven named interspecific hybrids in the United States alone.

Two other genera of the Opuntioideae, *Nopalea* and *Consolea*, are found only in Florida in the United States. *Nopalea* (Fig. 4) has a flower modified for hummingbird pollination. The flower is somewhat tubular in shape with red to orange tepals that are almost completely closed, but with protruding stamens and stigmas. The *Nopalea* flower also has a nectar chamber covered by an extension of the style near its base. Just one species (*N. cochinellifera* (L.) Salm-Dyck) is found in the United States and has naturalized from cultivation in central Florida. The genus *Consolea* (Fig. 5), has short, orange to red, slightly bilaterally symmetric flowers, with wide-opening petals and a nectar chamber similar to that of *Nopalea*. There is one species in the United States, the nearly extinct native *C. corallicola* Small from the Florida Keys, a species of special concern in this symposium.

Ecology

Opuntias, and cacti in general, are widespread and have adapted to many diverse habitats. One hypothesis is that they occupy areas where there is little competition from other plants, particularly when growing under extreme conditions. In

Fig. 1. Example of *Cylindropuntia*, *C. spinosior* (Engelmann) Knuth, the cane cholla.

Fig. 2. Example of *Grusonia*, *G. kunzei* (Rose) Pinkava, the Kunze club-cholla.

the United States, opuntias occur commonly in all four North American deserts: Chihuahuan, Sonoran and Mojave hot deserts and the Great Basin cold desert. In respect to the opuntias, prickly-pears, for example, thrive in arid, shallow and well-drained soils, but also on over-grazed sites and other disturbed areas, many attributable to human activities. In general, the greater the habitat disturbance the less the plant competition, but if too severe, of course, cacti also disappear. Cacti also do well in dry, tropical deciduous forests where there is little shade much of the year because of leaf-drop, even though the competing plants are close together. Epiphytic cacti, which are found mostly in the wet tropics, grow in open areas on branches of trees. Their roots are kept relatively dry in the open air or in a scanty substrate. All cacti require good drainage; long term accumulation of water is detrimental to them. But, cacti can do well and grow faster under hydroponics, if well aerated.

Cacti utilize high PAR (Photosynthetically Active Radiation) (for details see Gibson & Nobel 1986). They do poorly and etiolate rapidly in shade. However, shade is beneficial and often necessary during the critical stages of germination and juvenile development, such as when growing in association with nurse plants. Some cacti, e.g., the saguaro (*Carnegiea gigantea* (Engelmann) Britton & Rose) often outgrow, even outlive, these nurse plants.

MORPHOLOGY

The morphology of cacti is often, at first, bizarre-looking, but close study reveals only an exaggeration of well-known features. All cacti have alternate leaves along the axis of a long-shoot/short-shoot growth pattern. As is true for virtually all plants, there is an axillary bud at the upper leaf base; however, in cacti this bud barely elongates and is called the short-shoot or areole.

In prickly-pears, the long-shoots are the pads (stem segments also called cladodes) and the fruit coverings (pericarpels). Each pad, in its first year only, produces areoles with subtending conic leaves (Fig. 6). The short-shoot areole produces leaves modified into spines of two kinds—permanent spines with their bases embedded in cork (those which can puncture your finger but remain on the plant) and small, barbed, easily dislodged glochids (those which break off easily and stay with your finger). Hormone concentrations during the very early development of the spine determine if it will be a regular spine, a glochid, or something intermediate between these structures which is rare in nature (Mauseth & Halperin 1975). Spines are produced from the short-shoot areole spirally

Fig. 3. Example of *Opuntia*, *O. basilaris* Engelmann & Bigelow, the beavertail prickly-pear.

from its margin to its apex. Spines elongate from the base and are larger in diameter at the base, but cells within the spine die from the apex to the base. The microscopic barbs of the glochid tip are created when an epidermal cell overrides the epidermal cell below it (Robinson 1974). The base of the glochid has an abscission layer (thin-walled cells) that is easily broken by contact. Short-shoots (areoles) also, on occasion, produce long-shoots including branches and flowers.

Tubercles (or podaria) are swellings below the conic leaves of the pad (long-shoot). The upper part of the conic leaf is the blade, which abscises in a week or two at a notch. The leaf base, or petiole, and adjacent stem tissues are fused together forming the tubercle. The tubercle may elongate and swell such as in species of pincushion cacti (*Mammillaria* spp.). If the raised tubercles align vertically around the stem they can coalesce with those directly above and below forming ribs, like those of the saguaro.

The flowers of cacti are quite variable, but there are some general features that are shared by the whole family. The ovary of the flower (the ovule-bearing part of the pistil) is completely embedded within the stem—a modified pad or long-shoot. Non-cactus flowers are positioned on top of the stem and vascular strands (veins) enter from the stem below. However, cactus flowers have veins from the surrounding stem that enter at the top and sides of the ovary, split and extend upward into the style and downward toward the ovules of the ovary. This unique vasculature provides evidence as to the derivation of the inferior ovary of a cactus flower from a stem that protrudes outward and engulfs the ovary. What is generally called a "fruit" is actually a fused combination of long-shoot coverings (technically called pericarpels) and the true botanical fruit, the mature ovary. So, when we eat the fleshy fruits of prickly-pears, called tunas, we are eating primarily stem tissue (after removing the glochids and spines, of course). Because the pericarpel is composed of stem tissue, it, like a first-year regular pad, produces conic leaves and areoles on its sides that, in turn, produce glochids and sometimes spines, or even flower buds.

Adaptations

Cacti have no escapability and therefore are subject completely to their environs. Two major problems exist for cacti, particularly those in arid climates: temperature extremes and lack of available water. However, several adaptations allow them to cope with these difficulties.

Freezing temperatures in the United States limit distributions by destroying the growing api-

Fig. 4. Example of *Nopalea*, *N. auberi* (Pfeiffer) Salm-Dyck, the lengua de vaca.

cal meristems (stem tips) of many cacti at the northern edges of their ranges and on northern north-facing slopes. This freezing effect may be moderated somewhat by stem tips having protection via pubescence and/or spines or by having depressed summits.

High temperature effects may be reduced by evasion from direct insolation by tilting toward the sun such that only the smaller top surface gets direct sun and not the sides, e.g., barrel cacti (*Ferocactus* species); or by an orientation of pads of prickly-pears such that minimal surface area (at edges of, not faces of pads) is exposed to direct sunlight during the hottest periods of the day. Water is conserved by a reduction of leaf surfaces from broad blades to spines and the reduction of stem surface area by having an efficient shape in relation to surface area/volume ratios, such as in barrel and globular cacti. Also, there is shading of surfaces by pubescence and/or spines and by the formation of ribs and elongate tubercles. A specialization of prickly-pears in Arizona is a metabolic shutdown (aestivation, similar to hibernation), which occurs during non-growing seasons so that only minimum metabolic maintenance takes place (Nisbet & Patten 1974).

Water absorption from rainfall is maximized in most cacti by the presence of a shallow, widespread root system, which often extends out several feet from the main plant body. Cacti also quickly produce tiny "rain roots," which efficiently absorb water after rains, but which quickly die when water is no longer available. The retention of water within the cactus is enhanced by lowering transpiration rates via: 1) having leaves reduced to spines which lowers surface area; 2) having a heavy wax coating (cuticle) on surfaces, impeding direct water loss to the atmosphere; 3) having daytime closure of stomata; and 4) being succulent wherein water adheres to complex carbohydrates called mucilage. Mucilage holds water very tightly, requiring energy to free the water. In some cacti, ribs allow the stems to expand and contract like the pleated part of an accordion both daily and seasonally, allowing for gains and losses of water. Cacti also conserve water by quickly sealing any breaks in the stem's surface caused by animals, humans, or weather. Szarek (in Gibson and Nobel 1986) experimented with a teddybear cholla (*Cylindropuntia bigelovii* (Engelmann) Knuth) by severing it from its base, then tying it to a ring stand in the desert. It survived three years without any contact with the soil. The scar tissue that formed where the plant was cut quickly cut off the loss of water.

Crassulacean Acid Metabolism (CAM) provides a method for photosynthesis to occur while stomata are closed during the daytime. This tim-

Fig. 5. Example of *Consolea*, *C. falcata* (Ekman & Werdermann) Knuth.

ing of stomatal opening is common in cacti and other succulents but is the reverse of most other plants. In CAM, the stomata open at night, allowing for the exchange of gases when temperatures and transpiration rates are lower. Incoming CO_2 is converted to stored malic acid in the cells during nighttime. The next day, the malic acid is converted back to CO_2, which can then be used to carry out photosynthesis and the making of carbohydrates using light energy.

As a result of these adaptations, cacti thrive in arid environments. They have adapted well to the extremes of their physical surroundings and have the morphology and physiology to survive these environmental adversities.

Reproductive Strategies of Opuntioid Cacti

The opuntioid genera have evolved rapidly and successfully by taking advantage of a combination of several reproductive strategies: 1) sexual reproduction which promotes active gene exchange and helps to maintain genetic variability, including the development of dioecy and gynodioecy that increases outcrossing and the genetic diversity of populations; 2) cloning via vegetative propagules such as detached stem segments and fruits, and via sprouting from roots or non-sexual seeds; 3) polyploidization allowing for additional DNA that can, in turn, mutate providing genetic novelties and yet maintain the status quo in unchanged genome copies; 4) interspecific hybridization allowing for the exchange of genes between once genetically separated or partially separated populations via hybrid fertility.

Flowers in the Cactaceae are usually perfect, containing both functional pistils and stamens. Such flowers can either outcross with other individuals or be self-fertile and pollinate themselves (del Carmen Mandujano et al. 1996; McFarland et al. 1989; Osborn et al. 1988; Ross 1981). However, a very limited number of cacti have been reported to be dioecious, androdioecious, gynodioecious, or trioecious (Fleming et al. 1994; Hoffman 1992; Parfitt 1985; Valiente-Banuet et al. 1997). The opuntias have evolved some exceptions to synoecy (= hermaphroditism, having perfect flowers) as well. Within the genus *Opuntia*, Parfitt (1985) documents *O. stenopetala* Engelmann as dioecious (with separate pistillate and staminate individuals). More recently, *Consolea corallicola* was discovered to be cryptically dioecious (with functionally separate pistillate and staminate plants, but appearing morphologically bisexual) (Negron-Ortiz 1998) and five taxa in the genus *Cylindropuntia* (including *C. calmalliana* (Coulter) Knuth, *C. molesta* (Brandegee) Knuth, and *C. wolfii* (Benson) Baker) from southern Califor-

Fig. 6. Long-shoot pad of *Opuntia aurea* Baxter showing the spiral arrangement of short-shoots (areoles) at the bases of conic, long-shoot leaves. Photo by Martin Ganz.

nia and Baja California appear to be gynodioecious (with perfect- and pistillate-flowered individuals) (Rebman 1998).

Asexual reproduction is a common occurrence for many opuntias. The most prevalent type of cloning in this group is vegetative propagation by stem or cladode detachment (Fig. 7). The terminal stem segments of many species (e.g., *Cylindropuntia leptocaulis* (DeCondolle) Knuth, *Opuntia fragilis* (Nuttal) Haworth, and *O. pubescens* Wendland) detach with ease from the parent plant and readily take root creating clonal individuals (Fig. 7). By this mechanism, some opuntias can develop natural populations that appear to be dense monocultures of clonal individuals. Some of these species frequently referred to as "jumping cacti" (e.g., *Cylindropuntia bigelovii, C. fulgida* (Engelmann) Knuth, and *C. molesta*) bear retrorsely-barbed spines on their easily dislodged stem segments and are dispersed by attachment to some mobile vector such as animals. In these taxa, the success of this type of dispersal mechanism may be responsible for much of the species' distributional patterns.

The fleshy fruits of some opuntias, e.g., *Cylindropuntia cholla* (Weber) Knuth and *C. fulgida* can also become vegetative propagules. Since the pericarpel surrounding the ovary is actually stem tissue and has the ability to generate new organs such as adventitious roots and stems, the fruits can drop from the parent plant and develop into clonal individuals.

Another type of asexual reproduction that has been documented in *Opuntia* is adventive embryony (Davis 1966). In this form of vegetative propagation, a diploid mother cell is translocated into the embryo sac and without fertilization develops into a clonal embryo that is produced inside of the seed. Thus, the individual that germinates from the seed is actually a clone of the parent plant.

The high frequency of vegetative propagation in opuntias can help to maintain particular genetic combinations, perpetuate hybrids, develop dense populations, and readily colonize new localities.

Cytogenetic analyses in the Cactaceae have been a very useful taxonomic tool for distinguishing species and documenting natural hybrid populations (e.g., Baker & Pinkava 1987; Pinkava & McLeod 1971; Pinkava & Parfitt 1982; Pinkava et al. 1973, 1985, 1998; Powell et al. 1991). The Cactaceae have a base number of $x = 11$ and polyploidy is the most common type of chromosomal variation, although aneuploidy, secondary association, cytomixis, extranuclear bodies (Ross 1981), inversions (Pinkava et al. 1973), and translocations (Pinkava et al. 1985) have been discovered.

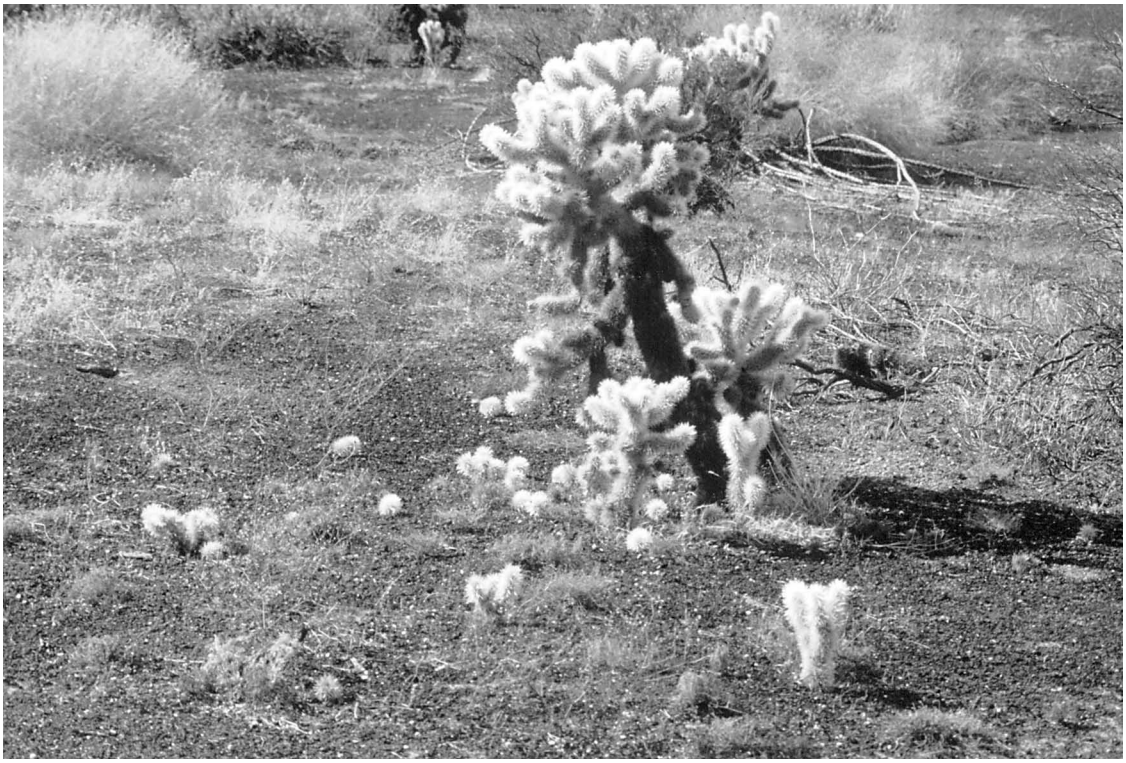

Fig. 7. Young clonal individuals of the teddy-bear cholla (*Cylindropuntia bigelovii* (Engelmann) Knuth) take root near the base of an older plant as a result of vegetative propagation by stem detachment.

Although polyploidy occurs in only about 28% of all cacti investigated thus far, it plays a more important role in the evolution of the subfamily Opuntioideae (64.3%), than in the Cactoideae (12.9%) and the Pereskioideae (0.0%) (Pinkava et al. 1998). The highest levels of ploidy in the opuntioid group occur in the South American taxa—*Austrocylindropuntia* (11*x*), *Miqueliopuntia* (ca. 20*x*), and *Tephrocactus* (30*x*).

According to Pinkava et al. (1998), the origin of most polyploid cactus species is probably from fertilization involving unreduced gametes. This mechanism was determined as the main factor in polyploidization because: 1) macropollen has been found positively staining with cotton blue in diploid species; 2) many opuntioid taxa are both 2*x* and 3*x*, but not 4*x*, suggesting that triploid individuals are produced from the union of a reduced gamete (1*x*) and an unreduced gamete (2*x*) and then reproduce vegetatively, rather than from 2*x* × 4*x* hybridizations; 3) the morphology of interspecific and intergeneric hybrids derived from parents with different ploidy levels show genome dosage effects on character expression, making them more similar to the parent of higher genome dosage than to the parent of lower dosage.

Polyploidy adds supplementary DNA to a species' genome. This process can facilitate the introduction of novel features by mutation without displacing proven adaptations. In other words, polyploidy, as part of an evolutionary mechanism, may help to bring about something new without much detrimental impact. It appears that polypploidy may be one of the main driving factors in the diversification of opuntias due to its common occurrence. This process may also be responsible for some reproductive strategies in the Cactaceae, i.e., gynodioecy and trioecy, since all cactus species determined thus far that stray from synoecy are polyploid.

Hybridization coupled with polyploidy, the perennial habit, and asexual reproduction all play a role in increasing the complexity of the evolutionary processes of the Cactaceae. In our studies of opuntias, intraspecific, interspecific, and intergeneric hybrids have been determined by intermediacy in morphological characters such as flower color and size, fruit shape, texture, and spination; reduced pollen stainability; proximity to putative parents; and overlapping flower phenology. The commonality of hybrid events in many opuntioid taxa blurs species' boundaries and has led to much difficulty in accurately delineating taxa.

Hybrids can be rare and sterile, quite common and self-fertile, or backcross to the parent taxa. The effects of gene introgression between sympa-

tric parental species have allowed certain hybrid genotypes to survive and thrive (Anderson and Stebbins 1954). In cacti, hybridization in association with polyploidy and vegetative propagation may even yield new species able to invade habitats different from both parent taxa, such as for *Cylindropuntia prolifera* (Engelmann) Knuth (Mayer et al. 2000).

Various techniques traditionally employed to help elucidate hybrid events and taxa include morphological studies, chromosome counts, and lactophenol pollen stains. Unfortunately, most of these studies have their limitations when examining very complex hybrid processes. It is hoped that future chemical and molecular analyses will help to unravel and provide much more insight into the reticulate evolution that seems prevalent in the phylogenies of many opuntias.

Taxonomic Challenges

The opuntias have long been a taxonomic problem for a variety of reasons. 1.) Dried specimens of cacti used for morphological studies usually are poorly prepared and many characteristics are lost or altered during herbarium specimen preparation. As a result, type specimens are often inadequate and non-descriptive causing subsequent nomenclatural difficulties (i.e., *Cylindropuntia* typology, in Rebman 1995). 2.) Like all cacti, it is difficult to make good herbarium specimens of opuntias due to all of the cutting, scraping, flattening, and drying that is required. For this reason, many botanists do not collect opuntias and herbarium collections are usually very depauperate in cactus specimens. This oversight creates a lack of distributional knowledge and an incomplete record of morphological variability present in most species, and should be considered one of the biggest limitations to the taxonomic research in the opuntias. 3.) Many vegetative characters can be quite drastically influenced by environmental factors. Morphological features such as growth habit, stem pubescence, spine length and number per areole can be phenotypically plastic and may change significantly depending upon local growing conditions. 4.) Many opuntias hybridize with other sympatric taxa producing novel, combined, or intermediate character states between species which can blur the boundaries between species. 5.) The opuntias can reproduce by vegetative propagation, adventive embryony, and self-fertility. These reproductive mechanisms help to sustain particular genetic combinations, perpetuate hybrids and as a result, create taxonomic enigmas for the systematist. 6.) There is a lack of interest by amateur collectors and hobbyists thus providing little knowledge of species from cultivated plants. 7.) There is a deficiency of detailed botanical investigations (e.g., systematic monographs and population studies) focusing on the various genera within the opuntioid group.

Of the groups within the Cactaceae, the opuntias are an extremely diversified and dominant component in many plant communities found throughout the New World, especially in arid regions. However, they are still one of the least understood groups in the cactus family. Although a lot of recent knowledge has been gained about the opuntioids and their evolutionary and ecological strategies, they are still an enigmatic group. There is no doubt that many discoveries about their natural history and phylogeny which have yet to be encountered will help us to better understand this fascinating and challenging group of cacti.

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THE ORNAMENTAL PRICKLY PEAR INDUSTRY IN THE SOUTHWESTERN UNITED STATES

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ABSTRACT

Several species of prickly pear cacti are grown as ornamental plants in public, private, residential, and commercial landscapes throughout the more arid areas of Arizona, California, Nevada, New Mexico, and Texas. Several commercial nurseries, ranging in size from small family-owned specialty operations to large diversified wholesale nurseries, produce and sell prickly pear cacti. The greatest nursery production occurs in Arizona, followed by southern California. In Arizona, there are over 40 small commercial operations in the Phoenix area alone. A survey of Arizona nurseries revealed an inventory of 550,000 prickly pear plants on hand with wholesale and retail values of $4.5 million and $9.5 million, respectively. If prickly pear cacti were lost as a viable nursery crop, small specialized nursery operations would be more likely to suffer than large diversified nurseries.

Key Words: *Opuntia*, economics, nursery industry, landscaping

RESUMEN

Varias especies de cáctus del género *Opuntia* se usan como plantas ornamentals en la jardinización de areas públicas, privadas, residenciales y comerciales en areas de clima seco en los estados de Arizona, California, Nevada, Nuevo Mejico y Tejas. Varios viveros comerciales, que varian en tamaño desde pequeños y especializados en Cactaceas a operaciones de tamaño y diversidad vegetal vasta, producen y venden cactus pertenecientes a este género. Los viveros de mayor tamaño se encuentran en el estado de Arizona y en el sur de California. En Arizona en areas cercanas a la ciudad de Phoenix, existen aproximadamente 40 viveros comerciales pequeños. Datos colectados en Arizona indican que hay alrededor de 550,000 plantas de cactus a la venta en viveros con un valor de venta al mayoreo de $4.5 millones y de venta al público de $9.5 millones de dólares. Cualquier amenaza a esta industria hortícola de cactus resultaria no solo en pérdidas grandes para el sector comercial sino también en la reposición de plantas que se usan corrientemente en areas jardinizadas. Si la venta de plantas de cactus se viera severamente restringida, los viveros pequeños y especializados en estas plantas serian afectados mas severamente que los viveros comerciales.

Many species of prickly pear cacti (*Opuntia*: Cactaceae) are used as ornamental plants in the southwestern United States (Mielke 1993; Irish 2000; Jones and Sacamano 2000). These plants are prominent parts of the ornamental flora of Arizona and Nevada and are found in varying degrees in California, New Mexico and Texas. Prickly pear cacti are commonly used landscaping plants on both residential and commercial properties. The common ornamental species are desert prickly pear (*Opuntia phaecantha* Engelmann and *O. engelmannii* Salm-Dyck), purple prickly pear (*O. violacea* Engelmann), beavertail prickly pear (*O. basilaris* Engelmann & Bigelow) and Indian fig prickly pear (*O. ficus-indica* (L.) Miller). Less abundant, but widely available are bunnyear prickly pear (*O. microdasys* (Lehmann) Lehmann) and chenille prickly pear (*O. aciculata* Griffiths). In addition, there are numerous hybrids, varieties, and unnamed forms of these species and others grown throughout the region.

Because prickly pears are relatively easy to grow, they are produced in Arizona by a variety of nursery operations. Large wholesale growers with a diverse inventory, small specialty growers, and one-person backyard operations all provide these plants to the public. Only large growers or recognized specialty growers have inventories that are included in published economic surveys. From my experience with the landscape industry, I estimate that there are 40-50 small-scale nurseries producing prickly pear plants in the Phoenix area alone.

MATERIALS AND METHODS

I used two methods to estimate the economic impact of prickly pears on the nursery industry in the southwestern states. The first was an informal telephone survey conducted in fall 2000, among growers in the Phoenix and Tucson areas. The second method was to summarize published economic surveys of the agriculture/horticulture industries for the relevant states.

RESULTS AND DISCUSSION

The telephone survey of Arizona growers revealed that on-hand nursery inventory of landscape prickly pear cacti was approximately

550,000 plants, with wholesale and retail values of $4.5 million and $9.5 million respectively.

In 1998, the entire ornamental landscape industry in Arizona generated sales of $415 million, of which $158 million consisted of plants specifically for arid environments (xeriscape plants) (Payne 1999).

In California, the 1999 total value of all landscape plant production was $2.6 billion wholesale; in 1998, retail plant sales amounted to $5.6 billion (J. A. Wick, Executive Director, California Association of Nurserymen, pers. comm.). Although data specific to cacti are not kept in California, there are approximately 30 specialized growers of cacti (Wick, pers. comm.). Whereas there is a substantial prickly pear nursery industry producing landscaping plants in Arizona, many of the California cactus growers produce potted plants for the gift industry and for cactus and succulent plant enthusiasts; the landscaping component of the California cactus industry is thought to be smaller than that in Arizona.

The total 1998 value of the Texas nursery industry was $144 million wholesale and $3.7 billion retail (Anon. 1998). There are no specific data for cactus production, but there are several commercial nurseries in the state. There were no data available for the New Mexico and Nevada nursery industries. There are retailers in both states that sell prickly pears for landscaping purposes, but most material is wholesaled from Arizona and California.

As an ornamental plant, prickly pears have more impact on the public and nursery owners than just their immediate monetary value. Many, if not most, cactus growers are small operations, typically with only a few employees. The loss of prickly pear sales would dramatically and adversely impact such businesses, especially in Arizona. While larger growers with a more diverse inventory would also be impacted by a loss of prickly pears, recovery would be more easily absorbed. But the specialty growers of southern Arizona and southern California would undoubtedly be unable to shift crops quickly enough to sustain such as a loss. If prickly pears were lost as viable landscape material, I expect that many of these small businesses would fail.

There is also the danger of the loss of confidence in a plant by the public. Once plants are seen to be problematic, such as being high-maintenance or prone to pests or disease, they quickly lose favor with the public. Unfortunately, most of the public would be content to just quit having cacti in the landscape, rather than maintain any kind of pest control monitoring or management. This reluctance, and the perception of difficulty associated with the affected prickly pears, could impact the industry just as severely as the actual loss of plants.

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THE IMPORTANCE OF *OPUNTIA* IN MEXICO AND ROUTES OF INVASION AND IMPACT OF *CACTOBLASTIS CACTORUM* (LEPIDOPTERA: PYRALIDAE)

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ABSTRACT

The appearance of the cactus moth *Cactoblastis cactorum* in Florida has roused concern over its possible effects on the *Opuntia*-rich areas of Mexico and the southwestern United States. In this paper we discuss the economic importance of *Opuntia* in Mexico and propose a method to predict the invasion of the alien species *C. cactorum*. In Mexico, the products derived from *Opuntia* are mainly human food and fodder for livestock. Both cultivated and wild populations of *Opuntia* are currently used for these two purposes. By using bioclimatic modeling, we predicted the potential distribution of *C. cactorum* and overlaid this on the actual distribution of *Opuntia* species. The resulting maps indicate that the possible routes of invasion to Mexico are 1) along the northern border through Texas (most likely) and 2) via southeastern Mexico (less likely). The impacts of an invasion of *C. cactorum* on *Opuntia* products could be significant as well as being a threat to endemic species. Bioclimatic modeling can help to predict the areas of highest probability of attack and facilitate planning to mitigate future impacts.

Key Words: bioclimatic modeling, GARP, FloraMap, cactus

RESUMEN

El uso de agentes de control biológico y sus efectos sobre especies nativas ha generado polémica. La invasión de la palomilla del nopal al continente norteamericano ha provocado preocupación acerca de la posible introducción de esta especie exótica a zonas de alta riqueza de *Opuntias* endémicas de México. En este trabajo hacemos énfasis en la importancia económica de los productos de *Opuntia* en México y proponemos un método que predice la invasión de *C. cactorum*. Usamos modelos bioclimáticos para generar las distribuciones potenciales de *C. cactorum* y especies de *Opuntia*. Los mapas resultantes permiten predecir la ruta de invasión de la palomilla del nopal al territorio Mexicano. Los mapas de probabilidad generados por FloraMap sugieren dos posibles rutas de invasión, la primera con alta probabilidad vía la frontera norte del país en Texas y una ruta secundaria por el Sureste mexicano. El impacto de *C. cactorum* y el potencial de los modelos bioclimáticos son discutidos.

The textbook example of successful biological control, the moth *Cactoblastis cactorum* (Berg) on *Opuntia* species in Australia, has now become a problem of major concern for continental North America (e.g., Zimmerman et al. 2000). The consequences of the arrival of *C. cactorum* on the *Opuntia* rich regions of the southwestern U.S. and Mexico, as well as the possible economic and social impact on Mexican urban and rural human populations has only recently been addressed (Zimmerman et al. 2000). The purpose of this paper is twofold. On one hand, it addresses the importance of *Opuntia* products in Mexico from an economic and social status, and on the other it proposes a means of modeling the routes of invasion and assessing the areas of Mexico that could be most susceptible to a possible invasion of *C. cactorum*.

THE IMPORTANCE OF *OPUNTIA* IN MEXICO

In present-day Mexico, there is a large array of traditional and commercial uses of *Opuntia* (Platyopuntia: Cactaceae). Historically the hunter-gatherer communities that roamed the southwestern U.S. and Mexico were using products derived from *Opuntia* (mainly forage, fruit and vegetables) in 9,000 BC. The process of domestication of a few species of *Opuntia* may have started as far in the past as 6000 BC (Smith 1967). By 3000 BC, hunter-gatherers settled into small communities, where family owned plots contained species of *Opuntia* that had been collected from wild populations (Hoffmann 1995). During the 1850s *Opuntia* was commonly used in the growing cattle ranching industry of the Sonoran and Chihuahuan deserts which gave way to

an extensive use of *Opuntia* as fodder. Due to the increase in population over the past 50 years, the demand for *Opuntia* products has increased dramatically. As family owned plots were not enough to satisfy demand, plantations were developed surrounding the most important urban areas. There are three main consequences of the use of products derived from the Cactaceae on a large scale: 1) an increase in hybridization between species that were brought in from wild populations to family owned plots, 2) a continuous use of wild populations for forage as well as for vegetables, and 3) a decrease in morphological diversity within plots (Casas et al. 1999) which could eventually lead to a decrease in genetic variation (Colunga-Garcia et al. 1999). However, despite the important commercial aspect of cactus products, the wild populations found around family-owned plots are still used for subsistence in the dry regions of Mexico and represent the transition between the wild and cultivated species, thus making them important gene pools of domesticated varieties.

The genus *Opuntia* is one of the most used plants in Mexico and Central America. Due to the high protein and fiber contents found in cladodes, and the amount of water in tissues (88-91%, Pimienta 1990), the range of uses given to *Opuntia* has been extremely wide, from food to cosmetics and adhesives (Barbera 1995). In Mexico, traditional uses of *Opuntia* vary widely although there are two main products that account for the economical importance of *Opuntia* products: food and fodder (Pimienta 1990; Barbera 1995). Fodder is mainly for cattle and goats in all parts of Mexico. The use of cactus for forage has also been documented in many other parts of the world including the U.S., northern and southern Africa, and several South American countries (Felker 1995). For example, in Brazil close to 300,000 ha are used to produce fodder (Barbera 1995). As food, *Opuntia* can be consumed as vegetables (by dicing young cladodes) or as fruit (cactus pears). Production of fruits is found in 15 out of 32 Mexican states employing close to 20,000 people, whereas use as vegetables is found in 14 states and employs close to 8,000 people. In addition, most rural people use prickly pear products from local wild populations or maintain family-owned plots for self-consumption.

In Mexico there are >250,000 ha of *Opuntia* cultivated for all purposes (Flores-Valdez & Aguirre-Rivera 1979; SAGAR 1995-1998). The area that is used for cultivation of fodder is close to 150,000 ha out of which 500 ha are being used intensively in the state of Jalisco. Most of the area under cultivation is used as forage for cattle farming. These areas are a remnant of areas that were designed to improve carrying capacity of impoverished rural areas during the 1970s and 1980s and were designed to introduce extensive cattle ranching and prickly pear production (Barbera 1995). After the failure of such programs, most of the areas that were cultivated were left behind and are still being used today as forage (Pimienta 1990). Wild *Opuntia* populations are used extensively for fodder and at least 12 species are known to be used as forage (Table 1); this figure is probably conservative as most local wild populations are also commonly being used.

Mexico has the highest variety of cultivated species of prickly pear (8 species and over 11 varieties, Flores-Valdez & Gallegos 1993) and is an important area in Cactaceae biodiversity.

Economically, *Opuntia* products constitute close to 1.5% of total agricultural production and represent 2.5% of the value of agricultural products (SAGAR 1995-1998, Fig. 1). The production of both cactus pears and cladodes used as vegetables have increased over the past eight years (Fig. 2). This increase has occurred primarily because of better management practices (Pimienta 1990); total area under production has not increased to the same degree. The average income generated by *Opuntia* products over the period 1990-1998 is approximately $50 million U.S. per year, with vegetable usage constituting more than half of the value ($27 million), followed by cactus pears ($20 million), and finally fodder ($1 million). In addition, the export market of *Opuntia* products is valued at $50 million per year. Exports are mainly to the U.S., Canada, Europe, and Japan.

In addition to their value to humans, opuntias are common and often dominant components of natural floras, where they have substantial environmental importance. Species of the Cactaceae and specifically those of *Opuntia* are a major ecological component of the floras of the Chihuahuan and Sonoran Deserts (nopaleras). They are a major contributor to soil stability. They constitute an important dietary component of white tailed and mule deer (*Odoicoileus virginianus* Zimmermann and *O. hemoinus* (Rafinesque)), rodents (*Peromyscus* spp., *Neotoma albigula* Hartley and *Dipodomys* spp.), javelinas (*Pecari tajacu* L.), and coyotes (*Canis latrans* Say) (Mandujano et al. 1997; Montiel & Montaña 2000). They also provide nesting sites and food for a variety of insects, birds, rodents, and lagomorphs (Gonzalez-Espinosa & Quintana-Asensio 1986; Russell & Felker 1987).

Mexico has one of the highest species diversity of *Opuntia* and populations cover an area of close to 3,000,000 ha (1.5% of Mexican territory). The numbers of *Opuntia* species varies in the literature, partially because of frequent hybridization between species and the lack of a standardized classification scheme. Bravo-Hollis (1978) recognized 104 species of *Opuntia* in Mexico, 56 of which are in the subgenus *Platyopuntia*, (pricklypears), 38 of which are endemic.

Although some authors have suggested that *C. cactorum* may already be present in southeast-

TABLE 1. SPECIES OF *OPUNTIA* EVALUATED IN DISTRIBUTION STUDY, THOSE USED AS FORAGE OR FOR FRUIT OR VEGETABLES, AND THOSE KNOWN TO BE ATTACKED BY *CACTOBLASTIS CACTORUM*. TAXONOMIC STATUS WAS DETERMINED USING BRAVO-HOLLIS 1978 AND BRAVO-HOLLIS AND SANCHEZ-MEJORADA 1991.

Opuntia sp.	Used as forage	Used as fruit and/or vegetables	Known to be affected by *C. cactorum*
amyclaea		X	
atrispina			
atropes			
azurea	X		
bensonii			
bravoana			
cantabrigiensis	X		
chavena			
chlorotica			
decumbens			
depressa			
dillenii			
durangensis	X		
engelmannii	X		
excelsa			
ficus-indica		X	X
fulginosa			
huajuapensis			
hyptiacantha		X	
jaliscana			
joconostle			
lagunae			
lasiacantha			
leucotricha	X	X	
lindheimeri	X		X
littoralis			
macrorhiza			
megacantha		X	X
megarhiza			
microdasys			
oricola			
pachona			
phaeacantha	X		
pilifera			
puberula			
pubescens			
pumila			
pycnantha			
rastrera	X		
rileyi			
robusta	X	X	
rufida			
spinulifera			
spraguei			
streptacantha	X	X	X
stricta	X		X
tapona		X	
tehuantapecana			
tomentosa			X
undulata			
velutina			
violacea	X		
wilcoxii			
Total	12	8	6

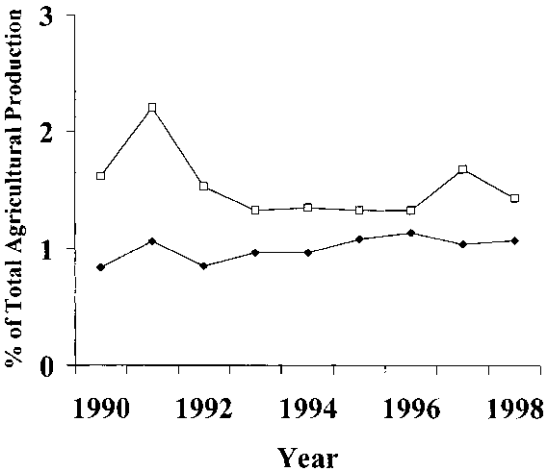

Fig. 1. Percentages of total Mexican agricultural production (closed dots) and value (open dots) of *Opuntia* products occupied by *Opuntia* species between 1990 and 1998.

ern Mexico (Pemberton 1995), we have no direct evidence that it has invaded Mexico to date. However, its movement through the southeastern United States into Mexico is likely.

In order to assess potential impact of *C. cactorum* in Mexico, the second part of this paper presents results of models of possible invasion routes and ultimate distribution.

Modeling Invasion and Distribution of *C. Cactorum* in Mexico

Methods

In order to assess the potential invasion and impact of *C. cactorum* on Mexican species of *Opuntia* we used bioclimatic modeling (FloraMap ver. 1.0, Jones & Gladkov 1999) to predict the distribution of *C. cactorum* as well as model the distribution of *Opuntia* species. FloraMap relies on 36 climatic variables and a principal component analysis for prediction. We used the Smithsonian collection to obtain localities of specimens of *C. cactorum*. The distribution of *Opuntia* species was modeled with GARP (Genetic Algorithm for Rule set Prediction; Stockwell & Noble 1991, Stockwell & Peters 1999; http://biodi.sdsc.edu) that contains databases for North America only. In these models the ecological requirements of a species are key to the inferential portion of the method. The data points used for bioclimatic modeling of *Opuntia* species were taken from herbaria collections (MEXU, ENCB, SD, XAL) as well from the databases collected by CONABIO (http:/www.conabio.gob.mx). Species of *Opuntia* with less than three data points were eliminated from further analyses to avoid sampling bias. Distribution maps generated by GARP were constrained to ecological regions were *Opuntia* species have been recorded, excluding those areas that were predicted by GARP but lacked the presence of *Opuntia* data points (commission error; Peterson and Cohoon 1999). Overlaying all the predicted maps for *Opuntia* we obtained a map of density of species of *Opuntia*. We predicted the potential risk to all species of *Opuntia* that are found in Mexico by overlapping the richness-of-*Opuntia* maps with the predicted distribution of *C. cactorum*.

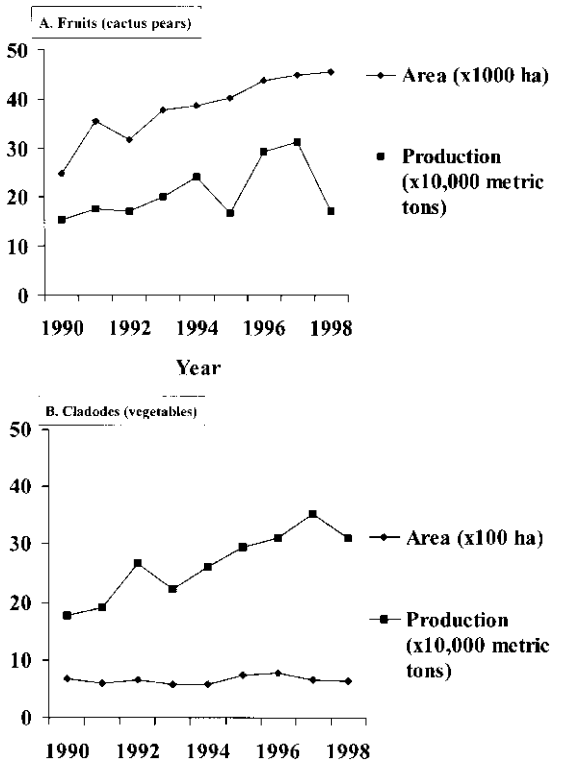

Fig. 2. Production (×10,000 metric tons) and area (×100 ha) under cultivation in Mexico of (A) *Opuntia* fruits (cactus pears) and (B) *Opuntia* cladodes (used as vegetables).

Results

Of the 52 species of *Opuntia* evaluated in this study, 15% (8 species) are known to be attacked by *C. cactorum* and an additional 27% (14 species) are taxonomically related to these 8 species (Table 1). At least four species of economic importance (*O. ficus-indica* (L.) Miller, *O. lindheimeri* Engelmann, *O. streptacantha* Lemaire and *O. stricta* Haworth) are known to be attacked by *C. cactorum* (Table 1).

The potential distribution of *C. cactorum* includes large parts of the southern and southwestern United States. Since *C. cactorum* is already

present and established in Florida, it will probably be just a matter of time for it to get to the Mexican border. In Mexico, the highest suitability areas are found in the east and northeast, with other areas of high probability in the southeast and along the coastal regions. The predicted distribution of *C. cactorum* suggests a higher probability of invasion through the northern border region than along the southeast as has been previously suggested.

The species having the highest risk (those known to be attacked by *C. cactorum*; Table 1) are located in the eastern border regions of Mexico, and are highly concentrated in central Mexico (Fig. 3). Even though there are species of *Opuntia* (*O. stricta* and *O. lindheimeri*) that overlap with the potential distribution of *C. cactorum*, most of the susceptible species of *Opuntia* are concentrated in central Mexico, where the bioclimatic analysis predicts a lower impact of the moth.

About 20% of the predicted distribution range of species known to be attacked by *C. cactorum* overlaps with adequate habitat for the insect (Table 2). If we consider all species of *Opuntia* evaluated in the analysis, the values of overlap increase to close to 50% (Table 2). The areas in the western part of Mexico show some overlap with potential *C. cactorum* distributions, with only a small portion of *Opuntia* species richness overlapping with the predicted distribution of the insect (Fig. 3).

Little is known of the potential for *C. cactorum* to utilize *Opuntia* species not studied, or of its potential to adapt to or survive in various climates. Therefore, the overlap and impact could possibly be greater than predicted.

Discussion

Mexico and the southwestern United States have a long tradition of use and consumption of *Opuntia* species as well as having the highest diversity of *Opuntia* species (Bravo-Hollis & Sánchez-Mejorada 1991) and in Mexico a significant portion of the local and national agricultural economy depends on *Opuntia* resources. Unfortunately, our results suggest that there is a high risk of *C. cactorum* spreading into Mexico from the United States. The establishment of the moth in Mexico is very likely given the large areas of similarity of environmental conditions with those found in its native habitat. The main routes of invasion are concentrated in the northeastern portions of Mexico suggesting a possible invasion through the desert regions of Texas, where species known to be attacked by the cactus moth are present (*O. lindheimeri* and *O. stricta*) and climatic similarity with areas of *C. cactorum* are also found.

The distribution patterns of *Opuntia* species and those predicted for *C. cactorum* show an area of overlap, mainly associated with *Opuntia* species that are susceptible to attack. Although little is known of the potential of *C. cactorum* to adapt to diverse environments, we can assume it to be high, as the moth has been successfully introduced into many areas of the world (Hawaii, the Caribbean region, South Africa and Australia) suggesting that the potential overlap between the insect and native opuntias can increase dramatically. Clearly, diet selection experiments are needed to assess the potential impact of *C. cactorum* on all *Opuntia* species that have not had contact with the moth in order to determine the full potential damage.

The predictions suggest northeastern Mexico as a primary route of invasion, followed by the southeastern areas of Mexico. Efforts towards early detection and containment of the invasion of *C. cactorum* have to concentrate on those two areas of Mexico with special emphasis on areas bordering the species-rich areas of central Mexico. The economic impact that will result from an invasion of the cactus moth cannot be determined

Table 2. Percentage of land area with *Opuntia* species in Mexico and potentially colonized by *Cactoblastis cactorum*. Coverages were developed from bioclimatic modeling with GARP and FloraMap.

Overlap Parameter	Percent of Mexican Territory	
	Species known to be attacked by *C. cactorum*	Total number of *Opuntia* spp. found in Mexico
Suitable for *C. cactorum*, but with no species of *Opuntia*.	32.51	9.85
Suitable for *C. cactorum* and with at least one species of *Opuntia*.	23.75	49.11
Unsuitable for *C. cactorum* and with at least one species of *Opuntia*.	12.79	35.99
Unsuitable for *C. cactorum* and with no species of *Opuntia*.	28.25	5.05

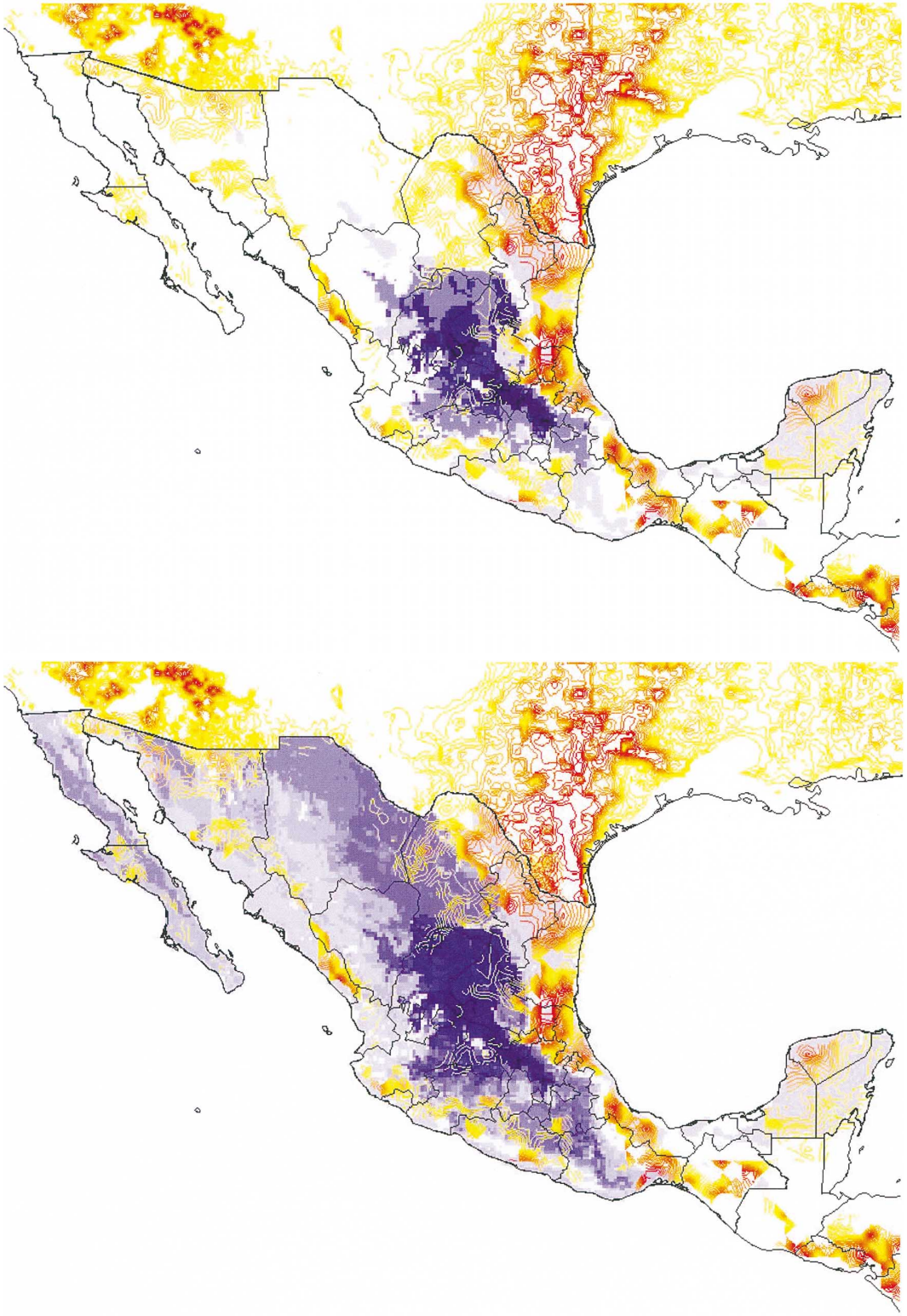

Fig. 3. Overlay of GARP *Opuntia* species distribution predictions (blue) and FloraMap predicted distribution of *C. cactorum* habitat (red). Top: species of *Opuntia* known to be attacked by *C. cactorum*. Bottom: all species of *Opuntia* used in the analysis.

yet, however, given the economic and social importance of *Opuntia* in Mexico we can expect the damage to be significant. Bioclimatic modeling is a valuable tool to predict areas where invasion is likely and can help to provide background information to plan future actions towards mitigating the impact an invasive species such as *C. cactorum* can have on local populations of *Opuntia*.

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USES OF *OPUNTIA* SPECIES AND THE POTENTIAL IMPACT OF *CACTOBLASTIS CACTORUM* (LEPIDOPTERA: PYRALIDAE) IN MEXICO

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ABSTRACT

In Mexico, cactus pears (*Opuntia* spp.) are regarded as very important plants, especially in semi-arid and arid regions where few crops can be cultivated. Historically, Mexicans have used cactus pears for food, as fodder for cattle, for medicinal purposes, in cosmetics, to produce dyes, and as natural fences. Cactus pears are also an important component of native ecosystems. Central Mexico is considered to be one of the main centers of cactus diversity. Approximately 200 species of *Opuntia* are recognized worldwide, 114 of which occur in Mexico. Because most *Opuntia* species are thought to be susceptible to attack by the cactus moth, *Cactoblastis cactorum* (Berg), spread of this moth into Mexico would likely have significant economic and social impacts. A number of the most widely used and/or distributed species, including *O. compressa* Macbride, *O. ficus-indica* (L.) Miller, *O. megacantha* Salm-Dyck, *O. stricta* (Haw.) Haworth and *O. tomentosa* Salm-Dyck, are known hosts of the cactus moth.

Key Words: prickly pear, cactus moth, invasive species

RESUMEN

Los cactus del género *Opuntia* son muy importantes en Méjico especialmente en las areas semi áridas y áridas donde pocos otros cultivos economicos pueden florecer. Historicamente estas plantas han sido utilizadas como alimento, forraje para ganado, en la manufactura de productos medicinales, cosméticos, tintes y como barreras limitrofes naturales. Asimismo, la fruta del cactus (tuna) constituye un importante componente de los ecosistemas naturales en Méjico. La parte central de Méjico se considera como un centro de diversidad para plantas de este género. Aproximadamente 200 especies de *Opuntia* se conocen mundialmente y de estas 114 especies ocurren en esta región de Méjico. Debido a que la mayoria de las especies de este género son suceptibles al ataque por *Cactoblastis cactorum* (Berg) la possible invasión de esta especie de lepidoptero al territorio Mejicano tendría consecuencias muy adversas tanto economicas como sociales. Varias de las especies mas ampliamente distribuidas o utilizadas en la manufactura de alimentos o productos son atacadas por esta especie. Entre ellas se incluyen *O. compressa* Macbride, *O. ficus-indica* (L.) Miller, *O. megacantha* Salm-Dyck, *O. stricta* (Haw.) Haworth y *O. tomentosa* Salm-Dyck.

In Mexico, cacti in the genera *Nopalea* and *Opuntia* are known as "nopal". They belong to the subfamily Opuntioideae and comprise more than 200 species worldwide, 114 of which occur in Mexico (Bravo 1978; Barthlott & Hunt 1993; Guzmán 1997). The nopal are probably among the most versatile cacti in the family, considering their wide geographic distribution and the great diversity of habitats they occupy. They also constitute one of the most valuable natural resources for peasants and farmers in Mexico, being a source of fruit ("tunas") and vegetables ("nopalitos") for human consumption, as well as fodder for cattle and other animals during the dry seasons.

The production of prickly pear in Mexico can be divided into three systems: 1) wild prickly pear; 2) prickly pear on family farms; and 3) commercial plantations of prickly pear for fruit and nopalitos (Flores et al. 1995; Flores 1997). The total area with significant prickly pear production, both wild and cultivated, exceeds 3,000,000 ha (Flores 1997). There are approximately 217,856 ha of commercial production, of which 150,000 ha are used for livestock feed, 56,856 ha for fruit, 10,400 ha for nopalitos (Flores et al. 1995) and about 100 ha for cochineal production (Portillo 1999). From an economic and social point of view, the use of prickly pear is considered a subsistence alternative, providing marginal communities with employment and other benefits (Flores 1997; Flores & Aranda 1997).

USES OF PRICKLY PEAR

Historically, Mexicans have used prickly pear (*Opuntia* spp.) in a number of ways:

1. Fruit. The cactus pear or fleshy fruits called "tunas" are in great demand on the local market, and are exported to the U.S., Canada, Japan, and some European countries.
2. Vegetable. The tender cladodes of certain species are cut up and eaten as a vegetable

called "nopalitos". Because there is an abundant supply of nopalitos throughout the year, they are also used as an ingredient in many traditional dishes.

3. Fodder. Prickly pear is used to feed cows on cattle farms in the north, especially during the dry seasons. The cladodes are first scorched to remove the spines and then chopped up before mixing them into fodder.
4. Medicinal Products. The consumption of nopalitos and the acid fruits (xonostle) of certain species have been shown to reduce blood glucose and cholesterol levels. The plant parts are consumed cooked, in capsules, and in pill form.
5. Agro-industry. Nopalitos are canned and used in a variety of processed foods for the commercial market. The fruit is used to produce marmalade, juice, nectars, pigments, pectin and fructose.
6. Cosmetics. Extracts from *Opuntia* cacti are used to make soaps, body creams, shampoos and cosmetic gels that are said to reduce body fat.
7. Pigments. About 12 *Opuntia* species are used to rear the cochineal insect (*Dactylopius coccus* Costa) for dye production.
8. Fencing. Some of the more spiny *Opuntia* species are used to delimit terrains, family farms and cattle camps. This is an ancient and common activity in Mexico.

In addition to the uses listed above, prickly pears are now being looked at as a potential source of anti-polluting agents to clean dirty water, as a source of oil, and as a mechanism to prevent soil erosion.

Cactus Fruit

There are approximately 24 species of *Opuntia* from which cactus fruit are collected. Table 1 lists some of the more popular species. Most wild fruit is collected from *Opuntia* species in the Streptacanthae series, while most commercial varieties, known as "mansas", are from the Ficus-indicae series. The harvested fruit is eaten fresh and used to produce candy ("queso de tuna"), marmalade ("melcocha") and an alcoholic beverage called "colonche". Demand for the fruit has been increasing steadily since the 1950's, as has been the number of hectares planted to commercial production of the fruit (Flores & Gallegos 1993). The agricultural management of both wild and commercial varieties is to select for fruits that are large, with few seeds and that have a sweet, juicy pulp (SAIMEX 1981).

TABLE 1. MAIN *OPUNTIA* SPECIES UTILIZED FOR THEIR FRUIT.[1]

Species	Common name
O. alfajayuca Haage & Schmidt	Nopal alfacayuca
O. amyclaea Tenore	
O. ficus-indica (L.) Miller	Nopal de castilla
O. hyptiacantha Weber	
O. leucotricha De Candolle	Nopal duraznillo
O. megacantha Salm-Dyck	Nopal tapón
O. streptacantha Lemaire	Nopal cardón
O. tapona Engelmann	Nopal tapón
O. robusta Wendland	Nopal camueso

[1]Flores & Gallegos 1993.

Prickly Pear as Vegetable

Two genera within the Opuntioideae are used for the commercial production of nopalitos: *Nopalea* and *Opuntia*. In particular, there are four species of *Opuntia* that are most commonly used: *Opuntia ficus-indica* (L.) Miller variety Copena VI, developed by F. Barrientos in 1960, is the most sought-after due to its excellent flavor and low acidity; *O. joconostle* Haage & Schmidt has fruits that are used mainly as a vegetable or spice (Sánchez et al. 1990) (Table 2); *O. robusta* Wendland is commercially grown in a small area of the Potosi state tablelands, where the cladodes are sold on the local market and processed for exportation. Currently, *O. atropes* Rose is very popular in the state of Jalisco because local consumers like its flavor and texture. The exact area planted is unknown but is estimated at around 500 ha (Sierra 1999).

Table 3 shows the main species and varieties of prickly pear used for nopalitos production in Mexico. Prickly pears are cultivated in 18 states of Mexico, although 71.4% of the cultivated area falls within one state (Distrito Federal) (Table 4) (Flores et al. 1995; Flores 1997). The total production area is around 10,500 ha with an annual yield of 575,575 tons.

Prickly Pear as Fodder

Some of the characteristics that make prickly pear cacti a valuable addition to fodder for cattle, goats, horses and a variety of wild animals are its high palatability and digestibility, its great abundance, and its high productivity and quick recovery after harvesting (López et al. 1996; Fuentes 1997). There are two cattle systems that use prickly pear in Mexico: free roaming cattle and farm cattle. Free roaming cattle are raised on wild cacti and other wild plants on about 150,000 ha in the states of Tamaulipas, Nuevo Leon, Coahuila, Chihuahua, Sonora, San Luis Potosi, Zacatecas and Durango. In the second system, the cladodes of certain cultivated cactus varieties (Table 5) are harvested and added to commercial concentrates together with oats, maize, wheat and salts (Fuentes 1997).

TABLE 2. CACTUS SPECIES USED TO OBTAIN XOCONOSTLE FRUITS.[1]

Opountia leucotricha De Candolle
O. joconostle Haage & Schmidt
O. matudae Scheinvar
O. oligacantha Salm-Dyck
O. heliabravoana Scheinvar
O. spinulifera Salm-Dyck
O. zamudioi Scheinvar
O. imbricata (Haworth) De Candolle

[1]Scheinvar 1999; Cano et al. 1999.

Production of Cochineal Dyes

The cochineal insect *Dactylopius coccus* Costa is native to Mexico and has been used since pre-Hispanic times to produce crimson dyes. The insects are reared on certain species of *Opuntia* (Table 6), mature females are collected and dried, and the pigments extracted from the dried bodies. Commercial production and use of cochineal dye is limited, however, its use continues to be an important local tradition (Portillo & Arreola 1994; Portillo 1995; Vigueras & Portillo 1997). The exact acreage of *Opuntia* cacti under cultivation for rearing the cochineal insect is not known but it is estimated to be around 100 ha (Portillo 1999).

TABLE 3. MAIN SPECIES AND VARIETIES OF PRICKLY PEAR (*OPUNTIA* AND *NOPALEA*) USED FOR NOPALITOS.[1]

Species	Variety
O. atropes Rose	Blanco
O. ficus-indica (L.) Miller	Milpa Alta
O. ficus-indica	Atlixco
O. ficus-indica	Copena V1
O. ficus-indica	Copena F1
O. ficus-indica	Moradilla
O. ficus-indica	Blanco
O. ficus-indica	Negro
O. ficus-indica	Blanco w/ spines
O. ficus-indica	Polotitlan
O. ficus-indica	Alba
O. ficus-indica	Lutea
O. ficus-indica	Asperma
O. ficus-indica	Piriforme
O. ficus-indica	Serotina
O. ficus-indica	Italiana
O. ficus-indica	Villanueva
O. ficus-indica	Jalpa
O. inermis De Candolle	Tlaconopal
O. robusta Wendland	Tapon
O. streptacantha Lemaire	Cardon
N. cochenillifera (L.) Salm-Dyck	Tamazunchale

[1]Bravo 1978; Flores 1995; De la Rosa & Santamaria 1998; Blanco et al. 1999.

POTENTIAL IMPACT OF *C. CACTORUM*

The arrival in Mexico of the exotic pest, *Cactoblastis cactorum* (Berg), could pose a potentially very serious threat to both wild and cultivated prickly pears. Many of the more widely distributed and commonly used *Opuntia* species, which have previously been shown to be heavily attacked by this insect, are native to Mexico (Table 7). Small and young plants are particularly vulnerable to *C. cactorum*. This could have serious implications for the long-term sustainability of some ecosystems because reproductive events and/or conditions favorable for reproduction often occur only every few years. This could leave the soil in many arid and semi-arid regions unprotected to erosion, since prickly pear is one of the few plants that grow in these areas. The rich diversity of *Opuntia* cacti in Mexico also supports a rich diversity of native fauna. For example, 102 insect species have been found to interact with the genus *Opuntia*, representing nine orders, 29 families and 71 genera (Rodriguez et al. 1999).

The introduction of *C. cactorum* could also have significant social impacts. In 1996, the cultivation of prickly pear involved some 20,300 fruit producers and 8,095 producers of nopalitos. Additional people are involved in processing industries and cochineal production. Prickly pear cultivation has provided marginal and subsistence communities with employment, food, income and enabled them to remain on their land (De la Rosa & Santamaría 1998).

The potential routes that this insect might take to invade Mexico, as well as its ability to disperse over long distances (DeBach 1964), need to be better evaluated. Currently the moth occurs in Florida and is slowly moving west around the gulf coast. One of its primary hosts is *O. stricta* (Haw.) Haworth, which occurs along the coast from Florida to Texas. Once in Texas it could easily pass into Mexico. Another potential entrance point is through the Yucatan. Some concern has been raised that it might already be there, although initial surveys have been negative. The illegal transport of cacti from other countries through airports, harbors and international borders is an additional serious concern.

POSSIBLE CONTROL OPTIONS

The use of chemicals to control *C. cactorum* is not recommended, at least not in Mexico. Aerial applications of pesticides would not be economical and probably would not be effective, given the internal feeding behavior of this insect. Systemic insecticides or chemicals that accumulate in the plant tissues could have human or other non-target toxicity effects. In addition, much of the area from which cactus pads and fruit are harvested is

TABLE 4. PRODUCTION OF NOPALITOS IN MEXICO BY STATE (1996).[1]

State	Area (ha)	Production (tons)	Yield (tons/ha)
Distrito Federal	7,500	450,000	60.0
Morelos	450	31,500	70.0
Puebla	400	16,000	40.0
San Luis Potosí	350	10,500	30.0
Michoacán	320	10,500	35.0
Tamaulipas	300	9,000	30.0
Guanajuato	280	9,800	35.0
México	200	6,000	30.0
Baja California	150	9,000	60.0
Jalisco	120	7,200	60.0
Oaxaca	100	6,000	60.0
Aguascalientes	80	2,400	30.0
Zacatecas	75	2,250	30.0
Hidalgo	60	2,400	40.0
Tlaxcala	45		25.0
Querétaro	35		20.0
Durango	15		20.0
Sonora	10		80.0
Other	10		10.0
Total	10,500		

[1]Flores 1997.

wild habitat and the use of pesticides could have wide ecological effects on diverse fauna.

Biological control, based on the use of natural enemies such as *Apanteles alexanderi* Brethes (Hym.: Braconidae), *Phyticiplex doddi* (Cushman) and *P. eremnus* (Porter) (Hym.: Ichneumonidae), is also potentially controversial. The introduction of new natural enemies could have negative impacts on the complex but fragile native cactus ecosystems.

Potential control options would be the use of traps or attractant-and-kill systems. However, such systems have yet to be developed. Another alternative might be the use of biopesticides such as neem. Again, however, these have not been tested.

TABLE 5. CULTIVARS OF *OPUNTIA FICUS-INDICA* (L.) MILL. USED AS LIVESTOCK FEED.[1]

Copena CE-1
Copena CE-2
Copena F-1 maduro (without spines)
Copena F-1 tierno (with spines)
Nopal Rojo Pelon
Nopal Amarillo Milpa Alta
Nopal 30 Huatusco
Nopal Amarillo Milpa Alta Tierno
Nopal 31 Azul
Nopal 7 Texas

[1]Fuentes 1997; Vazquez & De la Garza 1999.

Among the essential preventative actions would be to alert all producers and technicians involved in prickly pear cultivation of the threat this insect poses and what they should do if they encounter it. The information campaign should involve cactus societies, environmental groups, grower groups and research institutions, and

TABLE 6. PRICKLY PEAR SPECIES (*OPUNTIA* AND *NOPALEA*) REPORTED AS HOSTS OF THE COCHINEAL INSECT *DACTYLOPIUS COCCUS* COSTA AND USED FOR DYE PRODUCTION.[1]

Species	Common name
O. atropes Rose	Nopal blanco
O. amyclaea Tenore	
O. crassa Haworth	
O. ficus-indica (L.) Miller	Nopal manso de Castilla
O. incarnadilla Griffiths	
O. fulginosa Griffiths	
O. jaliscana Bravo	Azucar
O. megacantha Salm-Dyck	Pescuezon, jarrito
O. pilifera Weber	
O. sacra Griffiths	
O. streptacantha Lemaire	
O. tomentosa Salm-Dyck	San Gabriel
O. undulata Griffiths	
N. cochenillifera (L.) Salm-Dyck	

[1]Portillo 1995; Vigueras & Portillo 1997.

TABLE 7. MEXICAN *OPUNTIA* SPECIES THAT ARE KNOWN TO BE SUSCEPTIBLE TO ATTACK BY *CACTOBLASTIS CACTORUM* (BERG).[1]

Species	Uses
O. compressa McBride	
O. ficus-indica (L.) Miller	Nopalitos, forage, fruit, cochineal
O. megacantha Salm-Dyck	Nopalitos, forage, fruit, cochineal
O. streptacantha Lemaire	Nopalitos, forage, fruit, cochineal
O. stricta (Haw.) Haworth	
O. tomentosa Salm-Dyck	Cochineal

[1]Mann 1969; Zimmermann & Pérez-Sandi 1999; Zimmermann et al. 2000.

should include the development and distribution of posters and pamphlets. Pressure also should be exerted on the government to enhance the phytosanitary practices aimed at preventing the entrance of exotic organisms into Mexico from other parts of the world. A number of Mexican institutions, including the University of Guadalajara, CONABIO, Government of Queretaro, ITESM, SEMARNAP and NAKARI, already have begun to collaborate on awareness campaigns for *C. cactorum* in their own regions.

CONCLUSIONS

Mexico has a tremendous diversity of prickly pear species. The cactus moth, *Cactoblastis cactorum*, would likely attack many, if not most, of these species, given its wide geographic and host ranges. Considering the prominent role prickly pears play in native ecosystems and local economies, the impact of this moth in Mexico could be extremely significant.

With increased global trade, it is difficult to predict when or from where the moth will arrive, but its presence and spread in Florida is disturbing. Certain parts of Mexico have habitats that are very similar to those in Argentina where *C. cactorum* completes two generations per year. Its biology could be similar in Mexico. Currently, there are no effective control measures for the moth other than the hand removal of egg sticks. Public and governmental awareness of the threat *C. cactorum* poses to Mexico and the development of responses prior to its establishment are critical.

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ADDRESSING THE THREAT OF *CACTOBLASTIS CACTORUM* (LEPIDOPTERA: PYRALIDAE), TO *OPUNTIA* IN MEXICO

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ABSTRACT

The South American cactus-feeding moth, *Cactoblastis cactorum* (Berg) (Lepidoptera: Pyralidae), is a serious threat to the high diversity of native *Opuntia* species in Mexico, both wild growing and cultivated. An action plan has been compiled and submitted to the FAO for funding. The objectives are to collate all available information on the insect, to evaluate the risks to Mexico, to verify the presence of the insect and the most likely route of entry; also to mobilize the cactus pear industry, cactus and related societies, and government officials into the action plan, to embark on an extensive publicity campaign, and to consult international experts, including those in neighboring countries. The final goal is to generate a strategy that will be followed by the Mexican government with a medium- to long-term plan to ensure the protection of the cactus pear industry and the native cactus flora.

Key Words: Mexico, cactus pear, FAO, threatened floras, invasive species

RESUMEN

La polilla sudamericana que se alimenta del cactus, *Cactoblastis cactorum* (Berg), es una serie amenaza a la gran diversidad de especies nativas en México de *Opuntia*, tanto las silvestres como las cultivadas. Un plan de acción fue elaborado el cual se entregó a la FAO para su financiamiento. Los objetivos son conjuntar toda la información existente acerca del insecto, evaluar los riesgos para México, verificar la presencia del insecto y su probable ruta de entrada, movilizar a la industria del nopal, así como las asociaciones relacionadas con las cactáceas y a los representantes del gobierno para que formen parte del plan de acción. Promover una gran campaña publicitaria y consultar asesores internacionales incluyendo aquellos de países vecinos. El objetivo final es proveer al gobierno mexicano de una estrategia a mediano y largo plazo para asegurar la protección de la industria del nopal y de la biodiversidad de las cactáceas nativas.

The cactus-feeding moth, *Cactoblastis cactorum* (Berg) (Lepidoptera: Pyralidae), is native to Argentina, from where it was introduced to many countries, including a few small islands in the Caribbean, for the biological control of various cactus invaders in the genus *Opuntia* (Julien & Griffiths 1998). It was also introduced, either deliberately or accidentally, to the Dominican Republic, Hispaniola, Cuba and Puerto Rico (Habeck & Bennett 1990; Pemberton 1995; Johnson & Stiling 1996). The insect was first recorded in south Florida in 1989, from where it has spread along the north and northwestern coasts (Johnson & Stiling 1998). Although it could be possible that it spread from Cuba to Florida naturally, there is strong evidence that it arrived there with infested cactus plants through the nursery trade (Zimmermann et al. 2000). It attacks all six native *Opuntia* species in Florida and one of the rare species, *Opuntia spinosissima* P. Miller, is now threatened with extinction (Johnson & Stiling 1998). Its rate of spread along the coast of Florida was estimated by Johnson & Stiling (1998) as being 256 km per year, although this figure is challenged by Zimmermann et al. (2000). Unconfirmed records of *C. cactorum* in Mexico (Yucatan State) and its interception at the Mexican-U.S. border at Laredo, Texas (Pemberton 1995) have raised the suspicion that the insect may already be in Mexico, although recent surveys have all been negative (Zimmermann et al. 2000). There is, however, general consensus that the moth will arrive in Mexico. Should this happen, various important local industries that are based on the extensive cultivation of *O. ficus-indica* (L.) Miller, and related species (Pimienta 1994), will be threatened. The most serious threat is to the 79 native species in the genus *Opuntia*, which are all more or less vulnerable to attack, and which will be impossible to protect once the moth has naturalized. This paper proposes a program to address this serious threat to Mexico. The proposal has been submitted to the FAO as a TCP project.

RESULTS

The Threat to Mexico

When evaluating the potential threat of *C. cactorum* to Mexican *Opuntia* populations it is important to study the impact the insect has had on *Opuntia* populations in other countries outside its

natural distribution in South America. In all cases the effect was dramatic, more so where small species were targeted (Julien & Griffiths 1998).

The area with free living and cultivated cactus pear in Mexico has been estimated at 3 million ha (Flores & Osorio 1997) of which about 217,000 ha are under cultivation (Vigueras & Portillo 2001). Of the approximately 79 species of *Opuntia* native to Mexico (Zimmermann et al. 2000) there are about six species under intensive cultivation. At least 18 wild growing species are also actively used, mainly for fruit, fodder and, to a lesser extent, the rearing of the cochineal insect, *Dactylopius coccus* Costa (Rodriguez & Portillo 1988; Fuentes 1997; Vigueras & Portillo 2001). The cultivation of cactus pear involves some 20,300 fruit producers and 8,095 nopalitos growers; to this can be added many more who are involved with byproducts derived from the plant, including cosmetics, medicines, confectioneries and juices (Flores 1997). *Opuntia* has been of special importance to Mexico since ancient times and it features strongly in its history, economy and cultural life (Hoffmann 1983). Besides being of aesthetic value, *Opuntia* also comprises some rare species that are central to the unique floral diversity of the northwestern deserts of Mexico and the United States (Bravo-Hollis 1978). There is no evidence that these species will be immune to attack by *C. cactorum.*

The platyopuntias (including the 10 species previously known as *Nopalea*) are most threatened and these comprise most of the species in the genus. The few cylindropuntias (chollas) are not suitable hosts for *C. cactorum* (Zimmermann et al. 2000). In Florida the insect is spreading at an alarming rate and all six native species are attacked, including the endangered semaphore cactus, *O. spinosissima* (Johnson & Stiling 1996, 1998). In South Africa *C. cactorum* attacks all 11 naturalized *Opuntia* (platyopuntia) species, including 9 species of Mexican origin (Zimmermann & Perez-Sandi 1999). It is unlikely that many native *Opuntia* species in Mexico will be immune to the insects. As in Florida and other countries, the smaller species are most vulnerable to attack and are easily killed. The larger shrub and tree-like *Opuntias* are seldom killed but are severely damaged and defoliated (Zimmermann et al. 2000). Secondary fungal and bacterial infections often complete the destruction. This may be particularly applicable to Mexico where a large diversity of pathogens is associated with Cactaceae (Zimmermann & Granata 2001). Although the large cultivations of *O. ficus-indica*, *O. streptacantha* Lemaire, *O. tomentosa* Salm-Dyck, *O. robusta* Wendland, *O. amyclea* Tenore and *O. megacantha* Salm-Dyck are unlikely to be destroyed, the damage could be severe and the additional control costs will be a heavy burden to growers, which they can ill afford. The most serious threat will be the invasion and damage to native species growing in natural areas where control will be impossible. Some rare and low-growing species could face extinction.

Preventive Measures for Mexico

A proposed TCP-FAO project, recently submitted to the FAO for approval, is aimed at obtaining basic information on *C. cactorum,* evaluating the risks, providing the government of Mexico with a long-term strategy for preserving the country's cactus pear resources, publicizing the threat, encouraging international cooperation and verifying the presence or absence of the insect from mainland Mexico. Mexico will be expected to provide the necessary financial support for the continuation of the project after two years. The project involves mobilizing several leading organizations, stakeholders and experts at national and international levels, with management by a national steering committee. The main aims of the project are the following:

Information

All published and unpublished information on *C. cactorum* will be collected. Contacts with experts in countries, who have researched the insect, including South Africa, Australia, Argentina and Florida, will also be established. This will be one of the main tasks of the international consultant to be appointed to the project.

Risk Analysis

The risks of *C. cactorum* to existing agricultural resources and cactus biodiversity, and implications for social and economic security will be determined. Models to predict its potential impact, rate of spread, and climatic tolerances within Mexico will be designed. Extrapolations based on information received from other countries will be made, keeping in mind some important counterbalancing factors that are already present in Mexico, including parasitoids, predators, diseases and host-plant characteristics. Neighboring countries will be consulted and asked to provide information that will ensure the consultants make reliable assumptions. These countries will include Cuba, Haiti, Dominican Republic, Puerto Rico and the United States (Florida), in addition to South Africa, Australia and Argentina.

General Awareness

The presence of *C. cactorum* on mainland Mexico has not yet been confirmed, although there are some indications that the insect may already be established there (Pemberton 1995). Confirming the presence of *C. cactorum* in Mexico is thus crucial to the project in order to determine the type of

control measure to be implemented. This will be done through a publicity campaign that will use pamphlets, posters, television and radio programs, as well as the press to disseminate information on the insect and its damage.

All stakeholders in Mexico (cactus grower associations, cactus societies, cactus researchers, extension officers, phytosanitary personnel, farmers, nature conservation and horticulturist societies and enthusiasts) will be identified and alerted. The rationale is not only to detect the insect's presence wherever it may occur, but also to determine its location as soon as possible no matter when or where it arrives. A quick identification service will be provided at a central locality to confirm the identity of any collected material. Training programs for extension officers and phytosanitary personnel at border posts will be put in place with emphasis on the states of Yucatan and all the states bordering Texas.

Dissemination of Information

The national coordinator together with the steering committee will organize at least two workshops involving scientists and other stakeholders. These workshops will also coincide, if possible, with national and international cactus pear congresses, which are held every 18 to 24 months in Mexico. The objectives are to inform and mobilize all academic and industry leaders involved with cacti and cactus pears, to transfer the latest information about the threat and actions to be taken, and to identify research needs.

International Liaison

The consultants and the steering committee will liaise closely with neighboring countries that already have *C. cactorum* control programs in place. This will apply in particular to the United States and Cuba, which are likely origins for possible invasions. The national coordinator and the consultants will actively participate in follow-up workshops on *C. cactorum*.

Establishment of a National Plan

The final goal will be to inform the Mexican government of the risks and consequences of invasions by *C. cactorum*, and to provide it with a national medium- and long-term strategy to prevent invasions and/or to provide it with an effective control plan. The national plan will also identify certain research needs that will be essential to ensure its success. The Mexican government will be expected to provide the necessary resources to execute the plans.

Project Team

The project will be run by a national coordinator who will be appointed by the responsible government departments, namely SEMARNAT (Secretaría del Medio Ambiente y Recursos Naturales) and SAGARPA (Secretaría de Agricultura, Ganadería, Desarollo Rural, Pesca y Alimentación). CONABIO (Comisión Nacional para el Conocimiento y Uso de la Biodiversidad) will analyze risk to native cactus diversity and implement all geographical information systems that may be needed. The project will have the support of a national steering committee that will be appointed by SEMARNAT, SAGARPA and CONABIO. The national steering committee, together with the national coordinator, will appoint the national and international expert consultants as well as the publicity officer. Other institutions may also be invited to participate by the national steering committee. The FAO will be represented at the deliberations of the national steering committee.

Conclusions

Mexico has the capacity and the infrastructure to prevent the arrival and invasion of *C. cactorum* in the country. Its most valuable asset is the dedicated team of cactus pear researchers whose influence filters through to every individual grower in the country. The regularly held cactus pear and cochineal congresses, normally attended by about 100 delegates with various ties to and interests in cactus, must be one of the main focal areas from where a publicity campaign is launched. The paper presented by Zimmermann & Perez-Sandi (1999) at the VIII National and VI International Congress on Cactus Pear in San Luis Potosi, on the threat of *C. cactorum* to Mexico, received widespread publicity and has put important actions in motion among leading researchers, officials and politicians within a very short time. Most researchers, agricultural leaders and conservation bodies are now aware of the threat and are supporting drastic control measures. If this project can succeed in preventing the arrival of *C. cactorum* and in ensuring its eradication, it will not only have averted a possible disaster, but will also have gone a long way in preventing further negative sentiments toward the science of biological weed control: *C. cactorum* is still regarded as the textbook example, epitomizing the successes that can be achieved with natural enemies as biological control agents, but also the dangers in introductions of nonnative species (Dodd 1940; Pettey 1948; Moran & Zimmermann 1984; Julien & Griffiths 1998).

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PRICKLY PEAR CACTI PESTS AND THEIR CONTROL IN MEXICO

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ABSTRACT

Opuntia spp., known by Mexicans as nopal, represents historically one of the most important biotic elements of Mexico. This natural resource has been and is being used for multiple purposes. Some of the current uses include: food for humans as both vegetable and fruit, forage for animals, source for alcoholic beverages, sweetener, live fences, industrial products such as cosmetics and dye, and as a medical source against diabetes and other diseases. Its cultural and natural values have been reflected in paintings, ancestral Indian codes, and old writings; thus its historic relevance is quite apparent. Furthermore, it is depicted both in the Mexican national seal and flag where it represents the very characteristic feature of Mexican culture and society. *Opuntia* spp. are distributed throughout the American continent and Mexico is considered a center of diversity as these species are well adapted to the arid and semiarid conditions of Mexico. Here we summarize and discuss briefly the most important insect pest species and one snail species which currently are considered as serious pests of cultivated *Opuntia* spp. in Mexico, and, thus require control measures. The control of these pest species is mainly through chemical pesticides and currently at least a dozen types of insecticides are being applied.

Key Words: *Opuntia* spp., insect pests, control, arid zones

RESUMEN

Las especies de *Opuntia* o nopal mexicamo representan uno de los recursos bióticos más importante históricamente. Este ha sido y está siendo usado con muchos propósitos. Algunos de sus usos son: alimento para el hombre, tanto como vegetal como su fruto (tuna), forraje para animales, como materia prima para la preparación de bebidas alcohólicas, como edulcorante, para la construcción de cercas, medicinal contra diabetes, etc. Su valor cultural y natural se ha reflejado en pinturas, códigos indígenas ancestrales y escrituras antiguas. Más aún, forma parte del símbolo nacional de México. Las especies de *Opuntia* están distribuidas a través del continente Americano y México es considerado el centro de origen y diversidad de estas especies. Además de que están bien adaptadas a condiciones aridas y semiáridas de México. Este trabajo resume y discute de manera breve las especies de insecto plaga mas importantes y una especie de caracol, el cual es considerado en la actualidad como la plaga mas seria de *Opuntia* spp en México. El control de estas plagas está basado principalmente en Control Químicol y al menos una docena de insecticidas se aplican actualmente para controlar estas plagas.

Sixty percent of the total area (2×10^6 km^2) of Mexico is arid. There are over 200 species of *Opuntia* or nopal worldwide, of which more than 50% of the species are found in Mexico. Nopal grows naturally in an area of over 3 million ha in the country. Furthermore, there are about 250,000 ha in which nopal is grown commercially. In Mexico, nopal is used for various purposes, such as a source of energy, for production of cosmetics, dyes, and pharmaceuticals, for human consumption as both fruit and vegetable, and as livestock forage (Flores & Aranda 1997). There are over 240 food recipes of nopal in the country (Flores 1992, Flores et al. 1996).

Nopal grows best under the following conditions; a temperature range of 11.2-27.1°C, an annual rainfall of 116.7-1,805 mm, and a range of altitude of 0-2,675 m. In Mexico, there are at least 11 insect pest species and one species of snail which attack and cause damage to nopal. To control these pests in Mexico, traditionally over a dozen types of chemical insecticides have been applied (Sanchez & Alaniz 1997).

One of the main activities of commercial growers of prickly pear cacti (*Opuntia* spp.) in Mexico is the identification and control of insect pests. This paper provides a brief discussion of the main insect pests, and at the end of each section, where available, is a list of insecticides used against the pest. The insect common names given are those used in Mexico.

Opuntia Borer, *Cactophagus* (= *Metamasius*) *spinolae* Gyllenhal (Coleoptera: Curculionidae)

This is one the most serious pests of "nopal manso" or *Opuntia megacantha* Salm-Dyck in the states of Hidalgo, San Luis Potosi, Tlaxcala, Mexico, and Jalisco. Adults, which appear in May, are 2.3-2.6 cm in length, black with red markings on

the anterior section of the prothorax and have two orange bands on the elytra. They feed on the margins of the young pads and lay their eggs inside these pads, where larvae feed. The 2.5-3.1 cm long white larvae form galleries inside the pads. A brownish-yellow (eventually turning black) sticky secretion is produced by infested stems and accumulates at the base of the damaged pads. The larvae hibernate inside the pads. This pest reduces plant production and in some cases destroys the plant (Granados & Castañeda 1991).

Cultural control measures include the extraction of the larvae from the damaged areas by means of horticultural knives. Also the slow-moving adults are hand removed from the surface of the pads from May through September. Chemical insecticides used to control this pest include azinphosmethyl, endosulfan, malathion, and folidol.

Spine Borer, *Cylindrocopturus biradiatus* Champion (Coleoptera: Curculionidae)

The adult stage appears in April and May. It is 4-4.5 mm long and has a dark dorsal mark in the form of a cross. It oviposits at the bases of the spines; larvae occur in June and July. Larval feeding produces dry sections of the plant. This is not considered a serious pest of the plant. A cultural method of control consists of the removal of the damaged plants. Folidol is applied to control this pest in April and May.

Gray Chinch Bug, *Chelinidea tabulatus* Burmeister (Hemiptera: Coreidae)

This pest appears most abundantly during warm months. Eggs are laid in clusters of 5-15 on both the pads and spines. There are five nymphal instars. Both nymphs and adults suck the plant sap forming clear circular markings in damaged areas. Adults reproduce all year, achieving the highest densities during July and August; the reproduction rate decreases during the winter months. Both immature and adult stages are gregarious, however the tendency to aggregate in clumps is more noticeable in nymphs. The gray chinch bug is basically a pest of *Opuntia megacantha*. This pest prefers mainly young plants. This insect is controlled by chemical insecticides including malathion, ethyl parathion, methyl parathion, and endrin.

Red Chinch Bug, *Hesperolabops gelastops* Kirkaldy (Hemiptera: Miridae)

These insects hibernate as eggs inside the pads, leaving the damaged parts as nymphs in the spring. Young nymphs are red colored throughout including head and legs, however, as they grow the color of the legs turn black. Both adults (6.5-7 mm long) and nymphs suck plant juice. Damaged areas are characterized by dried sections which eventually turn into invaginated superficial furrows (Garcia, 1965). During the winter, mated females lay their eggs inside the pads and then die. Insecticides used to control this pest include malathion, ethyl parathion, methyl parathion, and endrin.

Zebra Worm, *Olycella nephelepasa* (Dyar) (Lepidoptera: Pyralidae)

This is a more polyphagous pest species attacking the following opuntias: *O. megacantha*, *O. tomentosa* Salm-Dyck, *O. ficus-indica* (L.) Miller, *O. robusta* Wendland, *O. streptacantha* Lemaire, and *O. stenopetala* Engelmann. During January, young plants and pads are attacked by many colonies of white first instar larvae which in the next instar turn black with 12 well defined orange bands (hence the name zebra worm). Larvae are 4.5-6.9 mm long. They live entirely inside the plant and produce a bulged section that appears on the exterior part of the affected area of the stem. Larvae finally leave the plant and pupate in the soil. Opaque moths (0.5-5.2 cm long) eventually emerge. There are two generations per year, the first being the more damaging because of the absence of natural enemies.

Because this species causes damage in localized areas, a cultural control method consists of the destruction of the damaged plants. There are two species of parasitoids that attack the zebra worm in the Valley of Mexico. One is a tachinid fly (*Phorocera texana* Aldrich and Webber) (Diptera) that attacks the mature larvae and kills them after they transform to pupae. The other parasitoid is a braconid wasp (*Apanteles mimoristae* Muesebeck) (Hymenoptera) that attacks the younger larvae. Chemical insecticides, which are applied against this species during January, include carbaryl and endrin.

White Grub, *Laniifera cyclades* Druce (Lepidoptera: Pyralidae)

Opuntia megacantha is the most susceptible host for this pest. However, *Laniifera* is also known to attack other species such as *O. streptacantha* and *O. tomentosa*. This pest is usually found in the high plains states of Mexico. Eggs are deposited in groups of 30-50 in a regular or uniform pattern on the pads. Hatchling larvae live under the cover of a profuse web. These larvae gradually penetrate the internal tissue of the pads reaching the central axis and thus causing the collapse of the plant or inhibiting the production of new growth. Well developed larvae are 4.5-5.5 cm long. Larvae form cocoons inside the plant where they molt to the pupal stage of 2 cm length. The yellow moth emerges during July-October. Larvae throw their feces out of the openings that

they make in the pads and indeed, the opuntia growers use these signs of the feces or "rice mounds" to find and mechanically destroy the larvae. The same chemical materials which are applied against the opuntia borer are also used for white grub (Vazquez & Medina 1981).

Wireworms, *Diabrotica* sp. (Coleoptera: Chrysomelidae)

Females lay hundreds of eggs in the soil and near the roots of the plant from which 1.5-2 cm long bright yellow larvae hatch. The larval stage lasts three years, the larvae changing to pupae during the summer of the third year in the soil. The damage is to the roots and other subterranean parts of the plant and is manifested as the yellowing of the stems and reduction in vigor of the entire plant. The following insecticides are applied against this pest: carbofuran, chlordane, diazinon, fonofos, heptachlor, and trichlorfon.

Blind June Beetle, *Phyllophaga* sp.
(Coleoptera: Scarabaeidae)

This is one the most serious insect pests of opuntias in Mexico. The insects hibernate inside the soil as either larvae or adult females. During the spring, the females leave the soil at night and fly to nearby trees where they feed on the foliage. Mating occurs also during the night. The adults return to the soil with the onset of the dawn where they lay their white colored eggs. Eggs hatch in two to three weeks. The larva is white with a brown head and possesses two rows of short setae underside of the last abdominal segment which differentiate this species from closely related species. The larvae feed on the roots and other subterranean sections of the plant until autumn when they enter into hibernation. Chemical control of this pest is achieved by means of the same compounds applied for wireworm (see above).

Cochineal Insect, *Dactylopius indicus* Green
(Homoptera: Dactylopiidae)

Each female lays an average of 150-160 eggs. The eggs almost immediately hatch into nymphs. The damage of this insect is basically localized in the basal portion of the plant where it produces cotton-like masses. Inside each mass is the insect body that, when ruptured, exudes a red or purple colored liquid. The severe attack of this insect can result in fruit fall, general loss of plant vigor and finally the death of the plant. An important natural enemy is *Chilocorus cacti* L. (Coleoptera: Coccinellidae) whose larvae attack the females. This insect is also very renowned for the production of dye and thus has a very high socio-economic and cultural value to the opuntia growers in Mexico. Traditionally the following insecticides are applied when cochineal is deemed a pest: malathion, methyl parathion, and trichlorfon.

Opuntia Thrips, *Sericothrips* (= *Neohydatothrips*) *opuntiae* Hood (Thysanoptera: Thripidae)

Adults are 1 mm long and yellow or pale colored. Development time from egg to adult takes about 20-30 days. Warm and dry conditions favor development and reproduction. This insect sucks the plant sap. The attacked portions of the plant are covered by yellowish or gray-whitish spots which in turn are covered by dark colored droplets of insect feces which later turn dry. Feeding can cause great losses of fruit and vegetative parts of the plant. This insect is also the vector of a viral pathogen of the plant. The following insecticides are used for thrips control: malathion, methyl parathion, heptachlor.

Moneilema variolaris Thompson
(Coleoptera: Cerambycidae)

The larvae bore through the plant stems which results in loss of vigor and occasionally can cause the death of the plant.

Brown Garden Snail, *Cryptomphalus* (= *Helix*) *aspersus* Müller (Stylommatophora: Helicidae)

This organism feeds on the surface of the pads and thus inhibits the chlorophyll synthesis which in turn causes the reduction of new growth.

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PROTECTING RARE FLORIDA CACTI FROM ATTACK BY THE EXOTIC CACTUS MOTH, *CACTOBLASTIS CACTORUM* (LEPIDOPTERA: PYRALIDAE)

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ABSTRACT

Cactoblastis cactorum (Berg) represents a threat to rare *Opuntia* cacti in the Florida Keys. Conservation of such species may depend upon successful outplantings of young cacti in places that minimize attack rates by *Cactoblastis*. This paper discusses how to maximize the success rates of such outplantings of the endangered semaphore cactus, *O. corallicola* Small. A 1998 outplanting of 180 cacti in the Lower Keys showed that planting close to *Opuntia stricta* (Haw.) Haworth infected with *Cactoblastis* results in heavy losses, as *Cactoblastis* bleed over from *O. stricta* to attack outplanted *O. corallicola*. Growth rates of outplanted *O. corallicola* are greatest in shade conditions, but attack rates by *Cactoblastis* are also greater in the shade. An outplanting of 240 *O. corallicola* cacti on six different Keys in 2000, all far away from *O. stricta*, had no *Cactoblastis* related mortality. The most successful conservation strategy for *O. corallicola* thus appears to be outplanting in the shade, possibly in tropical hammocks, far away from *Opuntia* cacti that might contain *Cactoblastis*.

Key Words: invasive pest, Florida Keys, *Opuntia corallicola*, rare cacti

RESUMEN

La presencia de la especie *Cactoblastis cactorum* (Berg) representa una amenaza real para las especies de *Opuntia* que se encuentran en peligro de extinción y que ocurren en los Cayos de Florida (Florida Keys). La conservación y supervivencia de estas especies podria depender de la efectividad en establecer parcelas plantadas con estas especies en areas donde el possible ataque de *Cactoblastis* sea mínimo. Este articulo discute algunas de las maneras en que se pueden maximizar las probabilidades de supervivencia de parcelas plantadas con *O. corallicola* Small. Por ejemplo, una parcela plantada en 1998 con 180 especimenes de *O. corallicola* en un area cercana a especimenes de *O. stricta* (Haw.) Haworth infestadas con *Cactoblastis* demostró que este insecto se dispersó hacia los especimenes *O. corallicola* causando grandes daños. La tasa de crecimiento en *O. corallicola* es maxima cuando las areas en donde se encuentra son sombreadas; sin embargo, el daño causado por *Cactoblastis* también se maximiza en areas sin sol. Al examinar 240 especimenes de una parcela plantada con *O. corallicola* en diferentes isles del los Cayos de Florida, en areas sin *O. stricta*, no se encontro daño causado por *Cactoblastis*. Por lo tanto, la estrategia mas prometedora en cuanto a la conservación de *O. corallicola* parece ser la localización de parcelas de esta especie en areas sombreadas y libres de la presencia de *O. stricta* que puedan encontrarse infestadas con *Cactoblastis*.

The moth *Cactoblastis cactorum* (Berg) was recorded in Florida for the first time in 1989, in the Florida Keys. This moth, a native of South America that specializes on *Opuntia* cacti, had already been introduced around the world to control pestiferous *Opuntia* in such places as Australia, South Africa and Hawaii (Zimmermann et al. 2000). It was widely considered to be a dazzling success for biological control. In 1957 it was introduced into the Caribbean and a little over 30 years later was recorded in the Florida Keys, having island hopped via winged flight or been transported to Florida as larvae via the port of Miami in cacti imported from the Dominican Republic (Pemberton 1995). Regardless of its method of entry into the United States, fears are high that this moth will, either on its own or in movement associated with the ornamental cactus trade, invade the rest of the Southeastern and Gulf States, and eventually the cactus-rich desert areas of Southwestern U.S. and Mexico (see other pages in this special issue).

Our research on *Cactoblastis* activity in Florida, at the University of South Florida, has focused on the rate of spread of *Cactoblastis*, its rate of attack on *Opuntia* cacti, and moth-related mortality levels. We are also determining whether natural enemies, especially parasitoids, have bled over from native hosts onto *Cactoblastis* and are reducing *Cactoblastis* density. Our research showed that in the first few years of invasion the moth spread rapidly, up to 160 miles per year, but in recent years the rate of spread has slowed to only 24 miles per year (Johnson & Stiling 1998), which is more comparable to rates of dispersal in other areas, like Australia (Dodd 1940). The rate of spread has been faster up the Florida east coast, than the west coast. In fact, in

1999 *Cactoblastis* was reported in Sapelo Island, GA, whereas in September 2000 it had only dispersed as far north as Cedar Key on Florida's west coast. If the moth can survive and thrive at Sapelo Island it can probably survive at most Gulf Coast latitudes and the threat of dispersal to the U.S. Southwest looms large. In addition, there is a very real possibility that dispersal will be accelerated by human activity. In July 2000 *Cactoblastis* was reported on cacti at a Wal-Mart in Pensacola, FL, having been transported from a nursery in Miami. Only diligence by field agents from Florida's Division of Plant Industry and swift action by Nancy Coile, curator FDACS, resulted in its detection and removal. Damage by *Cactoblastis* to native cacti may be considerable, with 90% of the common prickly pear cactus plants, *Opuntia stricta* (Haw.) Haworth, suffering damage (Johnson & Stiling 1998). Although only 15% of our monitored plants died, these were all small plants and we believe mortality to juveniles is probably high, which threatens the integrity of future cactus populations. So far, attack rates of *Cactoblastis* larvae by native parasitoids has been slight, <10%, and only one species of tachinid fly has been reared from pupae.

A more immediate concern for the State of Florida is the likely effect of *Cactoblastis* on native Florida cacti, many of which are rare and endangered. Florida has six species of native *Opuntia*, the common prickly pear, *O. stricta* (Haw.) Haworth and *O. humifusa* (Raf.) Rafinesque, which are frequently present in coastal habitats, *O. pusilla* (Haw.) Nutt., and the rare *O. corallicola* Small, *O. triacantha* (Willdenow) Sweet and *O. cubensis* Britton & Rose, the last three of which are found only in the Florida Keys. All six species are vulnerable to *Cactoblastis* and most are attacked by larvae in the field (Johnson & Stiling 1996). While concern is high that even the common *Opuntia* species could be decimated by *Cactoblastis*, concern is even higher for the rare Florida species that exist nowhere else in the U.S.

This paper focuses on a strategy to conserve the rarest of the Florida *Opuntia*, *O. corallicola* Small. Only 12 mature individuals of this species exist in the world, all on one small Key. Protecting the parent cacti from attack from *Cactoblastis* by the use of cages is problematic for two reasons. First, cages prevent cross-pollination and second, cages are susceptible to tropical storm or hurricane force winds and can knock down the cacti inside if they fall over. For this reason, cages initially erected to protect the cacti from *Cactoblastis*, in 1990, have been removed. Since cage removal, at least two of these cacti have subsequently been attacked by *Cactoblastis*, one of which has been killed. The preservation of *O. corallicola* in the Florida Keys may depend on successful outplantings of new cacti designed to bolster the current population. This manuscript discusses our findings on the best strategies to use in outplantings that might minimize attack rates by *Cactoblastis* and maximize growth rates of cacti.

Materials and Methods

During the summer of 1997 we collected about 150 young *O. corallicola* cacti from around the bases of several parent plants growing on private land in the lower Florida Keys. These young cacti were returned to the U.S.F. Botanical Garden in Tampa, Florida, where they were planted in trays. For the next year the cacti grew and pads from large individuals were broken off and replanted to create more new cacti. By the summer of 1998 we had nearly 250 young 10-30 cm cacti with one to three pads. These pads were then used in experimental outplantings.

In summer 1998 we outplanted 180 of our young cacti on Saddlebunch Key. There were six replicates of each of three treatments. The treatments represented different associations or neighborhoods of cacti. In the first treatment, 10 young cacti were planted within 3 m of *Opuntia stricta* plants attacked by *Cactoblastis* (= near attacked). The 10 cacti were planted in two rows of five, with 10 cm between the two rows and 10 cm between each plant. These distances were chosen to approximate the natural spacing between "volunteer" plants that grow up under the parents from fallen pads or from seed. In the second treatment, 10 young cacti were planted within 3 m of *Opuntia stricta* plants showing no evidence of attack by *Cactoblastis* (= near unattacked). In the third treatment, 10 young cacti were planted at least 20 m from any *Opuntia stricta* (= alone). Each replicate contained each of these three treatments for a total of 30 cacti per replicate. There were 6 replicates, with 100 m between each replicate, for a total of 180 cacti. Three replicates were planted in open, sunny conditions and three under the shade of buttonwood trees.

The cacti not used in the first outplanting continued to be maintained at U.S.F. and by the summer of 2000 we had built-up a collection of nearly 300 young rooted plants, again 10-30 cm tall with 1-3 pads. In the summer of 2000 we performed our second outplanting. Here, forty cacti were placed on each of six separate Keys: Sugarloaf, Little Torch, Ramrod, Cudjoe, No Name and Big Pine. The forty cacti were planted in four groups of ten. Two groups were planted in the shade of a tropical hammock and two in a light gap within a tropical hammock. On each Key care was taken to keep all cacti at least 500 m from any other *Opuntia* cacti.

At both outplantings all cacti were visited every three months and attack rates by *Cactoblastis* were scored, along with plant height and pad

TABLE 1. ANOVA ON ATTACK RATE OF *OPUNTIA CORALLICOLA* OUTPLANTINGS BY *CACTOBLASTIS CACTORUM* ON SADDLEBUNCH KEY, FL.

Source	SS	df	MS	F	P
Shade	1469.444	1	1469.444	9.404	0.01
Neighborhood	4116.667	2	2058.333	13.173	0.001
Shade × Neighborhood	1672.222	2	836.111	5.351	0.022
Error	1875.000	12	156.25		

number, as a measure of growth. *Cactoblastis* attack results in "green slime" exuding from fed-upon pads or, in the later stages of attack, a characteristic skeletal appearance of the cactus with all the tissue between the epidermal layers eaten. In the first outplanting, growth as measured by difference in height over two years, summer 1998 to summer 2000, was analyzed using the mean increase in height for each replicate group of 10 cacti in a two-way ANOVA with neighborhood and shade as the factors. Analysis of variance was also used to examine death of cacti from *Cactoblastis* from 1998 to 2000.

RESULTS

In the first outplanting, *Cactoblastis* attacked and killed many outplanted *O. corallicola*. Deaths rates were significantly greater where cacti were placed adjacent to *O. stricta* already attacked by *Cactoblastis* and contained a reservoir of actively feeding larvae (Table 1, Fig. 1). The 3 m distance between the *O. corallicola* and the *O. stricta* was probably too great to be crossed by *Cactoblastis* larvae, so this suggests that adults that hatched from pupae under the attacked *O. stricta* probably laid eggs on neighboring *O. corallicola*. Attack rates of *O. corallicola* near unattacked *O. stricta* or on those planted away from any *O. stricta* (alone) were very low. The growth rates of cacti among these treatments were not significantly different (Table 2, Fig. 2), indicating that all neighborhoods where cacti were planted were equally good places for cacti to grow.

Outplanted cacti were attacked significantly more by *Cactoblastis* when planted in the shade than when they were planted in the sun (Table 1, Fig. 1). Growth rates of shade cacti were almost twice as high as sun cacti, indicating that growth conditions were better in the shade and that shade cacti were healthier. Higher plant quality in the shade may promote higher attack by *Cactoblastis*.

In the second outplanting, after one year, by summer 2001, none of the 240 cacti were attacked by *Cactoblastis* and growth occurred in all treatment groups, indicating cacti were planted in appropriate locations. In contrast, in the first outplanting, nearly two thirds of the total cacti killed by *Cactoblastis* had been killed by the end of year one, indicating that the difference in results between the two outplantings was not time-related.

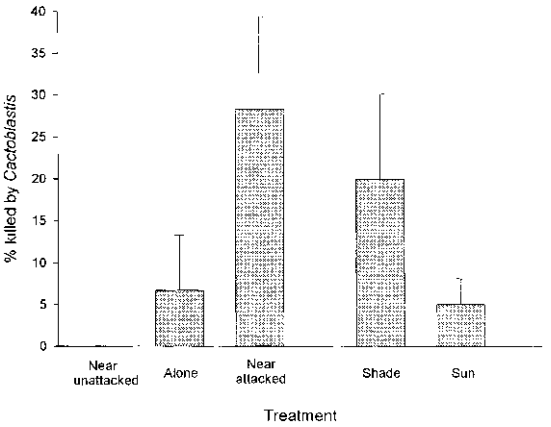

Fig. 1. Mortality of outplanted *Opuntia corallicola* cacti caused by *Cactoblastis* when placed near *Cactoblastis*-attacked *O. stricta*, when placed alone, and when placed near unattacked *O. stricta*. Also shown are levels of *Cactoblastis* mortality on *O. corallicola* when outplanted in shade or sun conditions.

DISCUSSION

Our major conclusion is that any recovery plan for the rare cactus *O. corallicola* in the Florida Keys should locate outplanted cacti as far away as possible from *O. stricta* because this common species may act as a reservoir for *Cactoblastis*. None of the 240 cacti outplanted in 2000, far away from *O. stricta*, were attacked by *Cactoblastis*. In contrast, in the first outplanting, where cacti were placed in close proximity to *O. stricta* containing *Cactoblastis*, they were likely to be attacked and killed by *Cactoblastis*. In the first outplanting even some cacti placed more distant from attacked *O. stricta* were attacked and killed. This would suggest that only outplantings at least 500 m from attacked *O. stricta*, and perhaps in the seclusion of a tropical hammock, would be isolated enough to prevent detection by *Cactoblastis*, at least in the short term. Such short-term protection might be critical because larger cacti appear more likely to survive *Cactoblastis* attack than

TABLE 2. ANOVA ON HEIGHT OF *OPUNTIA CORALLICOLA* OUTPLANTINGS ON SADDLEBUNCH KEY, FL.

Source	SS	df	MS	F	P
Shade	294.981	1	294.981	6.516	0.025
Neighborhood	33.593	2	16.796	0.371	0.698
Shade × Neighborhood	11.716	2	5.858	0.124	0.880
Error	543.232	12	45.269		

smaller cacti (Johnson & Stiling 1998). Bevill et al. (1999) also showed how protection of juvenile rare native Pitcher's thistle, *Cirsuim pitcheri* (Eaton) T. & G., from non-target effects of a weevil released to control exotic thistles increased growth rates. For the thistles, protection from weevils in the early growth stages resulted in a 50% increase in juvenile survival and a concomitant increase in flowering and seed production of mature plants.

Opuntia corallicola appears to grow better in the shade than in the full sun, a finding also reported by Stiling et al. (2000) from an earlier outplanting in 1996. However, here the conservationist faces somewhat of a dilemma because shade cacti are significantly more susceptible to attack by *Cactoblastis*, perhaps because they are of superior quality to small, relatively stunted sun plants. Other authors have noted higher attack rates of cacti by moths in shaded areas. For example, cladode mortality of *O. fragilis* (Nutt.) Haworth by the native moth *Melitara dentata* (Grote) (Lep.: Pyralidae) in Nebraska was higher in shaded sites than in open ones (Burger & Louda 1995). Perhaps the best conservation strategy for the rare *O. corallicola* would be to plant in shaded conditions but only well away from *O. stricta*, which acts as a reservoir for *Cactoblastis*. In this way rare cacti, both in the Florida Keys and elsewhere, might suffer less death by *Cactoblastis* yet have maximal growth rates.

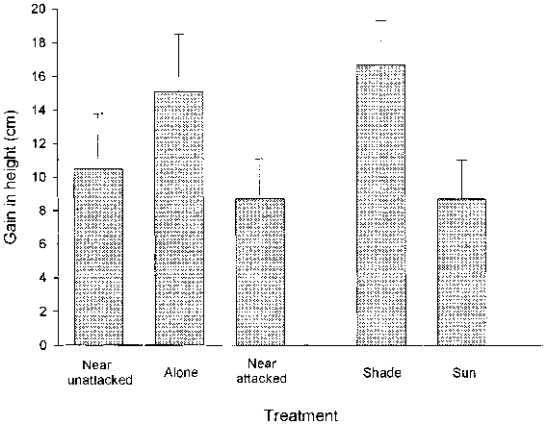

Fig. 2. Growth of outplanted *Opuntia corallicola*, as measured by gain in height, when placed near *Cactoblastis*-attacked *O. stricta*, alone, near unattacked *O. stricta*, and in sun or shade conditions.

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CHEMICAL CONTROL OF *CACTOBLASTIS CACTORUM* (LEPIDOPTERA: PYRALIDAE)

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ABSTRACT

Chemical control of *Cactoblastis cactorum* is hampered by the lack of data to support usage of many available pesticides. The application of pesticides to infested cacti is severely limited by the fact that these infested plants occur on sites in urban habitats, on public lands or in areas that are difficult to access. The use of such materials is governed by the United States Environmental Protection Agency and pesticide usage patterns, including allowable sites, must be specified on the pesticide label. There are an array of materials that could potentially be used to manage this insect with minimal impact on the environment and non-target organisms. However, there is very little research being conducted to determine the efficacy and safety of these pesticides.

Key Words: *Opuntia*, chemical control

RESUMEN

El control químico de *Cactoblastis cactorum* se ve afectado por la falta de información sobre el uso adecuado de varios pesticidas contra esta especie. La aplicación de pesticidas a las plantas de cactus que se encuentran infestadas es difícil debido a que estas plantas se encuentran localizadas en jardines urbanos, en areas de uso público o en areas de acceso limitado. El uso de pesticidas esta gobernado por la Agencia Protectora del Madio Ambiente de los Estados Unidos y las normas de aplicación de pesticidas, incluyendo las areas donde se permite su uso, deben estar especificadas en la etiqueta del producto. Hoy en dia existen varios productos que podrian ser utilizados en el control de esta especie que son poco dañinos al medio ambiente y a otros organismos. Sin embargo, en estos momentos, existen pocos estudios que proveen datos sobre la eficacia y seguridad de estos pesticidas para el control de *Cactoblastis cactorum*.

Only a few publications have addressed chemical control of the cactus moth, *Cactoblastis cactorum* (Berg) (Burger 1972; Bot et al. 1985; Pretorius et al. 1986; Pretorius & Van Ark 1992). However, no insecticide studies have been published that relate to management of *Cactoblastis* since the insect became established in Florida. This paper reviews the relevant literature, offers suggestions for candidate insecticide trials, and proposes considerations for chemical control research and management strategies.

Working in Africa, Pretorius & Van Ark (1992) evaluated stem injections of mevinphos, dimethoate, and monocrotophos. They concluded that stem injection of these insecticides was unpromising. However, they achieved good protection against larval attack with cover sprays of the same insecticides. A cover spray of cypermethin gave complete protection against larval attack. A cover spray of cypermethrin mixed with chlorpyrifos was very effective against cactus moth and *Dactylopius opuntiae* (Cockerell). Chlorpyrifos alone was also effective against both insects. Carbaryl gave poor to excellent control. Since several of the insecticides used in their work are not registered in the U.S., and continued registration of chlorpyrifos is questionable, it is time to revisit the use of insecticides in the management of cactus moth, especially considering the development of new insecticide chemistries since the previously described work. We believe that the relatively new insecticides abamectin, emamectin benzoate, imidacloprid, spinosad, indoxacarb, and chlorfenapyr, and some older insecticides such as acephate, fenoxycarb, dimethoate, and methidathion, have the potential to manage this insect in the U.S. (Table 1). Several of these insecticides are especially effective on many lepidopterous species and some possess characteristics that make them attractive for specialty uses such as control of cactus moth.

At first consideration, the very idea of utilizing insecticides to protect endangered species of plants from an introduced insect species would be questionable considering the older chemistries of the insecticides that have been examined. These materials can cause phototoxicity and are known to be very harsh to non-target organisms. However, with the new chemistries that are now available, the idea should be revisited. Several of the new chemistries are better suited for integrating with natural control and classical biological control. Abamectin, emamectin benzoate, spinosad, and indoxacarb are considered somewhat envi-

TABLE 1. SUGGESTED INSECTICIDES FOR SCREENING AGAINST *CACTOBLASTIS CACTORUM*, AS BASED ON CURRENT LABELING AGAINST TARGET LEPIDOPTERA THAT BORE INTO PLANT TISSUE.

Insecticide	Crops on which registered	Insecticide class	Characteristics of interest	Environment and safety concerns
Emamectin benzoate	Vegetables	Avermectin	Translaminar; easy on beneficials	Low
Abamectin	Ornamentals	Avermectin	Translaminar; easy on beneficials; Homoptera activity	Low
Spinosad	Ornamentals, fruit, vegetables	Spynosyn	Easy on beneficials	Very low
Indoxacarb	Vegetables	—	Easy on beneficials	Very low
Fenoxycarb	Ornamentals	Carbamate; insect growth regulator	Homoptera activity	Low
Imidacloprid	Ornamentals, fruit, vegetables	Chloro-nicotinyl	Systemic; Homoptera activity	Very low
Acephate	Ornamentals, fruit, vegetables	Organophosphate	Systemic; cacti on label; Homoptera activity	Low
Dimethoate	Ornamentals	Organophosphate	Systemic; Homoptera activity	Medium
Methidathion	Ornamentals	Organophosphate	Homoptera activity	Medium

ronmentally friendly. The potential environmental impacts associated with chlorfenapyr, especially effects on birds, might impact its approval for use in environmentally sensitive situations in the U.S. However, chlorfenapyr should be looked at since it appears to have numerous registrations outside the U.S.

To date, it appears that none of the new insecticides have been examined for the control of cactus moth. Therefore, for this discussion, it might be useful to speculate on the potential of insecticides for cactus moth based on insects that have aspects of their biology that are similar to cactus moth. The focus of chemical control should be the prevention of the first instar from boring into the stem (cladode). Thus, insecticides used against insects that bore into plant tissue after egg hatch would be considered potential candidates for evaluation against cactus moth. Insecticides were considered with the following insects on the label: diamondback moth; azalea, citrus, and other leafminers; Nantucket pine tip moth; codling moth; and artichoke plume moth (Table 1). Also some of these insecticides are effective on Homoptera, offering potential protection against cochineal insects, *Dactylopius* spp. Several of these insecticides are systemic, thus offering potential protection against cactus moth larvae that have successfully invaded a cladode.

Pyrethroids could be considered for managing cactus moth in the U.S., however, their use would be considered problematic in that they are harsh on beneficial insects and the high level of contact toxiticity could present problems for non-target Lepidoptera, such as threatened or endangered species that may be occurring within the same habitat. We suggest that the ideal insecticide would be one that, when applied, quickly enters the surface of the cladode and remains there for an extended period of time, but rapidly breaks down on the stem surface, presenting minimal problems to parasites and predators. Of the new chemistries, abamectin, emamectin benzoate, and indoxacarb are absorbed into leaf tissue, and should be examined for management of cactus moth. Even though abamectin is not effective against many caterpillars, it has shown unusual activity against some species, such as the diamondback moth, *Plutella xylostella* (L.). In addition, abamectin is registered for use on ornamental plants indoors and outdoors, making it readily available for use.

Focusing the management program on preventing the entrance of first instars into the cladodes requires knowledge of the pattern of oviposition of the cactus moth. Knowing the seasonal nature of oviposition as well as whether oviposition occurs over short, well defined periods, or occurs over protracted periods without well defined peaks is very important in planning insecticide application strategies. Apparently there are two or more well defined generations in Australia and South Africa (Pettey 1948; Robertson 1985). However, more generations might be expected in warmer climates. In Florida Johnson & Stiling (1998) have shown that the cactus moth appears to have a protracted oviposition period, with oviposition increasing in the spring and fall. Johnson & Stiling (1998) indicated that new larval damage varied over time and location, which is to be

expected considering the subtropical to tropical nature of Florida's climate. Therefore, a monitoring program would be very useful to precisely time insecticide applications, thereby reducing the amount of insecticide needed in the management program.

Protocols for evaluating the insecticides need to be devised in such a way to account for the natural behavior of the first instar. This is necessary for any insect, however, with the cactus moth, the habit of the neonate larvae collectively burrowing and entering a cladode through a single entry hole (Hoffmann & Zimmermann 1989) makes it necessary to place great attention to this behavior. It is speculated that this behavior overcomes the gum-secretions encountered by the neonates while burrowing into the cladode (Hoffmann & Zimmermann 1989). Similarly, the caterpillars that are first to colonize might succumb to the insecticide, but allow successful entry of the following larvae. Therefore, bioassays that don't allow this behavior to occur could provide misleading results. The effects of this behavior on insecticide efficacy need to be investigated.

In conclusion, as with many insects in a natural setting, the biology of the cactus moth probably precludes the use of insecticides in the management of this insect in the wild, and research should be conducted to evaluate the potential of classical biological control. However, in culturally managed plantings of cacti which can be monitored and which are amenable to application equipment and techniques associated with small and large-scale monoculture, several insecticides of different chemical groups might be used successfully, along with biological control, to manage the cactus moth. With the development of new insecticides that are increasingly amenable to usage in ecologically and politically sensitive environments, it would be worthwhile to revisit the use of insecticides for the control of cactus moth.

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POTENTIAL AND RISKS OF BIOLOGICAL CONTROL OF *CACTOBLASTIS CACTORUM* (LEPIDOPTERA: PYRALIDAE) IN NORTH AMERICA

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ABSTRACT

Cactoblastis cactorum Berg, an invasive moth and famous biological control of weeds agent, threatens numerous native and economic prickly pear cacti (*Opuntia*) in the United States and Mexico. Biological control of the moth, using a variety of approaches, is considered including: introduction of parasitoids and pathogens from the moth's native home in South America, introduction of parasitoids from related North American cactus moths (Pyralidae: Phycitnae), inundative releases of parasitoids known to attack the moth in Florida, and inundative releases of mass reared generalists parasitoids. The primary risk of employing biological control is the reduction of the many North American cactus moths, some of which probably regulate native *Opuntia* that can be weedy. The various biocontrol approaches are ranked according to their relative risk to the native cactus moths. The introduction of South American parasitoids or pathogens specific to the genus *Cactoblastis* (if they exist) may be the least risky approach. The introduction of South American parasitoids that can attack many cactus moths is the most risky approach because it could result in persistent "control" of these non-target native insects. Biological control probably can reduce the abundance of *C. cactorum* populations but is unlikely to prevent the spread of the moth. The relative benefits and risks of biological control need to be carefully assessed prior to any operational biological control programs. It will be difficult to reach agreement on acceptable levels of risk, if the likely benefits can't be predicted. Other management options need to be considered.

Key Words: *Opuntia*, biological control risk, cactus moths, host specificity, parasitoids, insect pathogens

RESUMEN

Cactoblastis cactorum Berg, una polilla famosa como agente de control biológico de malezas, amenaza numerosas especies nativas y económicas de cactos del género *Opuntia* en los Estados Unidos de América y en México. Se considera en este trabajo el control biológico de la polilla, utilizando diversas alternativas: la introducción de parasitoides y patógenos de Sud América, el área nativa de la polilla; la introducción de parasitoides de polillas de cactos de Norte América (Pyralidae: Phycitinae); liberaciones inundativas de parasitoides que atacan a *C. cactorum* en la Florida, y liberaciones inundativas de parasitoides generalistas criados en forma masiva. El principal riesgo de la utilización del control biológico es el empobrecimiento de las muchas especies de polillas de cactos de Norte América, algunas de las cuales probablemente regulan *Opuntia* nativas que podrían ser malezas. Las distintas alternativas del control biológico son ordenadas de acuerdo al riesgo relativo hacia las polillas de cactos nativas. La introducción de parasitoides y patógenos específicos del género *Cactoblastis* (si existieran) en Sud América, sería la alternativa menos riesgosa. La introducción de parasitoides sudamericanos que ataquen muchas polillas de cactos es la alternativa más riesgosa porque podría resultar en el "control" permanente de estos insectos que no son objetos del control biológico. El control biológico probablemente pueda reducir la abundancia de las poblaciones de *C. cactorum* pero es poco probable que pueda prevenir la dispersión de la polilla. Los beneficios relativos y riesgos del control biológico necesitan ser cuidadosamente evaluados antes del comienzo de los programas de control. Será tal vez difícil lograr acuerdos sobre los niveles de riesgo aceptables si los beneficios esperados no pueden ser estimados. Otras opciones de manejo necesitan ser consideradas.

Cactoblastis cactorum Berg has successfully controlled pest prickly pear cacti (*Opuntia* species) in Australia (Dodd 1940) and in many other places in the world (Moran & Zimmermann 1984). The moth was introduced to Nevis in the Caribbean in 1957 to control native *Opuntia* species that were weeds of pasture (Simmons & Bennett 1966). In 1989, *C. cactorum* was found in Florida (Habeck & Bennett 1990). The insect may have spread on its own from other places in the

Caribbean (Johnson & Stiling 1996) or may have been accidentally introduced by the nursery industry (Pemberton 1995). Since that time the moth has spread throughout the Florida peninsula where it attacks five of the six *Opuntia* species native to the state, including the endangered *Opuntia spinosissima* Miller (see Stiling & Moon this volume). There is considerable concern that the moth will continue to spread and attack additional *Opuntia* species. There are many native *Opuntia* in the southwestern U.S. and Mexico that could be harmed by the moth (Strong & Pemberton 2000; Zimmermann et al. 2000). An estimated 79 *Opuntia* species native to Mexico and the United States are at risk (Zimmermann et al. 2000). In addition, as many as 25 *Opuntia* species in Mexico and three species in the United States are used by people as food, animal fodder, and as the host of the cochineal dye producing scale (Zimmermann et al. 2000).

Currently in Florida the primary host plant of *C. cactorum* is *O. stricta* (Haworth) Haworth which is distributed around the Gulf of Mexico from Florida to Texas and Mexico. It appears likely that the moth will spread from Florida to Texas using this plant. If *C. cactorum* reaches Texas and Mexico, many other *Opuntia* species could become hosts and the moth could continue its spread via these new hosts. This would also bring the moth into contact with endangered *Opuntia* species that could be harmed. The ability of *C. cactorum* to quickly and completely control many exotic weedy *Opuntia* in disparate parts of the world, and also native weedy *Opuntia* species in the Caribbean, suggest that the moth could be particularly dangerous in North America.

In addition to the ecological damage caused by the moth, public confidence in biological control practice is being injured because of the moth's damage and threat to native *Opuntia*. Unfortunately, this situation is occurring when biological control, a critical tool in the fight against the many invasive species, is needed more than ever before.

The possible use of biological control against *C. cactorum* in North America was first raised by Bennett and Habeck (1992). Biological control has controlled many insects, including Lepidoptera that feed within plants. For example, the European pine shoot borer, *Rhyacionia buoliana* (Denis & Schiffermuller), and the European corn borer, *Ostrinia nubialis* (Hübner), have been successfully reduced using biological control (Kogan et al. 1999; Dahlsten and Mills 1999). In this paper, we will consider the possibilities of various biological control approaches that might be useful to reduce existing populations of the moth in Florida and adjacent Georgia, and perhaps limit its spread. The possible benefits and perceived risks of each approach will be discussed. We do not wish to advocate the use of biological control for *C. cactorum* in North America, but we think it is important to explore the potential use and implications of various biological control options.

Materials and Methods

Searches of the literature were made to detect the known parasitoids and diseases of *Cactoblastis* species and other species of cactus moths (Pyralidae: Phycitinae). Compilations of these organisms were created in different categories related to various biological control options. Other literature, primarily parasitoid catalogues, were searched to detect records of other host insects of these natural enemies, to help judge their host specificity. Criteria related to the potential benefit and risk of different biological control approaches were developed and then used to rank these approaches.

Results and Discussion

Biological control using parasitoids of *Cactoblastis cactorum* from its native range in South America

The 8-9 parasitoids associated with the cactus moth in South America are shown in Table 1. These include one braconid larval parasitoid, one chalcidid pupal parasitoid, 5-6 ichneumonid wasps and one tachinid fly. Apparently no egg parasitoids are known. The chalcidid wasp, *Brachymeria cactoblastidis* Blanchard, is suspected of being a hyperparasitoid (Zimmermann et al. 1979). The braconid wasp, *Apanteles alexanderi* Brethes, has been recorded to cause more than 30% parasitism of the larvae and the ichneumonid, *Temelucha* sp., was recorded to cause 5-30% parasitism of the larvae (Zimmermmann et al. 1979). Parasitism rates of the other parasitoids were not recorded, but two of the ichneumonid wasps are rare. *Apanteles alexanderi* attacks other cactus moths and at least three other genera of Lepidoptera, and probably others (DeSantis 1967; Mann 1969). The *Temelucha* sp. and the tachinid, *Epicoronimyia mundelli* (Blanchard), are known to use other genera of cactus moths (Mann 1969; Blanchard 1975; Zimmermann et al. 1979). No information about other potential hosts of the remaining parasitoids, the four ichneumonid wasps, was found, but this is probably due to a lack of knowledge rather than a true absence of other hosts.

Some of these wasps appear to have the potential to reduce *C. cactorum* populations (e.g., *A. alexanderi* and *Temelucha* sp.). If used in the United States, they probably would be able to orient to the plants and locate *C. cactoblastis* inside the pads where they feed. It is, however, unlikely that any of these parasitoids are monophagous, so their introduction for *C. cactorum* control could result in use of and harm to non-target Lepidoptera in North America, especially native cac-

TABLE 1. KNOWN PARASITOIDS OF *CACTOBLASTIS* IN THEIR NATIVE SOUTH AMERICA.

Parasitoid species	*Cactoblastis* species	Other hosts	Stage attacked	Degree of attack of *Cactoblastis*	Reference	Presumed specificity
Hymenoptera						
Braconidae						
Apanteles alexanderi Brethes	*C. cactorum* Berg		Larvae		Parker et al. 1953	broad
	C. cactorum Berg *C. doddi* Heinrich	*Tucumania tapiacola* Dyar *Salambona analamprella* (Dyar)		Not mentioned	Mann 1969	
	Cactoblastis spp.			>30%	Zimmermann et al. 1979	
	C. cactorum?				Bennett & Habeck 1992	
		Salambona analamprella *Tucumania tapiacola* *Plutella maculipennis* Curt. *Eulia loxonephes* Meyr. *Eulia* sp. *Argyrotaenia sphaleropa* (Meyr.) Lepidoptera sp.			DeSantis 1967	
Chalcididae						
Brachymeria (*Pseudobrachymeria*) *cactoblastidis* Blanchard	*C. doddi* Heinrich		Pupae		Mann 1969	
	Cactoblastis spp.		Pupae prob. hyperparasitoid		Zimmermann et al. 1979	
	C. cactorum?				Bennett & Habeck 1992	
Brachymeria sp.	*C. cactorum*		Pupae?		Thompson 1943	
Ichneumonidae						
Chromocryptus doddi (Cushman)	*Cactoblastis* spp.		?	Rare	Zimmermann et al. 1979	?
Cryptus sp.	*C. cactorum*		?		Mann 1969	?
Phyticiplex doddi (Cushman) (Probably a synonym of *Chromocryptus doddi*)	*C. cactorum*		?		Bennett & Habeck 1992	?
Phyticiplex eremnus (Porter)	*C. cactorum*		?		Bennett & Habeck 1992	?
Podogaster cactorum (Cushman)	*C. cactorum*		?		DeSantis 1967	?
	Cactoblastis spp.			Rare	Zimmermann et al. 1979	
Podogaster sp.	C. cactorum				Mann 1969	?

TABLE 1. (CONTINUED) KNOWN PARASITOIDS OF *CACTOBLASTIS* IN THEIR NATIVE SOUTH AMERICA.

Parasitoid species	*Cactoblastis* species	Other hosts	Stage attacked	Degree of attack of *Cactoblastis*	Reference	Presumed specificity
Temelucha sp. (*Temelucha* = *Cremastus*)	*Cactoblastis* spp.	*Salambona analamprella* *Tucumania* spp.		5-30% Rare 5-30%	Zimmermann et al. 1979	?
Diptera Tachinidae *Epicoronimyia mundelli* (Blanchard)	*C. doddi*	*Tucumania tapiacola* Dyar			Mann 1969 Blanchard 1975	?
	C. cactorum?				Zimmermann et al. 1979	

tus moths. Careful host specificity research might identify some of these parasitoids with narrow enough host ranges to minimize potential nontarget risks. Such parasitoids could be a viable control option. Parasitoids probably could be obtained from climatic areas of South America that are similar to Florida, which would increase the probability of establishment and control.

Biological control using insect pathogens

Two types of diseases, an entomopathogenic fungus and a protozoan, have been recorded to infect *Cactoblastis* species (Table 2). The fungus *Beauveria* sp. caused high death rates of larvae in many places in Australia (Dodd 1940), but *Beauveria* probably *bassiana* (Balsamo) Vuillemin caused only low levels of infection in larvae and pupae in South Africa (Pettey 1948). This fungus is a cosmopolitan disease with a broad host range. It has been isolated from more than 200 hosts, including spiders (Feng et al. 1994). *Beauveria bassiana* has been used in biological control of grasshoppers, scarab beetles and other insects (Hajek & Butler 2000). It might be possible to use the fungus in an inundative biological control of *C. cactorum* in limited situations such as where the moth threatens the few remaining plants of *Opuntia spinossisma* in the Florida Keys. The control obtained would be dependent on local weather conditions and perhaps broader climatic conditions as suggested by the differing levels of infection of *C. cactorum* in Australia and South Africa. Control at best would be temporary.

Many pathogens such as *B. bassiana* have wide host ranges, but fungal pathogens with narrower host ranges are known. One such fungus, *Entomophaga maimaiga* Humber, Shimazu & Soper, is successfully controlling the gypsy moth, *Lymantria dispar* L., in the U.S. (Hajek et al. 1990). No such fungal pathogens are known from *C. cactorum* but none has been sought. Exploration for pathogens of the moth could be productive. Demonstrating the safety of such pathogens probably would be difficult because the laboratory host ranges and field host ranges are different and host acceptance is not always determined by phylogenetic position of the host insect (Hajek & Butler 2000).

Two *Nosema* were described from *Cactoblastis* species in South Africa (Fantham 1939). One of these, *N. cactoblastis* Fantham, was described causing up to 100% infection of winter broods of larvae in some South African localities (Pettey 1948). This microsporidium was thought to be the cause of the lack of control of pest *Opuntia* by *C. cactorum* in these areas. Surveys for these *Nosema* spp. were recently made in South Africa and Argentina, where they may have originated (Pemberton & Cordo 2001, this volume). Considerations for their use against *C. cactorum* in

TABLE 2. KNOWN DISEASES OF *CACTOBLASTIS*.

Agent	Host	Stage attacked	Degree of attack	Place of attack	Reference	Presumed specificity
Fungi						
Beauveria sp.	*C. cactorum*	Larvae, winter generation	High death rate in many places	Australia	Dodd 1940	Broad
Beauveria prob. *bassiana* (Bals.) Vuill.	*C. cactorum*	Larvae and pupae	3.3 (summer) to 5.2% (winter)	South Africa	Pettey 1948	Broad
Microsporidia						
Nosema cactoblastis Fantham	*C. cactorum*	All stages	0-100% winter; 0-18.7% summer	South Africa	Fantham 1939 Pettey 1948	Narrow
Nosema cactorum Fantham	*Cactoblastis* sp.	All stages		South Africa	Fantham 1939 Pettey 1948	Narrow
Nosema sp. or spp.	C. cactorum	All stages, detected in larvae	0 to 5.8% summer	Argentina	Pemberton & Cordo 2001	?

North America are discussed in that paper. *Nosema*, like other pathogens, usually have their greatest impact at high host population levels. This characteristic might limit their impact on *C. cactorum* if they were introduced against the moth in North America.

Bacillus thuringensis Berliner and its products are commonly used in biological control programs against pest Lepidoptera (Beegle & Yamamoto 1992). *Cactoblastis cactorum* larvae could probably be killed by the disease and its products, but they would be unlikely to contact it because they feed entirely within the pads of their prickly pear hosts.

Biological control using parasitoids known to attack *Cactoblastis cactorum* in Florida

An alternative to importing exotic parasitoids for *C. cactorum* control could be to employ the parasitoids already known to attack the moth in Florida (Table 3). Only three species, two chalcidoid pupal parasitoids and one trichogrammatid egg parasitoid, are known (Bennett & Habeck 1992). One of the chalcidoids, *Brachymeria ovata* Say, attacked 55% of *C. cactorum* pupae at one site. The other chalcidoid, *B. pedalis* Cresson, was reared from a single pupa. The host range of *B. ovata* is very wide; it has been reared from diverse butterflies and moths (Peck 1963). *Brachymeria pedalis* may be limited to cactus moths (Thompson 1943; Krombein et al. 1979; Mann 1969). This parasitoid probably moved to *C. cactorum* from *Melitara prodenialis* Walker, a native cactus moth host of the parasitoid (Krombien et al. 1979) which attacks platyopuntias (prickly pears) in Florida. The egg parasitoid, an unidentified *Trichogramma*, was recorded to attack two egg sticks. Since this species was not determined, its other hosts are unknown, but most *Trichogramma* species have broad host ranges (Pinto & Stouthamer 1994).

All three of these parasitoids could be collected, reared to increase their numbers, and then released against *C. cactorum* in the field. The *Brachymeria* spp. might be reared on easily cultured Lepidoptera such as the pyralid flour moths, *Plodia* and *Ephestia* spp., if they proved to be acceptable hosts. It also might be feasible to mass rear the *Trichogramma* sp. on other more easily grown moth eggs and then release on particular *C. cactorum* populations. These might be employed against *C. cactorum* attacking vulnerable *Opuntia* such as *O. spinossisima* in the Florida Keys, or *O. stricta,* at the leading edge of the moth's populations in northern Florida and southern Georgia. The suitability of these parasitoids for this approach is unknown. Inundative releases of *Trichogramma* could have an adverse impact on non-target Lepidoptera, especially rare butterflies such as those in the Florida Keys (Bennett & Habeck 1992). Inundative releases of *Brachymeria pedalis* could also depress *Melitara prodenialis* populations and perhaps other cactus moths, but should impact no other species. *B. ovata* releases could potentially affect a wide array of Lepidoptera.

The relative lack of parasitoids attacking *C. cactorum* in Florida, which could be used in this approach, may reflect the limited knowledge of its natural enemies in Florida and also the relatively short time that the moth has been in the state. Increased research may reveal additional parasitoids that could be employed in this approach.

Biological control using cosmopolitan generalist parasitoids known to attack *Cactoblastis cactorum*

Perhaps more suitable for the inundative biological control approach are two generalist parasitoids known to attack *C. cactorum* (Table 4). A braconid wasp, *Bracon hebetor* Say, parasitized up to 25% of the larvae in South Africa (Pettey 1948) and *Trichogramma minutum* Riley parasitized up to 32% of the moth's eggs in Australia (Dodd 1940). These attack rates were naturally occurring. Higher rates of attack might be obtained with inundative releases into *C. cactorum* populations. Both parasitoids already occur in North America, and *T. minutum* has been used previously in inundative biological control of many pest insects (Li 1994), including the sugarcane borer *Diatraea saccharalis* (Fab.) in Florida (Wilson 1941). *Trichogramma minutum* is easily reared on a variety of insect eggs and is also available commercially. *Bracon hebetor* could be mass reared on some of its known hosts that are easily raised, including *Galleria mellonella* (L.), *Plodia interpunctella* (Hübner) and *Sitotroga cerealella* (Olivier).

These parasitoids, like those already recorded to attack the cactus moth in Florida, could be released into *C. cactorum* populations that threaten rare cacti, and populations at the leading edge of the moth's expansion. These parasitoid species would attack non-target insects. *Bracon hebetor* parasitizes at least three families of moths (Krombein et al. 1979) but prefers concealed hosts like most *Bracon* species (Askew 1971). *Trichogramma minutum* is known to attack insects in many different orders (Clausen 1940). The release of this parasitoid should not be made in areas where rare butterflies or moths occur. *Trichogramma* species are usually habitat specialists and many have poor dispersal abilities (Orr et al. 2000). Both control of *C. cactorum* and impacts on non-target species brought by these wasps would probably be temporary because neither wasp may persist in the environment. Periodic releases would be necessary for ongoing control of *C. cactoblastis.*

Biological control of *Cactoblastis cactorum* with parasitoids of related North American cactus moths

The 14 parasitoids listed in Table 5 are reported to parasitize seven cactus moth species in

TABLE 3. PARASITOIDS KNOWN TO ATTACK *CACTOBLASTIS CACTORUM* IN FLORIDA.

Parasitoid species	Other hosts[1]	Stage attacked	Degree of attack in *C. cactorum*	Reference	Presumed specificity
Hymenoptera					
Chalcididae					
Brachymeria ovata Say	Diverse butterflies and moths	Pupae	To 55%	Bennett & Habeck 1992 Peck 1963	Broad
B. (*Pseudobrachymeria*) *pedalis* Cresson	Other specialised phycitid moths attacking cacti	Pupae	One pupa in 1991	Bennett & Habeck 1992	Moderately narrow?
	Melitara prodenialis Walker			Krombein et al. 1979	
	M. dentata (Grote)			Mann 1969	
	Olycella junctolineella (Hulst)			Mann 1969	
	Alberada parabates (Dyar)			Mann 1969	
	Ozamia fuscomaculella clarefacta (Dyar)			Mann 1969	
Trichogrammatidae					
Trichogramma sp.	Yes, unknown	Egg	Two egg sticks	Bennett & Habeck 1992	Broad

[1]Recorded host not necessarily in Florida.

TABLE 4. COSMOPOLITAN GENERALIST PARASITOIDS KNOWN TO ATTACK *CACTOBLASTIS* THAT ARE KNOWN TO OCCUR IN NORTH AMERICA.

Parasitoid species	Other hosts	Stage attacked	Degree of attack in *C. cactorum*	Place of attack	Reference	Presumed specificity
Hymenoptera						
Braconidae						
Bracon hebetor Say	*Heliothis obsoleta* (Noctuiidae), *Ephestia, Galleria, Plodia, Vitula* (Pyralidae: Phycitinae), *Sitotroga* (Gelechiidae)	Larvae	To 25%	South Africa	Pettey 1948 Krombein et al. 1979	Broad
Trichogrammatidae						
Trichogramma minutum Riley	Many species	Egg	To 32%	Australia	Dodd 1940	Broad

three genera in the tribe Phycitinae (Pyralidae). These moths include three *Melitara*, three *Olycella* and one *Ozamia* species. All feed within the pads of prickly pear cacti. The 14 parasitoids include: one chalcid pupal parasitoid, five ichneumonid parasitoids (four attack larvae and one species is an egg-larval parasitoid), five braconid wasp larval parasitoids, and three tachinid flies that attack both larvae and pupae. *Brachymeria pedalis* (Chalcididae), *Temelucha sinuatus* Cushman (Ichneumonidae), and *Apanteles etiellae* Vierek (Braconidae) appear to be specialists of cactus moths, whereas the other parasitoids appear to be generalists. The degree of attack of these parasitoids on their native hosts is unknown to us, so it is difficult to sense how much parasitism they might induce in *C. cactorum*. The ability of these parasitoids to attack *C. cactorum* is also unknown, except for *Brachymeria pedalis* that attacks the moth in Florida (Bennett & Habeck 1992). However, *C. cactorum* probably would be a suitable host for most of these parasitoids.

Releases of specialist parasitoids of *Melitara prodenialis* into *C. cactorum* populations could be effective because the moths are closely related, use *Opuntia* species, and are partly sympatric, so occupy areas of climatic similarity. Introduction of any of the ten North American cactus moth parasitoids, distributed beyond the current distribution of *C. cactorum*, would be classical introductions to Florida. These parasitoids are mostly from western cactus moths and may be less suitable for *C. cactorum* control in Florida and Georgia because they may be unable to survive and develop effective populations in this humid region.

Potential risks of biological control of *Cactoblastis cactorum* in North America

The potential risks associated with biological control of *C. cactorum* in North America are both direct and indirect. The direct risk is the reduction of populations of non-target insects by parasitoids employed against the moth. The insects most likely to be harmed by the introduction of "specialist" parasitoids from the native South America range of *C. cactorum* are related cactus moths in North America (Table 6). The level of risk will depend on the level of specialization. There are at least 16 species of cactus moths (Pyralidae: Phycitinae) in eight genera that occur in the U.S., Mexico and the West Indies (Heinrich 1939). In addition, in the same geographic areas there are at least seven species of specialist cactus feeding moths in seven genera in four other families: the Pyraustidae (*Megastes*, *Noctuelia*, and *Mimorista*), Gelechiidae (*Metapleura* and *Aerotypia*), Tineidae (*Dyotopasta*), and Gracillariidae (*Maramara*) (Mann 1969). It is probable that the highest risk of specialist parasitoids from *C. cactorum* in its native range would be to cactus moths most similar to *C. cactorum* and which co-

TABLE 5. PARASITOIDS OF RELATED CACTUS MOTHS (PYRALIDAE: PHYCITINAE) WHICH MAY HAVE POTENTIAL AS CONTROL AGENTS OF *CACTOBLASTIS CACTORUM*.

Parasitoid species	Cactus moth hosts (Pyralidae: Phycitinae)	Other hosts	Stage attacked	Degree of attack	Reference	Presumed specificity
Hymenoptera						
Chalcididae						
Brachymeria (*Pseudobrachymeria*) *pedalis* Cresson	*Melitara prodenialis* Walker *M. dentata* (Grote) *Olycella junctolineella* (Hulst) *Ozamia fuscomaculella* (Dyar) = *O. odiosella* *Alberada parabates*		Pupae	?	Mann 1969	
Ichneumonidae						
Temelucha sinuatus Cushman) (*Temelucha* = *Cremastus*)	*Melitara prodenialis* Walker *M. dentata* (as *M. doddalis*) *Cactobrosis strigalis* (Barnes & McD.), *Rumatha glaucatella* (Hulst)		Larvae	?	Mann 1969 Krombein et al.1979	Relatively narrow?
T. facilis (Cresson)	*M. denata* (as *M. doddalis*)	*Crambus*, *Hellula*, *Ostrina* (Pyralidae), *Isophrictis* (Gelechiidae)	Larvae	?	Mann 1969 Krombein et al. 1979	Broad
Temelucha sp.	*Cahela ponderosella* Barnes & McD.		Larvae	?	Mann 1969	?
Trichomma prob. *maceratum* (Cresson)	*M. dentata*	*Etiella*, *Pima* (Pyralidae), *Barbara* (Torticidae)	Larvae	?	Mann 1969 Krombein et al. 1979	Broad
Chelonus electus (Cresson) (= *C. texanus*)	*M. dentata* (as *M. doddalis*) *Ozamia fuscomaculella* = *O. odiosella*, *Alberada parabates*	*Heliothis* (Noctuidae); *Laphygma*, *Prodenia*, *Ephestia*, *Loxostege* (Pyralidae)	Egg (emerges from larva)	?	Mann 1969 Muesebeck et al. 1951	Broad
Mesostenus gracilis Cresson	*Ozamia fuscomaculella* = *O. odiosella*	*Anagasta*, *Cadra*, *Ephestia*, *Euzophera*, *Homeosoma*, *Laetilia* (Pyralidae)	?	?	Krombein et al. 1979	Broad
Braconidae						
Apanteles etiellae Vierek	*Melitara prodenialis* *Cahela ponderosella* *Olycella*	*Eteiella*, *Cansarsia*, *Elasmopalpus*, *Psorosina*, *Ufa* (Pyralidae)	Larvae	?	Mann 1969 Krombein et al. 1979	Broad
A. megathymi Riley	*Olycella nephelepasa* (Dyar)	*Megathymus* (Hesperiidae)	Larvae	?	Mann 1969 Krombein et al. 1979	Broad
Apanteles sp.	*Olycella junctolineella* (Hulst)		Larvae	?	Mann 1969	?
A. mimoristae Muesebeck	*Olycella junctolineella*	*Mimorista*, *Hymenia* (Pyralidae: Pyraustinae)	Larvae	?	Krombein et al. 1979	Broad

TABLE 5. (CONTINUED) PARASITOIDS OF RELATED CACTUS MOTHS (PYRALIDAE: PHYCITINAE) WHICH MAY HAVE POTENTIAL AS CONTROL AGENTS OF *CACTOBLASTIS CACTORUM*.

Parasitoid species	Cactus moth hosts (Pyralidae: Phycitinae)	Other hosts	Stage attacked	Degree of attack	Reference	Presumed specificity
Bracon hebetor Say	*Melitara* sp., Texas (In cages)	*Anagasta*, *Cadra*, *Ephestia*, *Galleria*, *Laetilia*, *Moodna*, *Plodia*, *Vitula* (Pyralidae); *Phothorimaea*, *Sitotroga* (Gelechiidae)	Larvae	?	Dodd 1940 Muesebeck et al. 1951 Krombein et al. 1979	Broad
	M. dentata (as *M. doddalis*)				Mann 1969	
	Ozamia fuscomaculella = *O. odiosella*				Mann 1969	
Heterospilus melanocephalus Rohwer	*Olycella junctolineella*	*Noctuelia* (Pyralidae: Pyraustinae)	?	?	Muesebeck et al. 1951	?
Diptera						
Tachinidae						
Phorocera texana Aldrich & Webber	*Melitara prodenialis* *M. dentata* *Olycella junctolineella* *Olycella nephelepasa*	Hymenoptera: Diprionidae, Tenthridindae; diverse Lepidoptera	Larvae, pupae	?	Mann 1969 Arnaud 1978	Broad
Phorocera comstocki Williston	*M. dentata*	Hymenoptera: Diprionidae Lepidoptera: Cossidae, Megathymidae, Pyralidae—Ostrina	Larvae, pupae	?	Mann 1969 Arnaud 1978	Broad
Lespesia aletiae Riley	*Olycella junctolineella*	Coccinellidae (*Epilachna*), diverse Lepidoptera	Larvae, Pupae	?	Mann 1969 Arnaud 1978	Broad
Lespesia sp.	*Melitara prodenialis*	diverse Lepidoptera	Probably larvae, pupae	?	Mann 1969 Arnaud 1978	Broad

TABLE 6. CACTUS MOTHS (PYRALIDAE: PHYCITINAE) IN U.S., MEXICO, AND THE WEST INDIES THAT FEED IN *OPUNTIA* AND COULD BECOME NON-TARGETS OF A BIOLOGICAL CONTROL EFFORT AGAINST *CACTOBLASTIS CACTORUM*.[1]

Moth species	Host plant in *Opuntia* subgenus	Gregarious or solitary larvae	Feeding site	Region of occurrence	Size of geographic range	Warm or cold area
Alberada bidentella (Dyar)	Cylindropuntia prob.	Solitary	Stems	Western US	Large	Warm
A. holochlora (Dyar)	Cylindropuntia prob.	Solitary	Stems	Texas	Small	Warm?
Alberada parabates (Dyar)	Cylindropuntia	Solitary	Stems	W US-Mex	Large	Warm
Cahela ponderosella Barnes & McDunnough	Cylindropuntia	Solitary	Stems	W US-Mex	Large	Warm
Melitara dentata (Grote)	Platyopuntia	Gregarious	Pads	W US	Large	Warm-Cold
M. prodenialis Walker	Platyopuntia	Gregarious	Pads	FL to TX	Large	Warm-Cold
Olyca phryganoides Walker	Platyopuntia	Solitary	Pads?	Hispaniola	Small?	Warm
Olycella junctolineella (Hulst)	Platyopuntia	Gregarious-Solitary	Pads	W US-Mex	Small	Warm
O. nephelepasa (Dyar)	Platyopuntia	Gregarious-Solitary	Pads	W US-Mex	Large	Warm-Cold
O. subumbrella (Dyar)	Platyopuntia	Gregarious-Solitary	Pads	W US-Mex	Large	Warm-Cold
Ozamia odiosella = *O. fuscomaculella* (Wright)	Platyopuntia	Solitary	Fruit	W US-Mex	Large	Warm
Ozamia lucidalis (Walker)	Platyopuntia	Solitary	Fruit	FL-W Indies	Large	Warm
O. thalassophila Dyar	Cylindropuntia	Solitary	Fruit	CA	Small?	Warm
Rumatha bihinda (Dyar)	Cylindropuntia	Solitary	Stems	W US	Large	Warm
R. glaucatella (Hulst)	Cylindropuntia	Solitary	Stems	Texas	?	Warm
R. polingella (Dyar)	Cylindropuntia	Solitary	Stems	Arizona	Small	Warm

[1]Extracted from Heinrich, 1939.

occur with it in North America. *Melitara prodenialis*, with gregarious larvae in pads of the same hosts, and an overlapping geographic range, would be the most vulnerable cactus moth. It occurs from Florida to Texas, and introduced parasitoids which adopt the moth could move via this new host from Florida to Texas, where many other pad feeding cactus moths in the genera *Melitara, Olycella, Megastes, Mimorista and Mermara* occur**.** Cactus moths less likely to be attacked by introduced South American parasitoids are probably those most dissimilar to *C. cactorum*. These would be species that are not gregarious (*Olycella* and *Ozamia*), which attack flower buds and fruits instead of pads (*Ozamia, Noctuelia*), which use cylindropuntias (the chollas) instead of platyopuntias (*Alberada* and *Cahela*) or other genera of cacti (*Yosemitia*). Cactus moths that have many host plants and large geographic ranges would probably also be at less risk. Cactus moths that occur in cold areas, where *C. cactorum* and its introduced parasitoids are unlikely to colonize, should experience the least risk.

The risks associated with the introduction of parasitoids of native cactus moths from the western United States would be somewhat greater than that of specialist parasitoids introduced from *C. cactorum* in South America, because they would come from genera other than *Cactoblastis.* As such, they would likely have broader host ranges and be more likely to attack non-target moths.

The risks associated with inundative releases of parasitoids already associated with *C. cactorum* in Florida should be relatively minor because neither the geographic range nor the host range would be likely to increase. Large numbers of parasitoids could temporarily suppress host populations of insects in the area of release. The risk of inundative releases of cosmopolitan generalist parasitoids, such as *Trichogramma minutum* and *Bracon brevicornis*, could be the temporary suppression of many non-target insects in the area of release. Because these parasitoids are already in Florida, no increase in their geographic ranges would occur. A similar degree of risk would be associated with the use of generalists pathogens such *Beauveria bassiana*.

The risks involved with the use of the *Nosema* species could be very limited if they prove to be the narrow specialists that they are suspected to be, particularly if they have transovarial transmission and kill larvae within the pads where they feed. If they are not species or genus level specialists the risk will be commensurate with their host breadth.

The indirect risks of biological control relate to the potential effects caused by reducing populations of non-target insects, particularly effects to their host plants. The main effect could be increased populations of some *Opuntia* species due to the reduction of the cactus moths that help regulate their populations. This increase could allow some prickly pear cacti to become artificially abundant, enabling them to displace other species and to dominate natural communities. These plants could also become troublesome on rangeland where some *Opuntia* already tend to be weedy. Prickly pear cacti, including the Florida native *O. stricta*, are some of the worst weeds in the Old World, which has no native *Opuntia*. This is thought to occur, at least in part, because of the lack of regulating natural enemies (Moran and Zimmermann 1984). An additional indirect effect could be to negate the successful biological control of weedy *Opuntia* by *C. cactorum* in the Caribbean if introduced parasitoids spread to that region (Bennett & Habeck 1992). Finally, it is also possible that the introduction of parasitoids from South America that attack native cactus moths could result in competition with native parasitoids that lowers the overall level of control they provide. This might actually result in increased damage by native moth species to native cacti (e.g., Ferguson & Stiling 1996).

The criteria used to consider and rank the risk to non-target insects by different biological control approaches for *C. cactorum* control are shown in Table 7. These criteria relate in various ways to estimating the degree of use of non-target insects. Table 8 shows the rankings of the various approaches from the least to most risky. Both the criteria and the resulting rankings are not absolute, but are attempts to further compare and contrast relative risks. Both the least risky and most risky approaches in our scheme involve the importation of agents from the moth's native range. The least risky approach is the introduction of coevolved specialist parasitoids to the genus *Cactoblastis.* The most risky approach is the introduction of stenophagous agents from the moth and its relatives in South America, as they would likely have the greatest and most persistent effects on native, non-target cactus moths. The degree of host specificity of prospective biological control agents is the key aspect in our ranking.

Risks can be minimized or avoided by careful host specificity research on parasitoids considered

TABLE 7. CRITERIA TO CONSIDER AND RANK THE RISK TO NON-TARGET SPECIES OF BIOLOGICAL CONTROL APPROACHES FOR *CACTOBASTIS CACTORUM*.

Degree of host specificity of agent
If new hosts will be exposed
Relative number of new hosts that could be adopted
If the agent's geographical range will increase
Likely persistence of non-target use
If rare species will be exposed
Size of the treatment area

TABLE 8. BIOLOGICAL CONTROL APPROACHES FOR *CACTOBLASTIS CACTORUM* RANKED BY RELATIVE RISK TO NON-TARGET SPECIES (RANKED FROM LEAST TO MOST RISKY).

1. Classical introductions from South America of parasitoids specific to the genus *Cactoblastis*
2. Inundative releases of cactus moth parasitoids from Florida in Florida
3. Inundative releases of parasitoids that attack *C. cactorum* in Florida
4. Inundative releases of generalist parasitoids known to attack *C. cactorum* that also occur in Florida
5. Classical introductions of western cactus moth parasitoids that attack gregarious larvae
6. Classical introductions of other western cactus moth parasitoids
7. Classical introductions of stenophagous *Cactoblastis* parasitoids from South America

for introduction for biological control of *C. cactorum* in North America. However, it appears that the currently known parasitoids of *C. cactorum* are unlikely to be limited to the genus *Cactoblastis*, the level of specificity needed to avoid use of non-target insects. This may preclude their use as biological control agents of *C. cactorum* in North America. The relative risks and benefits of any such introduction would have to be carefully evaluated.

CONCLUSIONS

While it appears that the threat is substantial, the assumption that *C. cactorum* will devastate native North American *Opuntia,* as it did to exotic weedy *Opuntia* for which it was employed in Australia and elsewhere in the world, may be usefully questioned. Native *Opuntia* are different than the exotic weedy *Opuntia* in several important respects. Native *Opuntia* usually occur at lower densities and have complexes of specialist herbivores. These herbivores might effectively compete with *C. cactorum* and the predators and parasitoids of these native herbivores could limit the moth. The native herbivores might also reduce the suitability of the *Opuntia* plants as food for *C. cactorum.* However, the fact that *C. cactorum* did devastate native weedy *O. stricta* and other native *Opuntia* on Nevis (Simmonds & Bennett 1966) suggests that the threat is real. *Cactoblastis cactorum* was introduced to Nevis Island in the Caribbean more than 40 years ago to control weedy native *Opuntia* in a part of the world where the cactus family is an indigenous and diverse part of the flora (Britton & Rose 1937). Prior use of *C. cactorum* was against weedy exotic *Opuntia* in parts of the world without native cacti (Moran & Zimmermann 1984). The project in Nevis did not consider the conservation aspects of introducing the moth to the Caribbean (Fred Bennett, pers. comm.). Biological control practices during that era did not usually consider possible conservation consequences of introductions.

The use of biological control to try to correct, what might be seen in hindsight, a biological control error might seem appropriate. But it is important to carefully consider the actual capability of biological control to reduce the *C. cactorum* threat in North America. If the primary goal is to stop the spread of the moth, biological control is probably not the best tool. Inundative release approaches, as discussed above, might be both difficult and expensive to apply. The populations of the moth occur mostly along coastal Florida and Georgia. Their *Opuntia* host populations are scattered at various densities in complexes of natural vegetation. This situation is quite different from the homogeneous row crop environments where inundative biological control has been successful. The identification of a sex pheromone from *C. cactorum*, that could be combined with an insecticide to trap and kill the moth, might do a better job of stopping its spread. Biological control may, however, be able to reduce existing populations of the moth. The possibility of controlling *C. cactorum* must be carefully weighed against the direct and indirect risks of the approach. Although parasitoids may be able to reduce populations of the moth, they probably will produce some degree of non-target effects. The use of host-specific biological control agents is the best solution since they would pose the least risk. *Nosema cactoblastis* might be such an agent and it may be useful to control the moth.

Whether or not the risks of biological control are acceptable will depend on the level of the *C. cactorum* threat to native and economic *Opuntia* as it continues to spread and the degree to which introduced biological control agents might disrupt native *Opuntia* ecosystems. In light of our inability to predict the benefits of a given biological control agent, it might prove difficult to reach agreement about what level of risk is acceptable.

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NOSEMA (MICROSPORIDA: NOSEMATIDAE) SPECIES AS POTENTIAL BIOLOGICAL CONTROL AGENTS OF *CACTOBLASTIS CACTORUM* (LEPIDOPTERA: PYRALIDAE): SURVEYS FOR THE MICROSPORIDIA IN ARGENTINA AND SOUTH AFRICA

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ABSTRACT

Cactoblastis cactorum Berg is an invasive moth in North America where it damages and threatens many native *Opuntia* cacti. *Nosema* species of *C. cactorum* may have potential as biological control agents of the moth. Surveys for *Nosema* species were made in South Africa, where two of these Microsporidia were described from the moth and in Argentina where these pathogens may have originated. No *Nosema* were found in the *C. cactorum* larvae from South Africa and low levels of infection (0-6%) were found in the South American larvae. The low abundance of *C. cactorum* and the time of collection (austral summer) may be the reasons for the absence of or rarity of *Nosema* in these surveys. Winter collections of the larvae are suggested to obtain more abundant *Nosema* for evaluation as potential biocontrols of *C. cactorum*.

Key Words: biological control, surveys, insect pathogens, *Opuntia*

RESUMEN

Cactoblastis cactorum Berg es una polilla invasora en Norte America, donde daña y amenaza muchas especies nativas de *Opuntia*. Especies de *Nosema* que atacan a *C. cactorum* podrían tener potencial como agentes de control biológico. Se realizaron búsquedas de *Nosema* en Sudafrica donde dos de estos microsporidiosfueron descriptos y en Argentina donde estos patógenos podrían haberse originado. No se hallaron *Nosema* en larvas de *C. cactorum* de Sudafrica y se hallaron niveles muy bajos de infección (0-6%) en las larvas de Sud America. La baja abundancia de *C. cactorum* y el momento de las colecciones (verano austral) podrían ser las razones de la ausencia o rareza de *Nosema* en las búsquedas. Se sugieren colecciones de larvas durante el invierno para obtener mayor abundancia de *Nosema* para su evaluación como un agente potencial de control biológico de *C. cactorum*.

Cactoblastis cactorum Berg, is a famous biological control agent of weedy prickly pear cacti (*Opuntia*) in many parts of the world (Moran & Zimmermann 1984). This Argentine moth was introduced to Nevis in the Caribbean in 1957 for the control of native weedy *Opuntia* (Simmons & Bennett 1966). In 1989, *C. cactorum* was found in Florida where it attacks native *Opuntia* (Pemberton 1995; Johnson & Stiling 1996). The moth has the potential to spread to the western United States and Mexico where it could harm numerous native and economic *Opuntia* (Strong & Pemberton 2000; Zimmermann et al. 2000).

The potential and risk of using biological control as a possible solution to the *C. cactorum* threat was raised by Bennett and Habeck (1992) and is discussed in detail by Pemberton and Cordo (2001, this volume). Recorded parasitoids of the moth (Mann 1969; Zimmermmann et al. 1979) may have potential to control it, but they probably lack the host specificity needed to avoid use of native cactus moths and other Lepidoptera. Some insect pathogens such as *Nosema* species may be potent biological control agents of insects and also have enough host specificity to prevent non-target effects to native insects (R. Soper, pers. comm.). In many areas of the United States, *Nosema pyrausta* (Paillot) is the most important control agent of the European corn borer, *Ostrina nubialis* (Hübner) (Kogan et al. 1999). At times, *N. pyrausta* infects and kills 100% of the corn borers.

Two *Nosema* species have been recorded to attack *Cactoblastis*, both in South Africa (Fantham 1939). *Nosema cactoblastis* Fantham was described from *C. cactorum* which was originally imported for biological control from Australia. The second species, *N. cactorum* Fantham, was described from another *Cactoblastis* species, of uncertain identity, that was imported directly from Argentina. In South Africa, *N. cactoblastis* caused high mortality of *C. cactorum* larvae and pupae, and seriously hindered the ability of the moth to control weedy *Opuntia* (Petty 1948). Given this impact and the possibility that these *Nosema*

might have narrow host ranges, we decided to try to acquire them so their potential as biological control agents of the *C. cactorum* in the United States could be examined. They were sought in both South Africa and in Argentina where they may have originated.

Materials and Methods

In South Africa, searches were made of *Opuntia ficus-indica* (L.) Miller plants growing at 15 sites in the eastern Cape during March 1996 by the senior author and P. Hulley of Grahamstown University. Most of the searches were on wild plants growing in the Uitenhage area, where high levels of *N. cactoblastis* infection of *C. cactorum* had been reported (Petty 1948). Additional searches were made at Fort Hare in two plantations of *O. ficus-indica* cultivated for fruit, and two wild populations. Plants varied greatly in size (from approximately 1-4 meters tall) and density (from scattered individual plants to dense thickets of intertwined plants, to rows of spaced plants in the plantations). At each site pads with characteristic damage (exit holes, frass, hollowed out, and/or with decay) and egg sticks were looked for, then cut open for verification of living larvae. A total of 429 living larvae, from 41 pads collected at nine sites, and six frass samples were shipped to Argentina for *Nosema* detection. Argentine importation permits enable the larvae to be shipped to the Instituto Nacional de Tecnología Agropecuaria quarantine facility in Buenos Aires. After confirmation of the identification, the larvae were transferred in secured containers to Carlos Lange, contracting pathologist at University of La Plata, for *Nosema* detection. Each living larva was squashed to create a smear on a glass slide. These smears were then examined with phase-contrast microscope to search for the characteristic spores of *Nosema*.

In Argentina, surveys were made in the northern half of the country, which is the largest part of the native range of *C. cactorum*. In March 1995, we surveyed *Opuntia* species in the Argentine provinces of Entre Rios, Corrientes, Chaco, Formosa, and Santa Fe, and also along the eastern side of the Uruguay River in Uruguay. Additional surveys were made by the second author in Chaco and Formosa in Argentina and Paraguay during November-December 1995, and also in Buenos Aires, Cordoba, Santiago del Estero, Tucuman and Salta during December 1996. A total of 54 sites were surveyed in Argentina, three in Uruguay and one in Paraguay. A total of 867 plants were examined, 575 belonging to five identified *Opuntia* species and another 66 from *Opuntia* species that were not identified (Table 1). *Cactoblastis cactorum* was found in wild-growing *O. aurantiaca* Lindley, *O. paraguayensis* Schumann and *O. ficus-indica* at 14 sites. No larvae were found in either *O. monacantha* Haworth, *O. quimilo* Schumann or from unidentified *Opuntia*. A total of 528 larvae were collected for *Nosema* detection. *Opuntia* pads containing *C. cactorum* larvae were either transferred to La Plata for *Nosema* detection or reared in the laboratory to late instars to enhance detection and then transferred to La Plata for *Nosema* detection.

Results and Discussion

Nosema was not detected in the 342 South African larvae or the six frass samples examined. Low levels of *Nosema* were detected in only 4 of the 528 larvae collected in Argentina. *Nosema* spores were found in 2 of the 34 (5.88%) larvae collected from *O. paraguayensis* at Tres Isletas in Chaco Province in March 1995. The other *Nosema* infections were in larvae from *O. ficus-indica* in Cordoba Province sites collected in December 1996. At Cruz del Eje, 1 of 68 (1.28%) were infected and at Dean Funes, 1 of 26 (3.85%) were infected. The low levels of *Nosema* infection found is consistent with the apparent health of collected larvae from both South Africa and Argentina. To-

Table 1. *Cactoblastis cactorum* collection in Argentina and detected *Nosema*.

			C. cactorum larvae			
Opuntia species	No. sites with the species[1]	No. plants/ species	Total	Mean no. plant/species	Mean no. species/site	No. with *Nosema*
O. aurantiaca	15	124	135	1.08	9	0
O. ficus-indica	7	126	154	1.22	22	2
O. monacantha	2	11	0	0	0	0
O. paraguayensis	36	482	239	0.49	6.64	2
O. quimilo	7	58	0	0	0	0
O. spp.	11	66	0	0	0	0
Total	58	867	528			4

[1]Twenty sites had more than one *Opuntia* species.

tal mortality was less than 5% (25 of 600) in the Argentine larvae and less than 25% (87 of 429) in the South African larvae. This mortality probably resulted from handling and shipping conditions. Due to the low number of larvae infected, no effort was made to culture the spores to characterize the *Nosema* species involved.

The low incidence of *Nosema* in South America material may relate to the low numbers of *C. cactorum* encountered. Forty-four of the 58 Argentine sites examined (75.9%) had no detectable populations of the moth. The mean number of *C. cactorum* at these 58 sites was 9.1 larvae. At the 14 sites, where the moth was present, the mean number of larvae was 37.7 per site. Although only three of five (or more) *Opuntia* spp. plants examined had *C. cactorum* larvae, all are known to be host of the moth (Dodd 1940). *Opuntia ficus-indica* and *O. aurantiaca* had an average of one larva per plant (1.09 and 1.22 respectively) (Table 1). The most common prickly pear encountered, *O. paraguayensis*, had less than one (0.49) larva per plant. *Opuntia ficus-indica* had more larvae per site, a mean of 22 compared to about 7 for *O. paraguayensis* and 9 for *O. aurantiaca*. This may be due to a greater number of *O. ficus-indica* per site (18 compared to 13.4 and 8 for the others).

The absence of *Nosema* samples from South Africa may also relate to the relatively low levels of *C. cactorum* in the areas surveyed. The moth was more common than in South America occurring at 60% (9/15) of the sites compared to 24% (14/58) in South America. However, at five of the South Africa sites, only a single infested pad was found. The other 4 sites infested had 6, 6, 9 and 15 infested pads despite the large numbers of plants at some sites.

The absence of *Nosema* in South Africa and the low levels of the disease found in South America probably also relate to the season of collections - summer. In South Africa, *Nosema cactoblastis* infections of *C. cactorum* are known to be much less abundant in summer than in the winter (Petty 1948). For instance, at one South African site, *N. cactoblastis* was detected in 100% of the sampled larvae of the winter brood but in none of the larvae of the following summer brood. The infection rates of *Nosema* species we detected in Argentina (0.0, 1.28, 3.85, and 5.88%) are comparable to the infection rates (an average of 2%) at six coastal sites in South Africa during the summer (Petty 1948). These same sites had an average infection rate of 55.6% during the winter.

The absence of a formal biological control program for *C. cactorum* ended the research. Our efforts were opportunistic and done in conjunction with other research. We recognize that our collection times were not optimal for the detection of *Nosema*. The recent spread of the moth from Florida to Georgia and the increased concern that it will continue to spread and damage valued native *Opuntia* in North America, suggests that acquisition and examination of *Nosema* species associated with the moth should be continued. The *Nosema* spores we found are frozen and may be able to be cultured and evaluated. Renewed efforts to obtain *Nosema* species from field populations of *C. cactorum* should be more successful if winter collections are made in South Africa and Argentina.

The South African experience with *N. cactoblastis* suggests that the disease (its occurrence in the more humid winter months and its greater impact in more humid coastal regions) would be more effective in humid areas such as Florida and in the Southeast, than in the drier areas of the West. The effectiveness of the *Nosema* in low populations of *C. cactorum* is expected to be less than in high populations of the moth.

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APPLICATIONS OF F_1 STERILITY FOR RESEARCH AND MANAGEMENT OF *CACTOBLASTIS CACTORUM* (LEPIDOPTERA: PYRALIDAE)

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ABSTRACT

The unintentional arrival of the cactus moth, *Cactoblastis cactorum* (Berg), in Florida has raised concerns for the safety of native and rare *Opuntia* species in the Florida Keys and the potential spread of *C. cactorum* to the *Opuntia*-rich areas of the western United States and Mexico. In addition to threatening the biodiversity of these native ecosystems, such non-target effects would generate negative publicity that could heighten public concern over the use of exotic natural enemies and jeopardize future biological control programs against weeds. In this paper we discuss the use of inherited (F_1) sterility in Lepidoptera to study, predict, and manage the expanding populations of *C. cactorum*. Research areas in which the use of F_1 sterility would be most applicable include (1) elucidation of the host range of *C. cactorum* for key native *Opuntia* species from across the U.S., (2) prediction of the geographic range of *C. cactorum* in the U.S. and Mexico, and (3) delineation of the impact of native natural enemies on the spread of *C. cactorum*. The use of F_1 sterility for control of *C. cactorum* would be most appropriate for (1) eradication of *C. cactorum* from areas of new introductions, or from isolated and/or environmentally sensitive areas such as the Florida Keys, (2) establishment of a barrier by means of release of irradiated moths along the leading edge of the *C. cactorum* geographical range, and (3) provisioning sterile *C. cactorum* in the field as hosts for released natural enemies to increase their initial survival and establishment.

Key Words: cactus moth, sterile insect technique, biological control, inherited sterility

RESUMEN

La accidental introduccion de la palomilla del cactus, *Cactoblastis cactorum* (Berg), al estado de Florida ha incrementado la conciencia sobre la amenaza que esta introduccion causa a las especies nativas y poco comunes de cactus del genero *Opuntia* en los cayos de Florida y concientiza el peligro de esta invasion a las areas ricas en *Opuntia* en el oeste de los Estados Unidos y Mejico. Ademas de amenazar la biodiversidad en estos ecosistemas, la publicidad negativa sobre estos efectos no dirigidos tendra como consecuencia alarmar al publico sobre el use de enemigos naturales importados y afectara el progreso de futuros programas de control biologico de malezas. En este articulo discutimos el uso potencial de la esterilidad adquirida (o esterilidad F_1) en Lepidoptera para estudiar, predecir y manejar las poblaciones de *C. cactorum*. Algunas de las areas de investigacion donde la aplicacion de la esterilidad F_1 es mas apropiada incluyen (1) el estudio de el rango potencial de hospederos de *Opuntia* en los Estados Unidos, (2) predicciones sobre el potencial rango de expansion geografica de esta especie en Estados Unidos y Mejico y (3) el estudio del impacto de los enemigos naturales ya presentes en la expansion del rango de *C. cactorum*. El uso de la esterilidad F_1 para el control de esta especie seria apropiada en el caso de (1) erradicacion de la especie en areas de invasion reciente, en areas aisladas o en areas ecologicas en peligro como los cayos de Florida, (2) el establecimiento de una barrera para impedir la expansion de la especie a traves del uso de insectos irradiados liberados en el frente de invasion y (3) el uso de insectos irradiados en el campo como suplemento alimenticio para asegurar el establecimiento y supervivencia de enemigos naturales liberados para el control de *C. cactorum*.

The control of exotic *Opuntia* cacti (Caryophyllales: Cactaceae) in Australia by the cactus moth, *Cactoblastis cactorum* (Berg) (Lepidoptera: Pyralidae) (Dodd 1940), has long been cited as one of the classic success stories in biological control (Sweetman 1936; Johnson & Stiling 1996). However, the recent unintentional arrival of *C. cactorum* in Florida from the Caribbean has raised concerns for the well being of native *Opuntia* in the southern United States and Mexico (Pemberton 1995; Johnson & Stiling 1998). In the United States, Pemberton (1995) estimated that *C. cactorum* should be able to reach Charleston, SC, San Antonio, TX, and the lower-altitude areas of New Mex-

ico, Arizona and California north to Sacramento. Although specific interactions cannot be predicted at this time, establishment of *C. cactorum* in the southwestern U.S. and Mexico could have devastating effects on the landscape and biodiversity of these native desert ecosystems, and on the forage and vegetable *Opuntia* industries.

No satisfactory method of chemical control has been reported for *C. cactorum* (Habeck & Bennett 1990) and because many of the *Opuntia* species in the U.S. are associated with sensitive ecological areas, widespread use of pesticides has not been recommended. For example, in the Florida Keys *Opuntia* cacti occur together with rare and endangered fauna such as the Schaus swallowtail (*Papilio aristodemus ponceanus* Schaus, Papilionidae), Florida leafwing (*Anaea floridalis* Johnson & Comstock, Nymphalidae) and Bartram's scrub-hairstreak (*Strymon acis* (Drury), Lycaenidae) butterflies (Habeck & Bennett 1990), and the Gerstaeckeria cactus weevil (*Gerstaeckeria fasciata* Pierce, Cryptorhynchinae) (O'Brien, Florida A&M Univ., pers. comm.). In addition to environmental considerations, the economics of treating large tracts of coastal and desert land with pesticides would be prohibitive. The use of systemic insecticides injected into cactus stems was investigated by Pretorius et al. (1986) as a means of protecting ornamental cacti and small populations of endangered cacti, but these insecticides provided inadequate control. In addition, the use of insect pathogens does not appear to hold much promise. Vail et al. (1984) conducted bioassays to determine the susceptibility of *C. cactorum* to the nuclear polyhedrosis virus (AcMNPV) isolated from *Autographa californica* Speyer (Lepidoptera: Noctuidae) and found that *C. cactorum* was only moderately susceptible to the virus.

Classical biological control is another tactic that could be used against *C. cactorum*. In its native habitat in South America several natural enemies have been identified, including *Apanteles alexanderi* Brethes (Hymenoptera: Braconidae), *Phyticiplex doddi* (Cushman) and *P. eremnus* (Porter) (Hymenpotera: Ichneumonidae), *Brachymeria cactoblastis* Blanchard (Hymenoptera: Chalcididae), and *Epicoronimyia mundelli* (Blanchard) (Diptera: Tachinidae) (Habeck & Bennett 1990). However, the host range of these natural enemies and any potential non-target effects should be scrutinized carefully before approval for their release in the U.S. is granted. There are a number of native moth species closely related to *C. cactorum* that attack native *Opuntia* in the U.S. These species are under good biological control by a complex of native natural enemies. It is possible that the introduction of exotic parasitoids or other natural enemies might disrupt this equilibrium and cause secondary pest problems. Similarly, inundative releases of parasitoids, such as *Trichogramma* egg parasitoids (Hymenoptera: Trichogrammatidae), could have adverse non-target effects on desirable Lepidoptera (Habeck & Bennett 1990).

Three genetic control methods have been developed and field-tested against Lepidoptera. These are the sterile insect technique (SIT), inherited sterility (also known as inherited partial sterility or F_1 sterility), and backcross sterility (LaChance 1985). In SIT and F_1 sterility, mass production and release of large numbers of genetically altered (sterilized or partially sterilized) insects are used to insure that when matings occur in the field a significant proportion of these involve a sterile released insect. These methods are unparalleled in their specificity and safety because only the target species is affected. F_1 sterility takes advantage of two unique genetic phenomena in Lepidoptera. First, lepidopteran females generally are much more sensitive to radiation than are males of the same species. This may allow the dose of radiation to be adjusted so that treated females are completely sterile and males are partially sterile. Second, when partially sterile males are outcrossed with wild fertile females the radiation-induced deleterious effects are inherited by the F_1 generation. As a result, egg hatch is reduced and the (F_1) offspring produced are both highly sterile and predominately male. The lower dose of radiation used in this technique increases the quality and competitiveness of the released moths (North 1975). In addition, because F_1 sterile progeny are produced in the field, the release of partially sterile insects offers greater suppressive potential than the release of fully sterile insects (LaChance 1985). Not only is there a magnification of the sterility effect, but the production of F_1 sterile offspring enhances the buildup of native natural enemies that attack the insect pest (Carpenter et al. 1996).

The production of sterile progeny allows developmental and behavioral observations to be made under actual field conditions without the concern of establishing a breeding population. These observations allow for confirmation of oviposition behaviors and host associations, field-testing of larval feeding preferences, and studies of larval development and survival on related plants that are of concern. Also, both the impact that native natural enemies might have over an expanded geographic range of *C. cactorum* and the ability of *C. cactorum* to survive and overwinter under various climatic conditions can be studied with the use of F_1 sterility. While the control potential of releasing partially sterile insects is well documented (Carpenter et al. 1987a, b, c; Carpenter & Gross 1993; Bloem et al. 1999a, b), the latter applications of F_1 sterility are benefits of this technique that to date have not been utilized. In this paper we discuss the application of F_1 sterility to study and manage expanding populations of *C. cactorum*. Research areas in which the use of

F_1 sterility would be most applicable include (1) elucidation of the potential host range of *C. cactorum* for key native *Opuntia* species from across the U.S., (2) prediction of the geographic range of *C. cactorum* in the U.S. and Mexico, and (3) delineation of the impact of native natural enemies on the spread of *C. cactorum*. The most appropriate uses of F_1 sterility as a control tactic against *C. cactorum* include (1) eradication of *C. cactorum* from areas of new introductions, or from isolated and/or environmentally sensitive areas such as the Florida Keys, (2) establishment of a barrier by means of release of irradiated moths along the leading edge of the *C. cactorum* geographical range, and (3) provisioning sterile *C. cactorum* in the field as hosts for released natural enemies to increase their initial survival and establishment.

Applications of F_1 Sterility for Research

Elucidation of the Potential Host Range of *C. cactorum* for Key Native *Opuntia* Species

The larvae of *C. cactorum* are widely polyphagous, feeding on nearly all species of *Opuntia* cactus tested to date (Sweetman 1936; Johnson & Stiling 1996). As such, it is expected that *C. cactorum* will readily attack most *Opuntia* spp. in the U.S. and Mexico. However, the degree to which the moth impacts specific *Opuntia* species varies both in its native habitat and in the places where it has been used as a biological control agent (Mann 1969; Moran 1984; McFadyen 1985). For example, *C. cactorum* control of *O. stricta* (Haw.) Haworth in Australia was enormously successful but its control of *O. ficus-indica* (L.) Miller in South Africa was only moderately successful. Therefore, key *Opuntia* species that represent a cross section of subgenera from different geographical and ecological areas within the predicted geographical range of *C. cactorum* should be tested for their acceptability and suitability as hosts. The host range of *C. cactorum* on Florida *Opuntia* spp. has already been tested (Johnson & Stiling 1996). Although selected *Opuntia* species could be collected and shipped to the *C. cactorum* endemic area for the host-range testing, it would be more desirable and informative if the host-range testing could be accomplished within the natural environment of each candidate species or species complex. Using F_1 sterility, it would be possible to study oviposition behaviors, host associations, and larval feeding preferences under actual field conditions. Transport of fertile *C. cactorum* into these environments would be unthinkable. However, it might be possible to develop acceptable protocols that would allow for the transport of sterile moths or moths carrying F_1 sterility. In this way, there would be no risk associated with any potential escape of *C. cactorum* because the irradiated moths could only produce sterile progeny and, therefore, no reproducing colony could be established. The use of F_1 sterility for these assays should be appropriate because similar studies on different lepidopterans revealed no interactions between radiation treatment and the ability to survive on different hosts/diets and in different environmental conditions (Carpenter et al. 1985, 1987b; Carpenter & Wiseman 1992a, b).

Prediction of the Potential Geographic Range of *C. cactorum*

The geographic range that could be achieved by *C. cactorum* in the U.S. is unknown. Pemberton (1995) compared mean low temperatures for some of its known South American habitats with various North American localities and estimated that *C. cactorum* may colonize as far north as Charleston, SC, San Antonio, TX, and the lower altitude areas of New Mexico, Arizona and California north to Sacramento. Observations on *C. cactorum* distribution in South Africa suggest that the geographical range in the U.S. may be even greater than the estimates by Pemberton (Zimmermann, Plant Protection Research Institute, South Africa, pers. comm.). It is likely that the geographic range of *C. cactorum* in the U.S. will be limited by environmental factors such as temperature and photoperiod rather than by host availability. *Opuntia* spp. have a broad range extending from Massachusetts to Minnesota, south to Florida, and west to California. *Opuntia* spp. are tolerant of temperatures as low as -30°C and as high as 45°C. Because developmental studies of *C. cactorum* at different temperatures have not been reported, the temperature thresholds for survival and development of the different life stages of *C. cactorum* should be determined. Also, the ability of low temperature and short day length to induce diapause in *C. cactorum* should be studied. Diapause in the family Pyralidae has been studied in depth for several pest species (Teetes et al. 1969; Chippendale & Reddy 1974; Bell & Bowley 1980; Rojas et al. 1989). In these pyralids, as well as others, diapause is induced in the mature larvae. Both temperature and photoperiod influence diapause induction, but temperature is the most critical factor (Chippendale & Reddy 1974).

The influence of temperature and photoperiod on diapause induction of *C. cactorum* could be studied in any laboratory equipped with environmental chambers. However, exact environmental conditions experienced under field conditions cannot be simulated. The ability of *C. cactorum* to overwinter under different environmental extremes would be determined best by onsite field studies. Cages erected over cacti infested with *C. cactorum* larvae could be used to capture moths from the emerging spring generation. As discussed in the previous section, use of fertile *C. cactorum*

for these studies would not be acceptable. However, sterile larvae from irradiated parents can be used without the risk of establishing a breeding colony of *C. cactorum* outside the infested area. F_1 sterile larvae would be suitable test subjects for these assays because Carpenter & Gross (1989) found no interactions between F_1 sterility and diapause in *Helicoverpa zea* (Boddie) (Lepidoptera: Noctuidae). Data from these studies will be useful in determining the geographic range of *C. cactorum* and in calculating the possible number of annual generations at different locations.

Delineation of the Potential Impact of Native Natural Enemies on the Expansion of *C. cactorum*

The first record of *C. cactorum* in the continental United States was from the Florida Keys (Big Pine Key) in October 1989 (Habeck & Bennett 1990). *Cactoblastis cactorum* currently has a known geographical distribution limited to the coastal areas of Georgia and Florida, with the most northerly west coast record of *C. cactorum* at Cedar Key in Levy County, September 2000 (Stiling, University of South Florida, pers. obs.). The biotic and abiotic factors that influenced the expansion of the geographical range of *C. cactorum* during the past decade are unknown. However, because *C. cactorum* is an exotic species, the ability of native parasitoids and predators to attack *C. cactorum* may be crucial in moderating an expanding population. A knowledge of the natural enemy complex that could attack *C. cactorum* beyond the leading edge of its expansion would be valuable in predicting the rate at which *C. cactorum* would colonize new areas. This knowledge also would allow pest control specialists to consider whether or not an effort to use classical biological control against *C. cactorum* would be warranted. The interaction between *C. cactorum* and native natural enemies may be determined through surveys within the areas now colonized by *C. cactorum*. Methods for these surveys would include collecting egg sticks, larvae and pupae of feral *C. cactorum*, and placing sentinel egg sticks, larvae and pupae at field sites (Kring et al. 1992). The sentinel forms could be observed for predation while in the field, or they could be retrieved and observed in the laboratory for emerging parasitoids. Unfortunately, neither of these methods would be available in areas beyond the leading edge of *C. cactorum* expansion. No feral *C. cactorum* would be present beyond the leading edge and the use of sentinels would create the risk that escaped cactus moths would establish a breeding population in a previously uninfested area. However, this risk would be eliminated if irradiated *C. cactorum* and their sterile progeny were used as sentinels for surveys of potential natural enemies. In fact, irradiated *C. cactorum* and their sterile progeny could be used both in these uninfested areas (Carpenter et al. 1996; Greany & Carpenter 1999) and in infested areas where the goal would be to prevent further contribution to the feral pest population (Carpenter et al. 1996; Proshold et al. 1998; Mitchell et al. 1999).

Applications of F_1 Sterility for Control

F_1 sterility in *C. cactorum* could have several applications for control of *C. cactorum*. First, F_1 sterility could provide a tactic to protect rare *Opuntia* cacti in the Florida Keys. Through the release of irradiated moths, a zone of protection could be constructed around the area endemic for the cacti by excluding or eradicating of *C. cactorum* from this area. Another application would be as an available control/eradication tactic to be used against new introductions of *C. cactorum* (e.g., in Mexico or beyond the leading edge of the *C. cactorum*-infested area in the U.S.). As soon as an infestation is detected, irradiated moths could be released into the area surrounding the site where *C. cactorum* has been detected. After adequate assessment, it might be desirable to develop a partnership with a country in the Caribbean or with South Africa in which native *C. cactorum* could be collected/reared, irradiated and shipped to areas with new *C. cactorum* infestations. Such an arrangement would be similar to that of the sterile insect release programs for the Mediterranean fruit fly in which sterile flies are produced in other countries (i.e., Guatemala, Mexico) and released in Florida and California. F_1 sterility also may be used to erect a barrier to prevent the expansion of the *C. cactorum* geographical range. Surveys indicate that the current distribution of *C. cactorum* is mostly limited to within 40 km of the Atlantic and Gulf coastlines. By releasing irradiated moths along the coastal region, it may be possible to create a barrier that would impede the advance of *C. cactorum*. It may also be possible to slowly move the barrier into the infested area and, thereby, reduce the current distribution of *C. cactorum*. Finally, F_1 sterility could be used to provision *C. cactorum* as supplemental hosts in the field to increase the initial survival and establishment of released natural enemies. If the decision is made to use classical or augmentative biological control against *C. cactorum*, a low population of *C. cactorum* may impede the establishment or efficacy of the natural enemy. By releasing irradiated moths or their sterile progeny, it might be possible to enhance the activities of the natural enemies without contributing to the feral population of *C. cactorum* (Carpenter et al. 1996; Proshold et al. 1998; Mitchell et al. 1999).

Summary

Methods are needed for the containment, control and eradication of *C. cactorum*. The use of insecticides to control *C. cactorum* should be con-

sidered with much skepticism because of environmental and economic concerns. A classical biological control approach should also be considered with caution because of the need to thoroughly evaluate the safety of such releases, because its effectiveness is unknown, and because it would not prevent the spread of the moth. The use of F_1 sterility, however, would be species specific and environmentally friendly. F_1 sterility offers the potential to control the moth along the leading edge to limit geographical range expansion and the potential to develop an abatement program in environmentally sensitive areas (e.g., to protect rare and endangered *Opuntia* spp.). In addition, the use of F_1 sterility may also provide a framework for approaching future introductions of other exotic, invasive lepidopteran species, and may provide new risk management tools for assessing the safety of exotic lepidopterans being considered as biological control agents against invasive weeds.

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INHERITED STERILITY IN *CACTOBLASTIS CACTORUM* (LEPIDOPTERA: PYRALIDAE)

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ABSTRACT

Newly emerged male and female adult cactus moths, *Cactoblastis cactorum* (Berg), were treated with increasing doses of gamma radiation, and the moths were outcrossed to fertile counterparts. Fecundity of the moth pairs was not affected by increasing doses of radiation. The minimum dose at which treated females were found to be 100% sterile when mated to untreated males was 200 Gy. Fertility of treated males declined with increasing doses of radiation to approach 0% near 500 Gy. Inherited effects resulting from irradiation of P males and females were expressed in the F_1 generation as increased developmental time from oviposition to larval eclosion, increased egg mortality, and increased neonate to adult stage mortality. A shift in the F_1 sex ratio in favor of males was not observed.

Key Words: cactus moth, inherited sterility, sterile insect technique, invasive species

RESUMEN

Adultos recientemente emergidos de ambos sexos de *Cactoblastis cactorum* (Berg) fueron tratados con varias dosis de radiación gamma y apareados con individuos fértiles del sexo opuesto. La fecundidad de estas parejas no fue afectada por las dosis de radiación utilizadas. La dosis mínima que causó esterilidad completa en las hembras tratadas fue 200 Gy. La fertilidad de los machos tratados decreció a medida que la dosis de radiación aumentó hasta alcanzar esterilidad completa con la dosis de 500 Gy. Los efectos heredados al irradiar a los machos y hembras de la generación P fueron expresados en la generación F_1 como una reducción en la eclosión de huevecillos, un desarrollo mas lento durante la embriogenesis de los huevecillos y un aumento en la mortalidad observada durante el periodo larvario. No se observaron distorciones de la tasa sexual en favor de la progenie de sexo masculine.

The control of exotic *Opuntia* cacti in Australia and South Africa by the cactus moth, *Cactoblastis cactorum* (Berg) (Lepidoptera: Pyralidae), is one of the classic success stories in biological control (Dodd 1940; Pettey 1948). However, the recent unintentional arrival of *C. cactorum* in Florida from the Caribbean has raised concerns for the well being of native *Opuntia* in the southern United States and in Mexico (Habeck & Bennett 1990; Pemberton 1995; Johnson & Stiling 1998; Zimmerman et al. 2001).

Cactoblastis cactorum is a pyralid moth native to northern Argentina, Uruguay, Paraguay, and southern Brazil (Mann 1969). Larvae of *C. cactorum* are phytophagous, feeding on many species of *Opuntia* cactus, primarily from the subgenus *Platyopuntia* (Mann 1969). The female lays eggs in a vertical chain extending from the cactus surface or the tip of a cactus spine. Known as egg sticks, these chains average 50-80 eggs and each female can lay an average of three to four egg sticks in its lifetime (Dodd 1940; Myers et al. 1981; Robertson 1987). Eggs take four to five weeks to develop. Upon eclosion, the larvae crawl down from the egg sticks and burrow into a cactus pad. The larvae are gregarious internal feeders and will move to a new pad when the current feeding site is destroyed (Dodd 1940). Approximately four pads are needed to support the complete development of a cohort of larvae from an average egg stick (Monro 1967; Meyers et al. 1981). Fully developed larvae usually leave the plant to spin cocoons in the litter or the bark of nearby trees. Occasionally pupation occurs within the skeletonized pad. The number of generations per year in Florida is unknown, however, in Australia (Dodd 1940) and South Africa (Robertson & Hoffmann 1989) *C. cactorum* has two generations per year, with a possible third. Laboratory observations of *C. cactorum* collected in Georgia show the life cycle to be approximately 90 days from oviposition to adult stage at 26-27°C (authors, pers. obs.).

No satisfactory method of control, including pesticides, pathogens and biological control, is currently known for *C. cactorum*. However, the

use of the sterile insect technique and the phenomenon of inherited (F_1) sterility in Lepidoptera offer some potential for managing the spread of this insect in North America (see Carpenter et al. 2001 for a discussion of the potential applications of F_1 sterility for researching and managing *Cactoblastis* and other invasive lepidopterans).

F_1 sterility takes advantage of two unique genetic phenomena in Lepidoptera (LaChance 1985). First, females are generally more sensitive to radiation than are males of the same species. This allows one to adjust the dose of radiation used to treat the insects such that treated females are completely sterile and the males are only partially sterile. Second, when partially sterile males are outcrossed with wild fertile females the radiation-induced deleterious effects are inherited by the F_1 generation. As such, larval eclosion is reduced and the (F_1) offspring produced are more sterile than the irradiated parent and predominately male. The lower dose of radiation used in this technique increases the quality and competitiveness of the released moths as compared to fully sterile moths (North 1975). In addition, because F_1 sterile progeny are produced in the field, the release of partially sterile insects offers both greater suppressive potential than the release of fully sterile insects (LaChance 1985) and the potential to make developmental and behavioral observations under actual field conditions without concern for establishing a breeding population.

Nothing is currently known about radiation effects on *C. cactorum*. However, F_1 sterility has been demonstrated in a number of economically important Lepidoptera (Bloem & Carpenter 2001), including other Pyralidae such as the European corn borer, *Ostrina nubilalis* (Hübner) (Nabors & Pless 1981), the almond moth, *Cadra cautella* (Walker) (Brower 1980, 1982), and the sugarcane borer, *Diatraea saccharalis* (Fabricius) (Walker & Quintana 1968a, b; Sanford 1976, 1977). In this paper, we examine the effect of various doses of gamma radiation on the fecundity and fertility of *C. cactorum*. In particular, we were interested in determining the minimum dose at which females are 100% sterile when mated to fertile males and in verifying that the F_1 sterility effects are manifested in this species.

Materials and Methods

Test Insects

Cactus moths used in this study came from field-collected larvae found infesting stands of *Opuntia stricta* (Haworth) Haworth along the causeway connecting the Georgia mainland with Jekyll Island, GA. Two collections were made in the same general location on two different dates (1 & 10 March, 2001). Several hundred larvae of mixed age and additional uninfested cactus pads were collected, and the material returned to the USDA-ARS-CPMRU Laboratory in Tifton, GA. Infested pads were placed in rectangular plastic containers (34 × 24 × 13 cm) on top of a thin layer of sterilized sand. Uninfested pads of *O. stricta* were added to the containers to serve as additional food for developing larvae. Containers were kept in a growth chamber at 26.5°C, 70% relative humidity (R.H.) and a photoperiod of 12L:12D and checked every few days for the presence of cocoons. Most pupae formed under the container lids, although a few pupated under the cactus pads. Cocoons were collected 2-3 days after initiation of pupation. Pupae were carefully extracted from the silken cocoons, sorted by gender, and male and female pupae were held separately in 475 ml plastic cups at the above conditions. Prior to adult eclosion, male and female pupae were placed inside separate screen cages (30.5 × 30.5 × 30.5 cm) and allowed to emerge at room temperature (23 ± 1°C).

Effect of Gamma Radiation on Adult Moth Sterility

Newly emerged (<24 h old) virgin adult male and female cactus moths were exposed to gamma radiation in groups of 1-5 moths in 30 ml plastic cups. A Cobalt^{60} gammacell 220 irradiator with a dose rate of 20.3 Gy/min was used to administer doses of 0, 50, 100, 200, 300, 400, and 500 Gy. After irradiation, each treated (T) moth was placed in a 475 ml plastic container with a non-treated (N) adult of the opposite sex. N♀ × N♂ crosses served as controls. Each mating container was provisioned with a pad of *O. stricta* as an oviposition substrate and a small petri dish with a cotton wick soaked in 10% sugar solution to provide nourishment to the moth pairs. The moths were allowed to mate and lay eggs at 26°C, 70% R.H. and a photoperiod of 14L:10D until the females died. Adult longevity was recorded for females and males. Females were dissected to ascertain whether a spermatophore was present in the spermatheca, thus confirming their mating status (Ferro & Akre 1975).

Egg sticks deposited by each female were collected and held separately (one cup for each oviposition event per female) in small 30 ml plastic cups at the above conditions. Egg sticks were incubated for approximately 30 days to allow for complete egg development and larval eclosion. The total number of eggs produced and the total number of larvae that eclosed were recorded for each female at each treatment dose. Sterility was expressed as the percentage of eggs from which no larva eclosed. Seven to 13 pairs of T♀ × N♂ or N♀ × T♂ were used per treatment dose.

Cactus Moth F_1 Progeny Follow-Up

F_1 neonates from each cross were carefully placed on pads of *O. stricta* and reared at 25-27°C

in plastic containers (34 × 24 × 13 cm). Days to pupation were recorded for all treatments. Pupae were collected and separated by gender as above, and all emerging adults were outcrossed to fertile (unirradiated) counterparts of the opposite sex. Moths were allowed to mate and lay eggs as above. Egg sticks were collected and incubated as above and the sterility in the F_2 generation was calculated. Longevity for the F_1 pairs was recorded, and mating status of the F_1 females was verified as above.

Statistical Analysis

Data collected from both the parental (irradiated) and the developing F_1 generations were analyzed using a two-factor analysis of variance and regression analysis, with dose used and gender irradiated as sources of variation (PROC GLM) (SAS Institute 1989). The longevity of irradiated moths, number of eggs laid, percentage larval eclosion, percentage of neonates surviving to pupation, percentage of neonates surviving to adulthood, sex ratio (% male) of F_1 adults, developmental time from oviposition to larval eclosion, and developmental time from neonate to adult were the dependant variables. When significant ($P \leq 0.05$) interaction was detected between dose used and gender irradiated, the effect of dose within each gender was examined using polynomial regression (PROC GLM).

Data collected for the F_1 generation were analyzed using a three-factor analysis of variance and regression analysis, with dose, F_1 gender and parental gender irradiated as sources of variation (PROC ANOVA) (SAS Institute 1989). The longevity of F_1 moths, number of eggs laid, egg development time, percentage larval eclosion, and percentage of larvae surviving to the second instar were the dependent variables. When significant ($P \leq 0.05$) interaction was detected between dose, F_1 gender and parental gender irradiated, the effect of dose within each F_1 gender and gender irradiated was examined using polynomial regression (PROC GLM).

Results and Discussion

Fecundity (= total # eggs laid) and adult longevity of the *C. cactorum* parental generation were not significantly affected by radiation dose or by the gender irradiated. However, there was a significant ($F = 6.23$; df = 1, 55; $P = 0.0156$) difference in the longevity of male (13.0 ± 3.5 d) and female moths (11.3 ± 2.6 d) irrespective of treatment. During this study, an average of 50% of the moth pairs mated in the laboratory. The mean (±SD) number of eggs laid by mated females was 119.8±68.9.

The percentage of eggs from which larvae eclosed and the developmental time from oviposition to larval eclosion for the parental generation of *C. cactorum* were significantly affected by the gender irradiated and by the dose of radiation. For each gender, the percentage of larval eclosion declined significantly as the dose of radiation increased (Fig. 1). This dose effect was greater for irradiated females ($y = 76.4 - 10.9x + 0.56x^2$; $F = 23.89$; df = 4, 30; $P < 0.0001$) than for irradiated males ($y = 98.3 - 4.5x + 0.01x^2$; $F = 33.29$; df = 4, 28; $P < 0.0001$). The dose of radiation also had a significant effect on the time from oviposition to larval eclosion for both genders (Fig. 2). Again, this dose effect was greater for irradiated females ($y = 27.1 + 0.22x$; $F = 14.22$; df = 4, 11; $P < 0.0031$) than for irradiated males ($y = 27.2 + 0.09x$; $F = 3.42$; df = 4, 21; $P < 0.0265$).

For the F_1 generation, the percentage of neonates that pupated declined significantly as the dose of radiation administered to the parent increased ($F = 5.81$; df = 10, 29; $P < 0.0001$). In addition, the percentage of F_1 neonates that emerged as adults was significantly affected by the gender irradiated and by the dose of radiation administered to the parent. For each gender, the percentage of F_1 neonates that emerged as adults declined significantly as the dose of radiation increased. This dose effect was greater for irradiated females ($y = 47.9 - 8.27x$; $F = 98.97$; df = 2, 6; $P < 0.0001$) than for irradiated males ($y = 49.5 - 1.64x$; $F = 3.51$; df = 3, 13; $P < 0.0465$). The mean number of adult F_1 progeny produced from irradiated *C. cactorum* reflects the total mortality in the F_1 generation and is presented in Fig. 3. The effect of radiation on F_1 mortality was greater when the female was irradiated. The developmental time from F_1 neonate to adult and the sex ratio of the adult F_1 was not significantly affected by dose of radiation or gender irradiated.

Adult longevity of *C. cactorum* during the F_1 generation and the ability of F_2 neonates to establish on cactus pads were not significantly affected

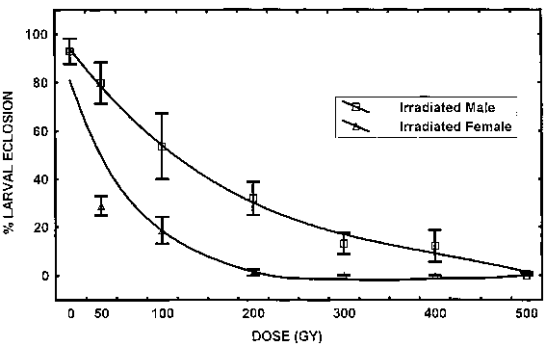

Fig. 1. Percentage larval eclosion obtained when *Cactoblastis cactorum* adults were treated with 0, 50, 100, 200, 300, 400, and 500 Gy of gamma radiation and outcrossed with untreated *C. cactorum*. Bars represent ±1 SD.

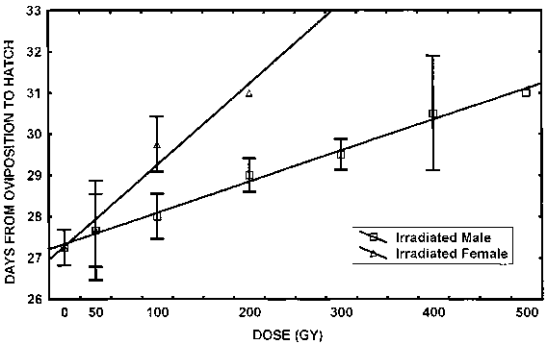

Fig. 2. Relationship between the dose of gamma radiation administered to *Cactoblastis cactorum* adults and the number of days from oviposition to larval eclosion for the F_1 generation eggs. Males and females were treated with 0, 50, 100, 200, 300, 400, and 500 Gy of gamma radiation and outcrossed to untreated counterparts. Bars represent ±1 SD.

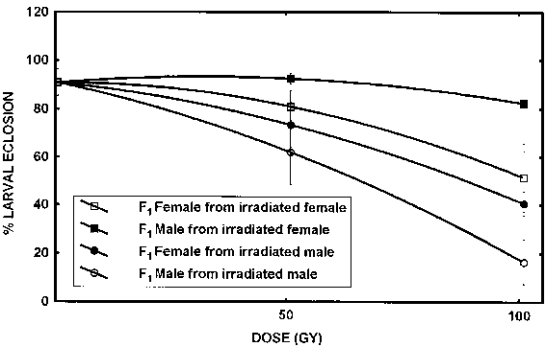

Fig. 4. Effect of the dose of gamma radiation used, the parental gender irradiated, and the gender of the F_1 adult on percentage larval eclosion for F_2 generation eggs of *C. cactorum*. Bars represent ±1 SD.

by radiation dose, the gender irradiated or the gender of the F_1 adult. Fecundity of F_1 adults was not significantly affected by radiation doses of 50 and 100 Gy administered to the parent generation. However, no eggs were laid by F_1 moths descending from matings (n = 7) between normal females and males irradiated with 200 Gy (females irradiated with 200 Gy produced no adult progeny).

The percentage of larvae eclosing from eggs laid by the F_1 adults was significantly affected by the dose of radiation applied to the parental generation ($F = 15.94$; df = 2, 40; $P < 0.0001$) and the P gender irradiated ($F = 4.67$; df = 1, 40; $P = 0.0368$) (Fig. 4). In addition, we found a significant interaction between the gender irradiated and the gender of the F_1 adult descending from an irradiated parent ($F = 4.24$; df = 1, 40; $P = 0.0460$). The percentage of larvae that eclosed was significantly reduced with an increasing dose of radiation, and was lowest when the P gender irradiated was male. For F_2 larvae that did hatch, the developmental time from oviposition to larval eclosion ranged from 28.3-33.3 d.

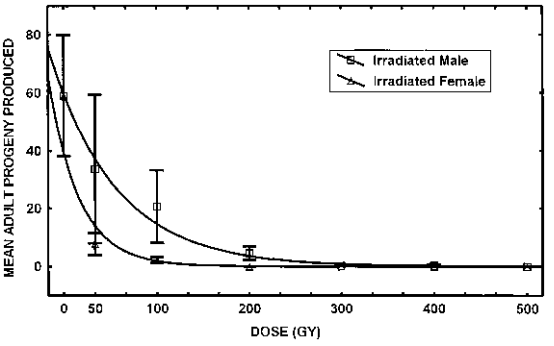

Fig. 3. Mean number of adult F_1 progeny produced per mating pair when *Cactoblastis cactorum* adults were treated with 0, 50, 100, 200, 300, 400, and 500 Gy of gamma radiation and outcrossed with untreated *C. cactorum*. Bars represent ±1 SD.

Attributes that are common to inherited sterility in Lepidoptera include (1) F_1 males and females are more sterile than the irradiated parental generation, and (2) more F_1 male progeny than female progeny are produced (LaChance 1985). Other attributes that have been reported include delayed developmental times and reduced sperm quality in F_1 progeny. We found that *C. cactorum* females are more radiosensitive than are males. These findings agree with those reported for other lepidopteran species (North 1975; Carpenter et al. 1986; Bloem et al. 1999). Our results also showed that irradiated *C. cactorum* share some attributes that are common to other irradiated lepidopterans. We demonstrated that F_1 progeny from irradiated males were more sterile than their irradiated parent. For example, at 100 Gy, irradiated P males were approximately 45% sterile when outcrossed to untreated females (Fig. 1), while their male progeny were approximately 82% sterile and the female progeny were approximately 60% sterile (Fig. 4). In addition, the F_1 progeny from irradiated females were more fertile than F_1 progeny from irradiated males (Fig. 4) (North 1975; LaChance 1985; Carpenter et al. 1986; Bloem et al. 1999). We also found that increasing radiation dose significantly delayed the developmental time (between oviposition and larval eclosion) for F_1 eggs. However, we did not detect a skewed sex ratio in favor of males for the F_1 adults. Although atypical, other researchers also have reported minimal effects of radiation on sex ratio of F_1 adults (LaChance et al. 1973). In this study, the failure to detect a distortion in the sex ratio may be the result of high F_1 mortality or reduced number of adults available for study at the radiation doses most likely to induce this sex ratio distortion (i.e., 200 Gy).

Carpenter et al. (2001) suggest that F_1 sterility for control of *C. cactorum* might be appropriate for (1) eradication of *C. cactorum* from areas of new introductions or from isolated and/or environmentally sensitive areas, (2) establishment of a barrier through the release of irradiated moths along the leading edge of the *C. cactorum* geographical range, and (3) provisioning sterile *C. cactorum* as hosts in the field to increase the initial survival and establishment of released natural enemies. Based on the results of this study, moths irradiated with a dose between 100-200 Gy might be suitable to address these control strategies. When moths are irradiated at 100 Gy, full sterility and/or mortality does not occur in the F_1 generation. The regression lines in Fig. 4 suggest that full sterility might be reached at 200 Gy for the progeny of irradiated males. However, the mean adult progeny produced from males treated with 200 Gy is quite low (Fig. 3), and no eggs were laid by the surviving F_1 adults. Therefore, we suggest that further studies involving larger test populations and at doses between 100 and 200 Gy are warranted in order to select a dose that would allow for maximum production of F_1 adults while inducing full sterility in the F_1 generation.

Carpenter et al. (2001) also discuss several ways in which F_1 sterility might be useful for studying *C. cactorum*. Examples include: (1) elucidation of the potential host range of *C. cactorum* for key native *Opuntia* species from across the U.S., (2) prediction of the potential geographic range of *C. cactorum* in the U.S. and Mexico, and (3) delineation of the potential impact of native natural enemies on the spread of *C. cactorum*. In each of these cases where the research protocol would involve the release of irradiated moths beyond the leading edge of the *C. cactorum* geographical range, 100% reproductive sterility of the F_1 progeny of irradiated *C. cactorum* would be mandatory. As stated above, our data suggest that the optimum dose of radiation for this purpose would be between 100-200 Gy. In addition, studies would be needed to determine the reproductive rate when progeny of irradiated parents are inbred ($F_1 \times F_1$ crosses) because only irradiated moths and their progeny would be found beyond the leading edge of the geographical range.

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THE RENOWNED CACTUS MOTH, *CACTOBLASTIS CACTORUM* (LEPIDOPTERA: PYRALIDAE): ITS NATURAL HISTORY AND THREAT TO NATIVE *OPUNTIA* FLORAS IN MEXICO AND THE UNITED STATES OF AMERICA

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ABSTRACT

The cactus moth, *Cactoblastis cactorum* (Berg) (Phycitidae) is native to South America. It was released as a biological control agent against alien *Opuntia*-cacti in Australia in the 1920s, then in southern Africa, and latterly on several islands, including those in the Caribbean. In 1989, the cactus moth was discovered in Florida, in the United States of America, where it is now threatening the survival of indigenous *Opuntia* species. In this paper we identify some of the attributes that have contributed to the success of *C. cactorum* as a weed biological control agent. Many of these same qualities account for the problems that *C. cactorum* has caused in Florida and predispose it as a major threat to the speciose, native *Opuntia*-floras of Central and North America. An estimated 79 platyopuntia (prickly pear) species are at risk: 51 species endemic to Mexico; nine species endemic to the United States; and 19 species common to both countries. Many cultivated and wild *Opuntia* species, that are used in various ways, are also vulnerable to attack by *C. cactorum*, including at least 25 species in Mexico and three species in the United States, particularly the widely-exploited and culturally-important cultivars of *O. ficus-indica*. Some control strategies are suggested that may minimize the risk and consequences of invasion by the cactus moth. The wider implications of this threat to the practice of weed biological control and to conservation are discussed.

Key Words: Invasive cacti, biological control, non-target effects, threatened floras, native opuntias, Mexico, United States

RESUMEN

La palomilla del cactus, *Cactoblastis cactorum* (Berg) (Phycitidae) es un insecto nativo de America del Sur. Se liberó como agente de control biológico contra especies invasivas de cactus (*Opuntia*) en Australia en los años 1920, luego en Africa del Sur y varias islas del Caribe. En 1989, esta especie fue detectada en el estado de Florida en los Estados Unidos de América donde hoy en dia se presenta como una amenaza a las especies nativas de *Opuntia* que se encuentran en peligro de extinción. En este artículo identificamos y discutimos los artibutos que han contribuido al éxito de esta especie como agente de control biológico. Muchos de estos atributos contribuyen a los problemas que esta especie esta ocasionando presentemente en Florida y que posa en el futuro en areas de alta diversidad de flora de *Opuntia* como Centro América y el suroeste de los Estado Unidos. Se estima que existen 79 especies en peligro de las cuales 51 son nativas del territorio Mejicano, 9 son nativas de Estados Unidos y 19 son comunes a ambos paises. Varias especies de *Opuntia*, cultivadas o salvajes, que son utilizadas en la manufactura de productos alimenticios o agrícolas también estan en peligro de ataque por *Cactoblastis cactorum*. Entre ellas se encuentran 25 especies en Méjico y tres especies en Estados Unidos, particularmente variedades de la especie *O. ficus-indica*. Sugerimos algunas estrategias de control que podrían reducir el riesgo y las consecuencias de invasión de esta especie. Las implicaciones mas amplias con respecto al control biológico de malezas y a la conservación también se discuten en este artículo.

Cactus species are among the most cosmopolitan and destructive of invasive, alien plants. They constitute a significant actual and potential threat to conservation and agricultural production in many parts of the world (Cronk & Fuller 1995; Bright 1998). The cactus moth, *Cactoblastis cactorum* (Berg) (Phycitidae), that is native to South America, has been used as a biological control agent against several invasive species of *Opuntia* cacti in Australia since the 1920s and in Africa south of the Sahara since the 1930s. The cactus moth was later imported to New Caledonia, Hawaii, Mauritius, the Caribbean Islands, the Cayman Islands, St. Helena, Ascension Island and Pakistan (where establishment is uncertain). It was introduced to Kenya in 1966 but did not establish (Julien & Griffiths 1998). Some of these introductions have provided textbook examples

epitomizing the great success that can be achieved through the manipulation of plant-feeding insects as biological control agents (Dodd 1940; Fullaway 1954; Moran & Zimmermann 1984; Julien & Griffiths 1998).

The detrimental effects of introduced biological control agents on organisms other than the target pest have, rightly, been criticized and the safety of biological control as a practice has recently been questioned (Howarth 1991; Miller & Aplet 1993; Simberloff & Stiling 1996; Thomas & Willis 1998; Lockwood 1999; Stiling & Simberloff 1999). Concerns about non-target effects in biological control were the subject of an international conference held under the auspices of the International Organisation of Biological Control, in Montpellier, France, from October 17-20, 1999 (see Cory & Myers 2000). Compared with biological control of insect pests, the practice of *weed* biological control has a very good safety record (McFadyen 1998; McEvoy & Coombs 1999). In his critique of the safety of biological control generally, Howarth (1991) notes that "greater care and stricter guidelines (are) required for the introduction of herbivores (i.e., mainly plant-feeding insects). . . ." He advocates that "The protocols for weed control need to be strengthened and applied to programs aimed at other pests." Ehler (1999) notes that in weed biological control "concern over non-target effects is of prime importance". Strict protocols and the meticulous screening of insects and pathogens have ensured that risks are minimal and that there have been few recorded deleterious effects as a result of the release of biological control agents against weeds.

However, there are two recent, much-publicized examples of undesirable non-target effects in weed biological control. Firstly, the musk thistle weevil, *Rhinocyllus conicus*, which was introduced for the biological control of thistles in Canada in 1968, in Montana and Virginia in 1969, and in California in 1971 (see Zwölfer & Harris 1984) is now attacking the seed-heads of native thistles over large areas in the West and Central United States (Turner 1985; Turner et al. 1987; Louda & Potvin 1995; Guretzky & Louda 1997; Louda et al. 1997; Strong 1997; Louda 1998, 1999; Nechols 1999). Secondly, the cactus moth, *C. cactorum*, has arrived in Florida, probably from the Caribbean, and is damaging native opuntias, including the critically-endangered semaphore cactus, *O. spinosissima* (= *O. corallicola*, see Stiling et al. 2000), (Bennett & Habeck 1995; Pemberton 1995; Johnson & Stiling 1996, 1998; Stiling & Simberloff 1999; Stiling 2000). This very-well-known biological control agent has now, ironically, itself become a threat to conservation because of the danger it poses to indigenous and cultivated *Opuntia* cacti in the United States and Mexico.

The case of *C. cactorum* has excited recent comment and warnings about possible consequences from a number of authors (e.g., Simberloff & Stiling 1996; Lockwood 1999; Stiling & Simberloff 1999; Zimmermann & Perez-Sandi y Cuen 1999; Cory & Myers 2000; Stiling 2000; Strong & Pemberton 2000). Besides the direct threat to conservation, the fear is that the invasion and possible impacts of *C. cactorum* in the Americas could be used by political lobbies as an argument to impose unrealistic constraints on the practice of biological control (Ehler 1999; McEvoy & Coombs 1999). In this paper we deal with the natural history of *C. cactorum* as a biological control agent and we detail the threat it poses to the native *Opuntia* floras of Mexico and the United States. In doing so, we attempt to place the case of *C. cactorum* and the conservation issues associated with it, in a wider historical and geographical context than has been done yet.

The Biology and Cactus Hosts of *Cactoblastis cactorum*

The biology of *C. cactorum* is well-documented (Dodd 1940; Pettey 1948; Robertson 1985, 1987; Robertson & Hoffmann 1989). This cactus-feeding phycitid, in common with some other cactophagous moths (Moran 1980), lays its eggs one on top of the other to form spine-like 'eggsticks'. An 'eggstick', comprises, on average, 60-100 eggs and each female usually lays a total of 200-300 eggs (Dodd 1940; Pettey 1948; Robertson 1985). The neonate larvae, collectively, burrow and enter cactus cladodes through a single entry hole, thus probably overcoming the defensive gum-secretions of the host plant (Hoffmann & Zimmermann 1989). The larvae feed gregariously within the cladodes for about two months in summer and about four months in winter, before exiting to pupate in leaf-litter or in the soil (Dodd 1940; Pettey 1948). In Australia and South Africa, where *C. cactorum* occurs in temperate latitudes, there are two (rarely three) generations per year (Pettey 1948; Robertson 1985). In the warmer tropical climate of the Caribbean and Florida there may be more generations each year.

Cactoblastis cactorum is native to Argentina, Paraguay, Uruguay and southern Brazil (Mann 1969) and is one of four described cactophagous species in the genus. Unlike its congeners, which are host-specific (i.e., monophagous) and have limited geographical ranges, *C. cactorum* exploits several species of *Opuntia* cacti as hosts (i.e., it is oligophagous). It occurs over a wide range of climates in South America (Mann 1969) and in its countries of introduction, notably in Australia (Dodd 1940) and South Africa (Pettey 1948). In its native land, *C. cactorum* has been recorded feeding on almost all of the many *Opuntia* species in the platyopuntia group (prickly pears) (Dodd 1940; Mann 1969; Zimmermann et al. 1979; McFadyen 1985). However, in South America, it does not attack the platyopuntias *O. longispina* var.

corrugata, *O. quimilo*, or *O. sulphurea* (Zimmermann et al. 1979; McFadyen 1985), nor any other genera of Cactaceae, including those in the cylindropuntia group (chollas) (Zimmermann & Perez-Sandi y Cuen 1999).

Following the introduction of the cactus moth to Australia, southern Africa, and elsewhere, *C. cactorum* readily attacked a number of novel *Opuntia* hosts of North American origin. These include: *O. compressa*, *O. ficus-indica*, *O. lindheimeri* (= *O. engelamannii*), *O. megacantha*, *O. spinulifera*, *O. streptacantha*, the various subspecies of *O. stricta* (= *O. dillenii*), *O. tomentosa*, *O. triacantha*, *O. tuna*, and *O. vulgaris* (Pettey 1948; Fullaway 1954; Mann 1969; Annecke & Moran 1978; Moran & Zimmermann 1984; Julien & Griffiths 1998). It occasionally attacks the North American cylindropuntia, *O. imbricata*, in South Africa, but never becomes abundant on this species. It now also attacks the six native *Opuntia* species found in Florida (Johnson & Stiling 1996).

Cactoblastis cactorum as a Biological Control Agent

Cactoblastis cactorum was released in several countries as a biological control agent in spite of its oligophagous habit and ability to damage or kill numerous species of opuntias. In Australasia and in the Old World, where there are no native *Opuntia* species, nor other con-familial cactus species, the release of *C. cactorum* was rational and safe. Before its release in the 1930s in South Africa, the impact of *C. cactorum* on cultivated spineless varieties of the target weed species, *O. ficus-indica*, was anticipated, assessed and discounted (Pettey 1948; Annecke & Moran 1978).

The spectacular success of *C. cactorum* in the control of invasive, alien opuntias has been cited often in ecological and biological control literature (e.g., Debach 1974). Although several agents were implicated in the biological control of pest prickly pears in Australia, the cactus moth was the most important. The original stock of *C. cactorum* that was destined for Australia was derived from last-instar larvae collected in 1925 in pads of *O. delaetiana* and *O. monacantha* from Argentina (Dodd 1940). Adult females from this stock produced about 3000 eggs, which were placed on *O. monacantha* pads in Wardian cages and shipped, via Cape Town, to Australia, a journey which took 10 weeks. Over the next nine years the cactus moth was mass-reared and about 2750 million eggs were distributed on infestations of *O. stricta* (the main pest prickly pear in Queensland and New South Wales) (Dodd 1940). The rapid spread and success of *C. cactorum* was attributed to this massive rearing and release effort.

Dodd (1940) reports that, at the start of the campaign in Australia, about 24 million hectares (60 million acres) was infested with prickly pear, of which half of this area was so densely infested "that the land was useless from a productive viewpoint". For several years, until 1933, the scale of the operation was "vast" and the scenery changed rapidly "from flourishing [prickly] pear to dead [prickly] pear . . . to crops and fodder grasses. . . ." "The celerity with which the insect multiplied and spread from many release centres is illustrated by the situation along the Moonie River. . . . In August 1930, for 150 miles [240 km] along the river the pest [*O. stricta*] was in its full vigour, its continuity almost unbroken by cleared land; the pastoral properties had been overrun and mainly deserted, former large holdings having become mere names on a map; . . ." ". . . in August 1932, 90 per cent of the [prickly] pear had collapsed. The change in exactly two years was extraordinary." "Its [i.e., the cactus moth] progress has been spectacular; its achievements border on the miraculous. . . ." "The prickly pear territory has been transformed as though by magic from a wilderness to a scene of prosperous endeavor. . . ." ". . . the most optimistic scientific opinion could not have foreseen the extent and completeness of the destruction. The spectacle of mile after mile of heavy [prickly] pear growth collapsing *en masse* and disappearing in the short space of a few years did not appear to fall within the bounds of possibility." Dodd (1940) estimated that about 25 million *C. cactorum* larvae had been required to kill off one hectare of heavily infested *O. stricta* (i.e., about 10 million per acre).

Today, the '*Cactoblastis* Memorial Hall' and the '*Cactoblastis* Cairn' in Queensland, are among the memorabilia celebrating these events. Dodd's (1940) observations emphasize the astronomical numbers of insects involved and the extraordinary scale of the success. They also serve as an indication of the magnitude of the potential threat to native opuntia floras in North and Central America.

Dispersal and Spread of *Cactoblastis cactorum*

An understanding of the biology of natural, unaided dispersal in *C. cactorum* is obviously crucial in the debate about how the cactus moth came to be in Florida, in anticipating and assessing the threat of its further invasion onto native cacti in the United States, Mexico and the rest of Central America, and in devising strategies that minimize this risk. Unfortunately, evidence from the literature is mostly anecdotal and circumstantial and it is difficult to gain a clear impression of how far the cactus moth is able to disperse unaided and how quickly the species is able to spread once a new area is invaded.

Cactoblastis cactorum has not spread naturally from its native range in Argentina, Paraguay, Uruguay and southern Brazil to the large cultivated stands of *O. ficus-indica* in the state of

Pernambuco in central Brazil (Arruda et al. 1999), in spite of the presence of available hosts and of suitable climates *en route*. Within Argentina, it has not spread to cultivated *O. ficus-indica* plants in the valleys in the foothills of the Andes. The Andean mountain chain may have prevented the cactus moth from spreading to Chile, although suitable native *Opuntia* host-species and abundant commercial plantings of opuntias are present there (Marticorena & Quezada 1985; Hoffmann 1989). Physical barriers also may have prevented the spread of *C. cactorum* onto suitable cactus hosts in Central and North America.

In Australia, the unaided spread of *C. cactorum* on *O. stricta* was relatively slow (Dodd 1940; Pettey 1948). Larvae are able to move short distances from one host plant to another, but these trivial movements must be almost irrelevant in the context of the overall spread of the species. Where suitable hosts are densely abundant the adults seldom range far, but as food plants decrease in density the moths travel more widely (Dodd 1940; Pettey 1948; Robertson 1985). There is a record of individual females flying as far as 24 km (15 miles) to oviposit (Dodd 1940). In Australia, the cactus moth spread unaided, from the release points, for about 16-24 km (10-15 miles) in dense *O. stricta* infestations in 2.5 years (Dodd 1940).

In South Africa, the unaided rate of spread of the cactus moth through infestations of the larger, tree-like prickly pear, *O. ficus-indica*, was less, at about 3-6 km in 2.5 years (Pettey 1948). *Cactoblastis cactorum* was introduced into South Africa nearly 70 years ago and is well established on several species of opuntias. However, it has failed, on its own, to colonize some isolated infestations and plantings of *O. ficus-indica*, although this host plant is very widely distributed in South Africa (Henderson 1995). It also failed to spread naturally to a large (ca. 19,000 hectare) infestation of *O. stricta* in the Kruger National Park. This is surprising because the host plant, *O. ficus-indica*, was present in 1932 at high densities in the Eastern Cape Province (where *C. cactorum* has been established in large numbers since the late 1930s), and was contiguous in scattered infestations across the centre of the country, almost to the borders of the Kruger National Park (see distribution map in Pettey 1948).

CACTOBLASTIS CACTORUM IN THE CARIBBEAN AND FLORIDA

The decision in 1957 to release *C. cactorum* to control native opuntias on islands in the Caribbean (Simmonds & Bennett 1966) was not contested at the time. Only recently, after the moth was discovered in Florida, was this biological control program in the Caribbean questioned. Certainly, such an introduction would not be sanctioned nowadays because of the risk of attack by *C. cactorum* on non-target native opuntias and because biological control of native plants that are pests is now considered to be unwise. Julien & Griffiths (1998) record that *C. cactorum* was introduced into the Caribbean for the control of *O. dillenii* (= *O. stricta*) (Cayman Islands, Nevis, Puerto Rico and associated islands), *O. lindheimeri* (Antigua and Nevis), *O. triacantha* (Antigua, Montserrat, Nevis, Puerto Rico and associated islands) and *Opuntia* species (St. Kitts, U.S. Virgin Islands and Puerto Rico) (and see Moran & Zimmermann 1984). The cactus moth was also found by one of us (HGZ) on at least one non-target species, *O. repens*, in Puerto Rico as long ago as 1974.

Opuntia stricta var. *dillenii* was an important weed problem in Cuba in the early 1970s but, in contrast to the situation elsewhere in the Caribbean, a decision was taken not to import *C. cactorum*. In spite of this, the cactus moth was discovered on *O. stricta* var. *dillenii* in Cuba in 1974 and gave good control of the infestations (E. P. Montesbravo, pers. comm.). *Cactoblastis cactorum* was subsequently recorded from the Isle of Pines (Bibijagua Beach) in 1992 (Hernández & Emmel 1993). The origin of these *C. cactorum* populations is unknown and there have been no studies to determine the effects of the cactus moth on native, Cuban *Opuntia* species (E. P. Montesbravo, pers. comm.).

Over the years, the cactus moth has 'dispersed' to many islands in the Caribbean Basin such as Hispaniola and the Bahamas (Habeck & Bennett 1990). The latter authors as well as Johnson & Stiling (1996) assumed that the moth had spread naturally among the Caribbean Islands and eventually dispersed of its own accord from there to Florida in the United States of America. The supposition that the "moths dispersed on their own" to Florida "which is just 90 miles (144 km) from Cuba" (Stiling 2000) is problematic because *C. cactorum* is abundant only in the dry southeastern part of Cuba, around Guantanamo (E. P. Montesbravo, pers. comm.), about 800 km on a direct line from the Florida Keys. Pemberton (1995) also speculated that the moth might have dispersed repeatedly between islands in the Caribbean as it is reputed to have done in Hawaii (Tuduri et al. 1971). Although the moths are strong flyers, there is no direct evidence of natural, unaided inter-island dispersal in the Caribbean (Simmonds & Bennett 1966). Certainly, *C. cactorum* was frequently transported between islands by man, for example from the Caribbean to the U.S. Virgin Islands (Simmonds & Bennett 1966).

Recent studies by Pemberton (1995, 1996) provide evidence that *C. cactorum* could have been introduced to Florida through shipments of cactus plants that were colonized by larvae of the cactus moth and that were imported from the Dominican Republic to Florida, by the plant-nursery trade. *Cactoblastis cactorum* has colonized several native and introduced *Opuntia* species in Puerto Rico,

Antigua, Nevis, St. Kitts, Montserrat, Cuba, Hispaniola, Bahamas and the Dominican Republic (Habeck & Bennett 1990; Bennett & Habeck 1995; Julien & Griffiths 1998). Shipments of any of these cactus species from any of these islands may have been the original source of the infestation by *C. cactorum* of the *Opuntia*-cacti in Florida. From 1981-1986 there were 13 interceptions of *C. cactorum* larvae at Miami ports and larvae were found inside *Opuntia* cladodes originating from a Dominican Republic supplier owned by a Florida nursery (Pemberton 1995, 1996). Of the more than 300,000 *Opuntia* plants entering Miami from the Dominican Republic annually during the 1980s, most arrived in marine shipments (Pemberton 1995, 1996) and illegal introductions by cactus collectors were also probably very frequent.

Following the introduction of the cactus moth into Florida, Johnson & Stiling (1998) estimated an initial northward 'migration' of *C. cactorum* from the lower Florida Keys at 256 km per year, decreasing to 40 km per year thereafter. They estimated that the moth had 'dispersed' 360 miles (576 km) northwards through Florida, from 1989 to 1991. They noted that the rate of spread depended on host plant availability and abundance. In 1999, the cactus moth was reported on Sapelo Island, Georgia (Stiling 2000), which is about 650 km north of Miami.

The broad differences in the estimated rates of spread of the cactus moth in Australia (Dodd 1940) and South Africa (Pettey 1948) compared with Florida (Johnson & Stiling 1998) are difficult to reconcile. In Australia the slow natural dispersal of *C. cactorum* was purposely enhanced by re-distributions of the eggs and inadvertently supplemented through the behavior of the cactus moth itself. Female moths (but not males) are attracted to light and were transported in vehicles and trains: ". . . electric lights in passing trains have proved attractive; moths have been found resting in railway carriages a long distance from the locality where they had entered on the previous night" (Dodd 1940). It is possible that the relatively rapid spread of the cactus moth reported in Florida was also partly the result of inadvertent transport on trains, cars and aeroplanes. Perhaps the lower densities of hosts in Florida induced far more rapid and widespread natural dispersal of the cactus moth than was the case in Australia and South Africa, where there were very high host-plant densities. However, it is also possible that *C. cactorum* invaded the Florida Keys of its own accord and that, at about the same time, the species was imported inadvertently to the Miami area in shipments of cacti from the Caribbean. Multiple introductions, both natural and human-assisted, together with intrastate movement of infected nursery plants, rather than natural dispersal entirely, could provide a plausible explanation for the rapid spread of the cactus moth in Florida.

The Threat to *Opuntia* Species in Mexico and the United States

Regardless of how *C. cactorum* arrived in Florida, it is almost inevitable that the moth will spread to other parts of North America and to Mexico and Central America either unaided or through the assistance of human activity. Dispersal of *C. cactorum* from Cuba to Mexico across the Yucatan Channel is a distinct possibility. However, its presence has not yet been detected in the Yucatan Province, or elsewhere in Mexico, even though cactus growers and agricultural officials have been widely consulted and alerted to the danger (Zimmermann & Perez-Sandi y Cuen 1999). Natural spread on suitable hosts (such as *O. stricta*) that grow along the Gulf of Mexico from Florida to Mexico (Benson 1982) is a likely avenue of dispersal. Otherwise it could move as larvae in horticultural-cactus freight or inadvertently as adults in craft via road, sea or air (see Bright 1998). Indeed, a consignment of plants infested with *C. cactorum* was intercepted on a flight from (or via) Mexico to Miami in 1992 (Pemberton 1995).

If the cactus moth invades the southern United States and Mexico the effects may be severe. Several studies in Australia and South Africa have shown that *C. cactorum* can kill individual plants and whole populations of small- to medium-sized *Opuntia* species (Dodd 1940; Pettey 1948; Zimmermann & Malan 1981; Hoffmann et al. 1998a, b). Individual plants of the larger, woody, tree-like opuntias are not killed by *C. cactorum*. However, several authors (e.g., Pettey 1948; Zimmermann & Malan 1981; Johnson & Stiling 1998) have noted that the new growth of mature plants is particularly susceptible to *C. cactorum* damage and that population reductions of the larger species of opuntias can be expected through the destruction of juvenile plants.

In the southern United States, besides the numerous varieties of *O. ficus-indica* that are cultivated for fodder and fruit, wild populations of *O. lindheimeri* and *O. robusta* are also extensively utilized for fodder (Felker 1995). In Mexico, cacti have been of special importance since ancient times and have featured in the history, economy and cultural life of the country (Hoffmann 1983). Opuntias were cultivated for food in the valleys of Tehuacan in the State of Puebla since at least 6,500 BC (Smith 1967). Wild prickly pears, which occur at a density of about 200 plants per hectare over 300,000 km^2 in Mexico, rival corn and agave (*Agave tequilana*) in importance (Pimienta-Barrios et al. 1999). Besides their use as fodder, wild and cultivated opuntias are widely used for fruit and the tender young cladodes are harvested as a vegetable (Pimienta 1994). A large industry is based on opuntia by-products including juices, jams, confectioneries, pharmaceuticals and cosmetics (Pimienta 1994). Cultivars of *O. ficus-*

indica serve as host plants for rearing the cochineal insect, *Dactylopius coccus* (Homoptera), which is the basis of a carmine-dye industry that has been in practice from ancient times (Sáenz-Hernández 1995). Prickly pear opuntias are so important in the life and culture of Mexico that they are depicted in the National flag and on the modern-day Mexican coat-of-arms.

It seems likely that the platyopuntias (prickly pears) will be most at risk and few of the species in North and Central America will be immune. There are an estimated 51 species of platyopuntias endemic to Mexico, nine species endemic to the United States, and 19 species common to both countries, i.e., a total of 79 species that are vulnerable (Bravo-Hollis 1978; Benson 1982; Scheinvar 1999; Zimmermann & Perez-Sandi y Cuen 1999). It is possible that the list of vulnerable species could extend to some cylindropuntias (chollas) and to some 10 species in the genus previously known as *Nopalea* (now *Opuntia*). This supposition is based on the fact that, in South Africa, *C. cactorum* occasionally attacks *O. imbricata* (a cylindropuntia) and is able to develop on *Nopalea* (*Opuntia*) *cochenillifera*.

In Mexico, several cultivated species of platyopuntias are likely to be attacked by *C. cactorum*. These include *O. albicarpa*, *O. amyclaea*, *O. cochinillifera*, *O. robusta* var. *larreyi*, *O. streptacantha* and particularly the many cultivars of *O. ficus-indica* that are grown over a total of about 60,000 hectares (Scheinvar 1995; Pimienta-Barrios et al. 1999). Also at risk in Mexico are at least 18 other species of uncultivated, native opuntias. These wild prickly pears are utilized for forage (and other purposes) or are being considered for cultivation, and include *O. hyptiacantha*, *O. joconostle*, *O. lindheimeri*, *O. megacantha*, *O. mutudae*, *O. robusta* var. *robusta*, *O. sorea*, and *O. tomentosa* (Pimienta 1994; Flores Valdez & Aranda Osario 1997; Ochoa de Cornelli 1997).

The precedent of the cactus moth as a biological control agent in Australia, and elsewhere, where huge areas of suitable opuntias were destroyed, suggests that the threat *C. cactorum* invasions should be taken very seriously.

Control of *Cactoblastis cactorum*

Given the necessary expertise, funding and resolve, it is possible to envisage the control or even the eventual eradication of *C. cactorum* in Florida, and, if necessary, elsewhere in Central and North America. No such program has yet been mounted, although studies on control of the cactus moth in Florida have been initiated by Johnson & Stiling (1996, 1998).

There are a number of research areas related to the biology, invasive potential and possible impact of the cactus moth that need attention, including: (i) a detailed study of its taxonomy (see McFadyen 1985); (ii) the pattern and extent of its invasion in Florida; (iii) its natural dispersal abilities and potential for spread by deliberate and inadvertent human interventions—aspects which have obvious implications for management of the threat; (iv) its climatic tolerances; (v) factors affecting its survival, fecundity and success in the field in South America and in Florida and the Caribbean—in this respect, it would be important to determine the role of native Floridian parasites, predators and diseases in suppressing populations of *C. cactorum*, and to compare this information with the extensive data on the subject published by Australian and South African entomologists (e.g., Dodd 1940; Pettey 1948; Robertson 1985; Robertson & Hoffmann 1989); (vi) the actual and potential impacts of the cactus moth on individuals and populations of vulnerable host plants in Mexico and the United States and; (vii) the possible effects of *C. cactorum* invasions on the native cactophagous faunas (particularly con-familial phycitid moth species) in Mexico and the United States.

In South Africa, *C. cactorum* is readily controlled in cultivated stands of *O. ficus-indica* by removing the conspicuous eggsticks from the plants during the two oviposition-periods for *C. cactorum*, namely in February-March and in September-October (Annecke et al. 1976). Whether *C. cactorum* in tropical climates will display two such well-synchronized generations per year is unknown. It may be necessary in Florida to collect the eggsticks over a longer period. Whatever the case, eggstick collections should be followed by removal of all cladodes, or portions thereof, that have larval colonies. Applications of persistent contact insecticides will kill the eggs and hatching larvae and may be an effective adjunct against *C. cactorum*, particularly in cultivated plantations. Other methods, such as sterile male techniques or pheromone trapping, are also worth consideration.

As a supplement to these suggested control strategies, research should re-start on the possible biological control of *C. cactorum*. Some preliminary investigations have been done in this respect (R. W. Pemberton, pers. comm.). In South America, native populations of *C. cactorum* are attacked by at least five parasitoid species of which *Apantales alexanderi* (Braconidae) is the most common (Mann 1969; Zimmermann et al. 1979). Pathogens (e.g., *Nosema* species) also attack *C. cactorum* (Pettey 1948). Whether any of these potential biological control agents will prove to be specific to *C. cactorum* remains to be established. *Apantales alexanderi*, for one, is a generalist and the risks of non-target damage to the native phycitid and pyralid moth faunas of the United States may eventually disqualify biological control of *C. cactorum* as a viable strategy.

Early detection of invasions by the cactus moth will be crucial for successful control. Con-

certed, international preventative strategies, including awareness programs to alert politicians, educators, cactus-collectors, researchers and nursery-people to the dangers posed by *C. cactorum* to conservation in Mexico and the United States would seem to be important. A review of national and international phyto-sanitary procedures as they apply to this particular problem may also be appropriate.

Discussion

The extraordinary history of *C. cactorum* as a biological control agent against alien prickly pears in Australia, and elsewhere, has been used in this paper to stress the potential of the cactus moth as a pest of native opuntias in North and Central America. It would not be wise, however, to extrapolate directly from these experiences to predict disaster for indigenous opuntias in Mexico and the United States. The impact of the cactus moth could be dramatic in dense growths or in cultivated stands of opuntias in these countries, and it is disconcerting that *C. cactorum* is a major pest of cultivated cactus pears in Argentina, where the cactus moth occurs naturally. However, what may eventuate, should the cactus moth invade Mexico and the southern United States, will, of course, be governed by the local climate, parasites, predators and diseases, host-plant characteristics and many biotic and abiotic influences on the cactus moth itself, including the vagaries of its natural- or human-aided-dispersal. The cactus moth did not become established after its introduction into Pakistan and Kenya, so it may take especially suitable conditions to allow its invasion and spread in new areas. It will probably prove as difficult to predict the effects of a *C. cactorum* invasion into Mexico and the southern United States as it has always been to anticipate success or failure for biological control agents that were purposely released against weeds.

The presence of *C. cactorum* in Florida and the consequent risks to native opuntia floras elsewhere in the United States and in Central America, has tarnished the safety record of weed biological control. The case of *C. cactorum* will continue to stimulate criticism and debate on the non-target effects of biological control. These discussions could result in reforms and new protocols that lead to increased safety in biological control generally. However, the indirect danger to conservation is that the spread of the cactus moth to Central and North America may result in negative sentiment in lay, scientific and political communities and the imposition of unrealistic constraints ("revenge effects") on the practice of weed biological control (McEvoy & Coombs 1999). These authors advocate "treating new control organisms as 'guilty until proven innocent': presume(ing) each new control organism species is unnecessary, unsafe and ineffective until it is shown, beyond a reasonable doubt, to be necessary, safe and effective". The concern is that countries that have not yet adopted biological control as a management option may be constrained from doing so for fear of causing undesirable side-effects in their own regions. Reluctance to use biological control could have substantial consequences in countries where invasions by alien plants impinge directly on the lives of people and where there are no alternative solutions to alleviate the problems.

Although the emphasis in this paper has been on the threat of *C. cactorum* to native opuntias in Mexico and the United States, there maybe wider implications. Cacti (mainly cultivars of *O. ficus-indica*) are increasingly grown as 'wonder-plants' in many parts of the world, including North Africa, the Mediterranean countries, the Middle East, India and China. Cultivated opuntias in these countries are susceptible to invasion by *C. cactorum* (through the inadvertent importation of pads colonized by larvae of the cactus moth, as has been discussed in this paper). Should this happen, biological control of the cactus moth, using suitably-specific parasitoids and, or, diseases as agents, may be feasible and relatively uncomplicated by non-target effects. In other countries, where the cactus moth is used successfully as a biological control agent for the management of alien cacti, the emphasis may be on ways and means to keep out these agents. The story of *C. cactorum* and its role in conservation may have only just begun.

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INSECT SURVEYS IN THE SOUTHEAST: INVESTIGATING A RELICTUAL ENTOMOFAUNA

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ABSTRACT

Rare insects can occur in specialized niches of familiar habitats. For example, the burrows of rodents, such as the pocket gopher, contain a relictual entomofauna of surprising diversity. The discovery and cataloging of this "cryptic" diversity is an ongoing process that will require patience, time, and resources. The role of the amateur naturalist and collector is far from extinct in modern systematics, particularly in surveys of these specialized environments. They can provide much of the manpower for local surveys and often have extensive regional knowledge.

Key Words: Coleoptera, Histeridae, Geomyidae, Pocket Gopher, Rarity, Burrow fauna

RESUMEN

En nichos especializados de hábitat familiares, pueden encontrarse insectos poco comunes. Por ejemplo, las madrigueras de roedores, tales como las de la ardilla terrera, contienen una entomofauna de diversidad sorprendente. El descubrimiento y catalogamiento de esta diversidad "críptica" es un proceso continuo que requerirá paciencia, tiempo y recursos. El rol del naturalista principiante y colector está lejos de extinguirse en las sistemáticas modernas, particularmente en los estudios de estos ambientes especializados. Ellos pueden proveer gran parte de la mano de obra para inspecciones locales y usualmente tienen conocimiento regional extenso.

Only recently with The Great Smokey Mt. National Park—All Taxa Biotic Inventory (ATBI) has a serious concerted effort begun to sample and catalogue biodiversity in a large U.S. National Park. Undoubtedly, a major factor contributing to the overall disinterest regarding inventories and the search for new species here at home is the impression that our insect fauna is largely known. While this may be true for some areas of the U.S., most areas have been poorly studied. In addition, tucked within well-studied areas are various microhabitats and niches that have not been properly sampled for insects. To illustrate this point, Karl Stephan, an avocational coleopterist, has discovered dozens of beetles new to science in the vicinity of Red Oak, Oklahoma. Another avocational coleopterist, Roy Morris recently discovered two new species of long-horned beetles and three new species of scarab beetles in relictual sand scrub habitat in central Georgia. Further sampling in fossil dune systems in the southeast has netted several additional undescribed scarab beetles, some rare staphylinid beetles in the genus *Platydracus*, and a rare myrmecophilous carabid beetle *Pseudomorpha excrucians* Kirby, one of only two eastern members of a predominantly western genus. Sampling in remnant beech / magnolia ravines has led to the discovery of several undescribed species of weevils and significantly extended the known range for other insect species.

The chronicle of events leading up to some of these amazing discoveries can be as interesting as the discoveries themselves. While the initial phase of the discovery process may be entirely serendipitous, ultimately, it is persistence and cunning that yields results. As an example of how a full blown biotic survey can materialize from a relatively focused quest, we shall recount the history of our survey of the insects endemic to the burrows of the southeastern pocket gopher, *Geomys pinetus* (Rafinesque) (Geomyidae). The southeastern pocket gopher is a fossorial rodent restricted to well-drained soils in Florida, Georgia, and Alabama. Avise and Laerm (1982) characterized them as "homely, belligerent sausages". Pocket gophers remain hidden in their burrows during daylight hours, and thus, are rarely seen. However, their burrowing generates conspicuous earthen mounds indicating their presence. The burrow system created by an individual gopher can be in excess of a hundred meters in length. The mounds are connected to the burrow system by diagonal tubes that are generally plugged with dirt so that no open entrances are visible above ground (Avise and Larem 1982). Pocket gophers require open grassland or marginal habitats rich in grasses and herbaceous vegetation for their survival and are an important grazing herbivore in longleaf pine/wiregrass ecosystems. Their constant burrowing enhances soil fertility by moving

nutrients to the surface that would be otherwise lost via leaching or other factors (Grant & McBrayer 1981).

History of the Pocket Gopher Survey

The origin of this study was the search for a beetle, *Onthophilus giganteus* Helava (Histeridae), known from a single specimen collected in the mid-1970s. The holotype was collected in Alachua County, Florida near Archer during January and was found frozen in a pitfall trap. After its description, it was accidentally fragmented in route back to the Florida State Collection of Arthropods.

In 1987, Rupert Wenzel of the Field Museum of Natural History drove to the type locality of *O. giganteus* which was essentially an old pasture. Wenzel, a histerid specialist, was interested in seeing the habitat where this beetle had been collected. He informed PES (at the time a graduate student) that members of *Onthophilus* are often associated with burrowing rodents, and the only rodents apparent at the type locality were pocket gophers. PES began scouring the literature for papers on pocket gophers and on prior survey work of insects associated with pocket gopher burrows.

Following Hubbell and Goff's (1939) sampling technique, PES set pitfall traps in the burrows at the type locality in January. Surprisingly, three *O giganteus* were caught overnight, along with additional insects that were rare or undescribed. Energized, PES trapped in the pasture for an entire year. This year proved enlightening, as the burrow fauna was found to have distinct seasons of insect activity. The majority of the fauna was active from late Fall to Spring. All prior work had been done in late Spring and Summer, well past the period of peak activity.

News of unique discoveries travel fast in small coleopterist circles prompting PWK, the junior author to contacted PES with a request for live histerids for rearing purposes. PWK was beginning a revision of the subfamily to which *Onthophilus* belongs and was building a histerid larval collection to study their chaetotaxy. PES suggested that PWK visit the following winter to assist with burrow sampling efforts. In late December 1990, we drove to the pasture near Archer, set a few traps and overnight had 50 live adults! During the remainder of PWK's visit, we decided to go to the Florida panhandle to do some additional sampling for pocket gopher burrow insects. Our foray yielded some additional specimens of the same species that were collected in Archer, a few other species that we had not seen before including the scarab beetle *Aphodius pholetus* Skelley and Woodruff.

Some colleagues and PES continued to randomly collect in pocket gopher burrows for a few more years and found more interesting insects. All of them were rare in collections, but not so in the field. Some of the scarab beetles collected include: *Euphoria aestuosa* Horn, a scarab not previously known east of the Mississippi River; *Aphodius dysptisus* Skelley and Woodruff and *A. laevigatus* Haldeman, two abundant scarab species; and *A. platypleurus* Skelley and Woodruff a scarab that appears to prefer relatively undisturbed habitats. The hister beetles collected during this period included *Spilodiscus floridanus* Ross, the largest histerid in the Southeast, and *Onthophilus kirni* Ross, a species formerly known only from Texas and Louisiana. Other arthropods taken include *Ptomaphagus schwarzi* Hatch, an abundant cholevine leiodid beetle previously known from 6 specimens, *Typhloceuthophilus floridanus* Hubbell, a blind pallid cave cricket, and some nearly blind lycosid spiders.

In January 1995, PWK moved to Tallahassee, Florida and we began to sample burrows in the vicinity of Thomasville, Georgia just north of where PWK was living. Much to our amazement this area yielded more undescribed species including two species of hister beetles, three species of aphodiine scarabs, and a species of camel cricket. It was at this point that PWK, Robert Turnbow, and PES decided to embark on a major insect survey project that would cover the entire range of the southeastern pocket gopher.

Now the real work began. We needed to learn more about the habits and habitat of the pocket gopher in order to improve our sampling efficiency and accumulate literature records of the known distribution of the gopher. We also needed to be able to distinguish pocket gopher mounds from fire ant nests which they resembled. This can be difficult, especially while traveling in a car at 70MPH. We also had to develop a sampling procedure, decide how many sites to visit, and how may burrows to sample. Permits to trap gophers were obtained for Florida, Georgia, and Alabama. We sought assistance from Joshua Larem, Wilson Baker, Mark Bailey and William Michener to assist us in locating additional populations of pocket gophers and facilitate access to quail plantations. We were able to recruit Roy Morris and Philip Harpootlian, avocational entomologists, for assistance in monitoring traps at remote sites and were moderately successful at finding taxonomic support with groups for which we lacked expertise.

We searched for pocket gophers at all localities documented in literature, and were unable to find them at many of their former haunts. Many hours were spent combing these areas without luck. Factors such as fire suppression and development have apparently taken their toll on some local populations, especially those in central Georgia, west central Alabama, and south central Florida (see Fig. 4. on our web site http://www.famu.org/gopher). We began to keep records of all confirmed

sightings of pocket gopher mounds. The confirmation process usually consisted of stopping the car so that one of the mounds could be kicked to see if any fire ants were there. If not, the mound was scraped away to the soil surface to look for a plugged burrow entrance. Slowly, a more accurate map showing the distribution (past and present) of the southeastern pocket gopher began taking shape. After three winters of intensive field-work, we had samples from over 200 burrows throughout the range of the southeastern pocket gopher. At this point we began compiling and mapping our distribution data, but continued sampling a few sites for two additional seasons to get a complete picture of the entire range.

Most of the material collected from the burrows has been curated and some of it is now in the hands of specialists who are in the process of identifying the specimens. We are presently preparing manuscripts describing some of the new species and have began a GIS analysis of the insects distribution patterns.

Man has long regarded the pocket gopher as a pest. Our study has helped support the notion that the pocket gopher is also a keystone species with some ancient associations. We have significantly added to the list of species that are entirely dependent on the pocket gopher for their existence. We hope our study fosters further work on the arthropods inhabiting pocket gopher burrows.

Inherent Pitfalls of Insect Surveys

The easy part of an insect survey is gathering the material. It is another matter entirely to get it curated, identified to the species level, and the data compiled. Taxonomists willing and able to help with species identifications are becoming increasingly scarce, thus limiting the scope of an intended project. Surveys tend to generate a large volume of material, which represents raw data. This material needs to be properly cared for and housed in an insect collection. If the material is mounted, properly labeled, and identified, finding a repository is usually not be a problem. In the case of our survey, most of the material was originally collected in propylene glycol and then transferred to whirl packs containing 75% alcohol. Fortunately, most beetles hold up well when stored in alcohol but this is not the case for other insect groups. Survey projects targeting a specific group of insects invariably generate "residues" of non-target insects. If a survey is conducted in a remote locality or a microhabitat for which sampling is specialized and labor intensive (as with our study) every effort should be made to preserve residues for future study.

Obtaining permission to conduct field-work can be difficult. Permits were required by various state agencies to trap gophers. No permits were generally required to collect insects from pocket gopher burrows. However, we often had to do a great deal of explaining (sometimes in writing) as to why we sought access to trap gophers on private property. It was often difficult for private landowners to grasp the purpose of our study. While we were rarely denied access to areas we wished to sample, we were sometimes permitted entry only after hunting season was over. Hunting season coincides with peak activity of the insects and this may have cost us some data.

Obtaining funding to do most basic research is often problematic. With the exception of some modest monetary support provided by Theodore Cohn, an orthopterist assisting with our project, our survey was funded out of pocket. We pursued grant funding, but unfortunately we were unable to obtain any additional financial support. We hope that publishing our results will facilitate obtaining money so that we may continue to explore the pocket gopher burrow fauna for other insect taxa and in other parts of the U.S.

Final Comments

It is important to acknowledge the role amateur or avocational entomologists have played in improving our knowledge of insects. These entomologists voluntarily provide much needed man power for surveys and often do so with personal funds. In addition, these entomologists frequently have extensive regional knowledge, as well as collections of literature and insects that rival those in larger institutions. It benefits all of us to support and encourage their efforts.

Entomologists conducting insect surveys quickly discover that these endeavors are difficult. On one hand, the abundance and diversity of insects make them perhaps the most ideal subjects available for ecological and biogeographical studies. On the other hand, because of their diversity and abundance, it may take many years to sort, mount, label, and identify the insects gathered in a passive trap like a Malaise or flight intercept trap run in a given area for a single season. Evidence suggests that certain insects are habitat specific. These taxa may be useful for conservation and land management decisions. However, for many insects we know little of their distributions or habitat specificity. The only way to remedy this is through dedicated field studies, survey work, and the support of the avocational entomologists.

To summarize, local faunal surveys give us a better understanding of the insect life around us. They can help us to answer larger questions concerning the geographic and temporal distributions and help us to better understand their ecological associations. They can show us where our knowledge is deficient and where we have a handle on things. We need to remember that there is still much to discover in our own backyards.

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THE ALL TAXA BIOLOGICAL INVENTORY OF THE GREAT SMOKY MOUNTAINS NATIONAL PARK

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SYNOPSIS

The history, organizational structure, and purpose of the all taxa biodiversity inventory (ATBI) of the Great Smoky Mountains National Park are detailed. The benefits of the ATBI to the areas of Conservation, Education, and Science are explained.

In December of 1997 scientists, educators, and administrators gathered in Gatlinburg, Tennessee to discuss the idea of an all taxa biodiversity inventory (ATBI) of The Great Smoky Mountains National Park and, after three days of exchanging ideas and opinions, the ATBI was born. An inventory of this magnitude was attempted only once before, by D. Janzen in Guanacaste State in Costa Rica. For a number of reasons (financial and political) this endeavor changed into a survey of selected taxa over the whole of Costa Rica. Thus, the Great Smoky Mountains endeavor might be considered the sole extant ATBI.

In this paper I want to briefly discuss what we are trying to achieve and why such a herculean task is important to society.

Purpose

For every species of life in the Park we want to answer three questions: 1. What is it? 2. Where is it? 3. What does it do? And, we want to make this information easily accessible to a wide range of users.

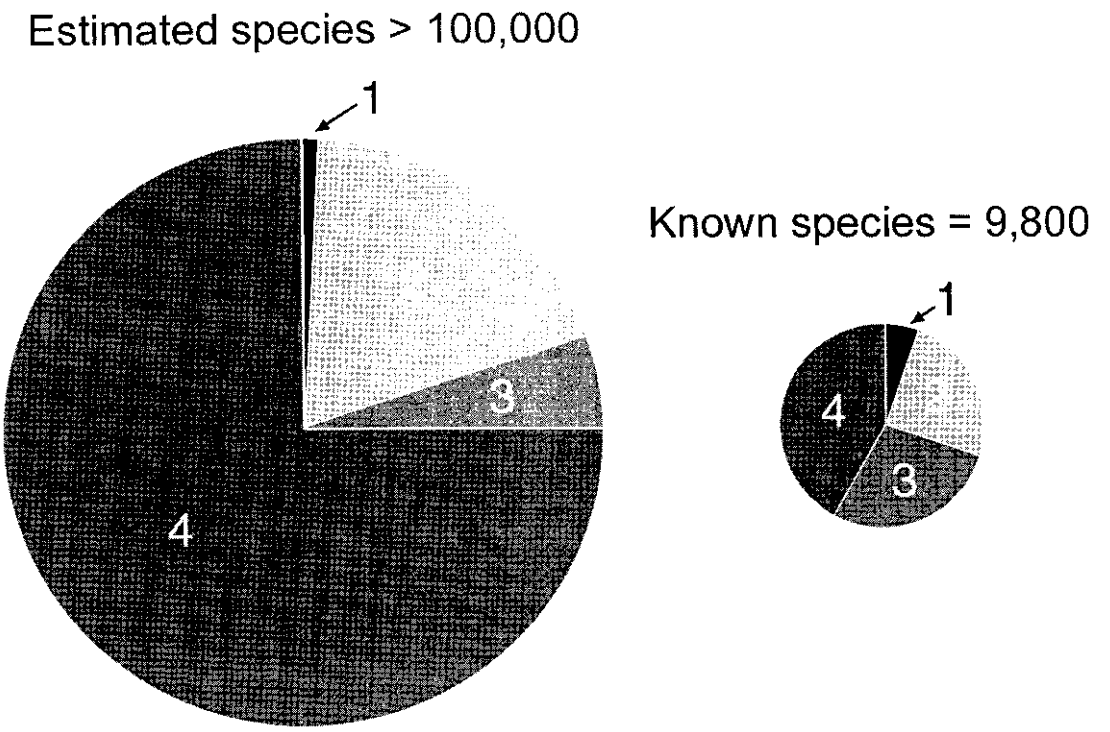
Most readers will recognize that two of these questions are potentially endless pursuits to which more and more detail could be added. We are looking for only the most basic answers. Our quest can best be explained with a simple example. If someone in the Great Smokies were to find an organism eating another organism, we would like to have the tools and information assembled to allow that person to identify the organisms to species. We would like to have a database that would allow her/him to find out where and when they occur in the Park (and perhaps elsewhere). Finally, we would like to have a homepage for the two species so that the user could access biological information, view images, and link to relevant web sites and published articles.

The Magnitude of the Task (Fig. 1)

At one of the annual meetings of the ATBI we asked the participating biologists to estimate the number of species that occur in the Park for their particular taxon of expertise. The tabulated result was 100,000 species. We know the number of species that have been recorded from the Park to be about 9,800. Of this number, many are simply published records of species occurrences and therefore there is much to do before these species can be considered "inventoried" for the Park. As Fig. 1 illustrates, some taxa such as mammals and vascular plants are well known but the megadiverse groups like fungi and arthropods are barely known. Indeed, less than 6% of the invertebrates are recorded!

Our first mission is to collect all species. Of course it will not be necessary to collect black bears or red oak trees, but collections will be necessary for the vast majority of taxa. These then have to be named. Willing systematists must be recruited, who, in many cases, will have to describe new species. Once there are names applied to organisms, the collection data must be incorporated into a central database. Further, we want to construct illustrated, interactive, identification keys for all taxa, including all species. Finally, we intend to construct species homepages that provide images and a synopsis of basic information about each species, as well as links to other more comprehensive sources of information.

One of the most prolific systematists in history was C. P. Alexander; a dipterist who described over 10,000 species in his lifetime. However, the average number of species "treated" by systematists today is far less than this. Even those who research diverse arthropod groups usually describe less than a few hundred species in a lifetime. Naturally, alpha taxonomy is not the sole task of most systematists; all of us are involved in higher classification, teaching, biodiversity studies and other research and duties. Nonetheless, imagine that the average taxonomist involved in the project could treat 40 species each year. This would include the major components of the inventory: naming (describing) the species, recording the data in the database, constructing interactive keys, and producing species' homepages. Some groups of organisms like the vertebrates and vascular plants could be dealt with at a much greater annual rate, but 40 seems a reasonable average since most of the biodiversity is composed of relatively poorly studied taxa. At this pace it would take 2,250 person-



	Estimated total in Park	Number currently known
1 Vertebrates	450	450
Fungi	20,000	2,250
3 Plants	5,400	2,816
4 Invertebrates	76,000	4,280

Fig. 1. Pie charts illustrating the relative abundance of organisms in the Park and the relative abundance of what is known.

years to deal with 90,000 species; it would take 100 systematists 22.5 years, and it would take 200 systematists 11.25 years to complete. I do not wish to discuss in detail the real monetary cost of this endeavor; but if all equipment, overhead, and personnel costs were calculated, the budget would be hundreds of millions of dollars. I hope that I have impressed upon the reader that this is no trivial task; rather it is one of the grandest scientific endeavors ever to be attempted. It is comparable to the moon-shot or the human genome project. What are the benefits to justify such a large expenditure of time and money? Is it worth doing? Can it be done?

Benefits

Conservation

According the book of Genesis (4:14), God gave Man his/her first task, which was to name all the beasts of the land, all the fish of the sea, and all of the birds in the sky over the Garden of Eden. Contrary to popular belief, this makes taxonomy the oldest profession in the world. This original task is repeated in the mythologies of most cultures, and with good reason. We can only benefit from natural resources if they are known, protect ourselves from natural hazards if nature is known, and,

most immediately, we can conserve and protect only those natural resources that we are aware of.

It is inconceivable for any successful economic enterprise not to have an inventory of their products and raw materials. Maintaining a ledger that lists inventory is a basic responsibility that companies owe to their shareholders . . . not to mention the IRS. In the same way, is not the scientific community, including you and me, not responsible for providing an inventory of the natural resources in the way of an all-species inventory? This was recognized by the federal government on August 25, 1916, when President Woodrow Wilson signed an act creating the National Park Service, a new federal bureau in the Department of the Interior responsible for protecting the 40 national parks and monuments then in existence and those yet to be established. One of the original justifications for the great expense of the park system was to ". . . to promote and regulate the use of the . . . national parks . . . which purpose is to conserve the scenery and the natural and historic objects and the wild life therein and to provide for the enjoyment of the same in such manner and by such means as will leave them unimpaired for the enjoyment of future generations." (National Park Service Organic Act, 16 U.S.C.1). How can we conserve and protect "the wildlife therein" if we don't know what they are?

There are many threats to the environment in the United States and around the world. In the Great Smoky Mountain National Park (GSMNP) these environmental threats include the following: global warming, acid precipitation, ground-level ozone, and deleterious non-native organisms. Just what effect these perturbations are having on the Park's ecosystem we don't know in much detail. Acid precipitation levels in the Park are amongst the highest in the nation and threaten a great deal of life forms. In the short run, those in freshwater systems where acidity can fluctuate rapidly are especially vulnerable. We know that acid rain is having an impact on the biodiversity of the Smokies, but are species being threatened with extinction? We have little idea because we don't have a comprehensive idea of what is/was there. How threatening is acid rain to soil invertebrates? The soil in most of the Park is not well buffered and the effects are likely dramatic.

We tend to see the effects of man's perturbations on large species. For example, the balsam woolly adelgid is an insect that was accidentally introduced to North America and it is well on its way to destroying the high altitude forests in the Park. These are dominated by Fraser fir trees, which are killed after the insects block the xylem transport system after feeding on the trees. We see the steady disappearance of the fir trees but we have little idea of the cascade effect that results when fir forests disappear. I would guess that there are many species of life that are dependent on the Fraser fir for their existence, either by maintaining some necessary environmental parameter or directly through the food chain. Most of these species will be lost long before the last Fraser fir succumbs to disease. A survey conducted by Fred Coyle (1997) on the spruce-fir moss spider (*Microhexura montivaga*) concludes that the decline in the high elevation Fraser fir canopy has caused extensive damage to the forest floor community, and has disturbed the fragile ecosystem that depends on protection afforded by Fraser firs. How many, if any, species have been, or will be, lost? How many of these were/are endemic to the Park? To determine what is being lost we must have some idea of what is there . . . and we just do not. The first benefit of an all species inventory is that it will allow us to monitor the effects of environmental pollution and other disturbances to the environment, including our most recent great concern, global warming.

Education

The educational benefits of the ATBI are enormous and they are already being realized. The curved line in Fig. 2 represents our present state of knowledge about the Park biota. Thanks to the efforts of D. K. Smith at the University of Tennessee and many other botanists we have a lot of information on the vascular plants of the Great Smokies. We have much less information on the species of fungi in the Park and still less on the insects. It is the goal of the ATBI to move this curve of knowledge up and to the right until the area of darkness becomes a small semicircle in the far upper right corner.

The educational benefits are represented in Fig. 3. The products of the ATBI will enlighten all sectors of society. Professional biologists (specialists) will be able to identify a diversity of organisms and to access the wealth of information that these names provide.

To give you an example of our current state of knowledge on a very diverse and relatively poorly known group, I will use the Braconidae. My systematic research centers on this family of parasitoid wasps and I estimate that there are about 2,000 species of braconids in the Great Smoky Mountains National Park, about one-half to two-thirds of which are described. Adult females of braconid wasps lay their eggs in or on other insects and their progeny consume and eventually kill their hosts. Braconids and other parasitoid wasps are very abundant and they are important in the natural balance of life. I will explain the process of trying to identify braconids from the Park using a simple, though somewhat hopeful example. Because I spent more than 13 years at the Canadian National Collection, where I was responsible for building the braconid collection

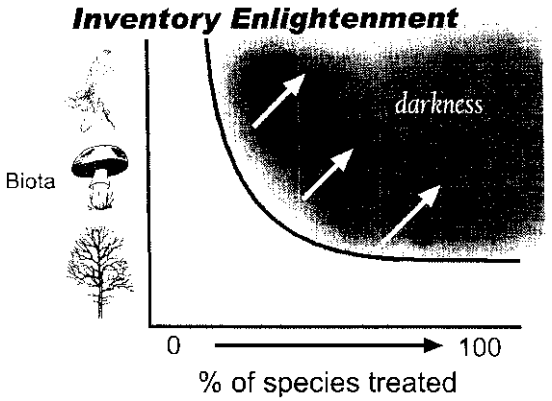


Fig. 2. The y axis refers to the physical size of an organism and the x axis refers to the percentage of species that have been recorded in the park. See text for explanation.

and identifying these wasps to species, I am one of the most qualified people in the world to do this and I have in hand all of the literature and identification keys for the North American species of the Braconidae.

Imagine that ten species of braconids are collected in the Park and luckily all of them are described. Because I recognize most of the 300 or so genera of braconids but a very small fraction of the species, I would go directly to species-level keys. I would plow through these keys and descriptions to obtain temporary identifications and then check these against my collection at the University of Kentucky. This would yield about five satisfactory identifications. For the remaining five specimens I would have several options: ask

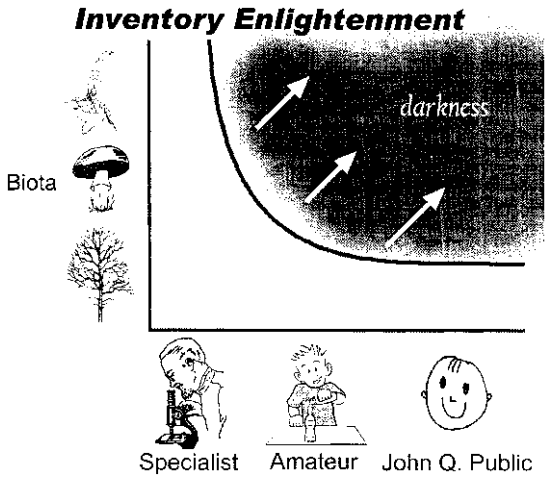


Fig. 3. The y axis refers to the physical size of a species, and the x axis refers to the state of knowledge of various segments of the population. It is our goal to move the curve to the upper right. See text for explanation.

for type specimens from the museum curators where they are deposited, send the specimens to colleagues who happen to know more than I do about the particular subfamily, or travel to the Smithsonian Institution and/or other major collections to make comparisons with types or reliably determined material. The point that I am trying to make is that even the 'world experts' have great difficulty identifying the vast majority of the described species that are in the Park. The described species present another set of problems.

After the completion of the ATBI the task of identifying the braconids will be greatly facilitated. The illustrated interactive keys would permit reliable identifications; the color images on the species homepages would verify most identifications, and in a worst case there would be access to reliably identified specimens of all of the species in one museum. (It is our intention to have representative specimens of each species deposited in the Park collection, and the Park is in the process of building a multimillion dollar science center to house the biological collections emanating from ATBI activities).

People with amateur interests in biodiversity will also benefit greatly from the products of the ATBI. I have an amateur interest in the Ichneumonidae (These are parasitic wasps closely related to the Braconidae and there are about 3,000 species estimated in the Park). If I were asked today to identify a handful of species of ichneumonids from the Park, I would be able to identify the beasts to the subfamily or maybe the generic level but further identification would be unlikely for all but the most well-known taxa. I would have to rely on the aid of one of the few world experts in the group who, in turn, would have to go through the process described above. With the aid of the tools supplied by the ATBI, especially the interactive keys and images, I could obtain reasonably accurate species identifications for this diverse family. I have some confidence in these claims because I have developed many interactive keys using the software DELTA (Dallowitz 1994) and INTKEY (Dallowitz et al. 2000), and I have asked amateurs, including my 15-year-old daughter, to test them. Many of these are on my website (www.uky.edu/~mjshar0). Although printed dichotomous keys are all but impossible for amateurs, illustrated interactive keys make identifi-cations quick and easy.

With easy access to electronic identification tools for rather esoteric groups of organisms we can expect greater interest in their natural histories. Most readers know of published works that have accomplished this to some degree for a particular taxon. In my own experience I have seen a greatly increased interest in braconids since the publication of a manual for the identification of the 404 genera of Braconidae that are known to occur in the New World (Wharton et al. 1997). One of the expected results of the ATBI will be that many of

the taxa that are in the inaccessible "darkness" region of Fig. 3 will become popularized.

What about the average person (J. Q. Public, in Fig. 3)? Our experience tells us that this is the segment of the population that is most likely to benefit from the ATBI. Most readers of this article are biologists and will appreciate that with an increased knowledge of the natural world comes an increased appreciation and fondness for nature. We all know that an educated community will enjoy and use the Park far more than an uneducated one.

In one of our outreach events for the ATBI, the public was invited to the Park to experience the ATBI. A laptop computer with an illustrated interactive key to the 30 species of salamanders that occur in the Park was taken into the field with a large group of people ranging in age from five to 75. They were so excited about catching salamanders and identifying them with the picture keys that it was the most successful event of the day. Incidentally, the participants were carefully instructed on how to handle salamanders so as not to injure them. We envision interactive keys for the more conspicuous fauna and flora in the Park, such as vertebrates, wild flowers, mushrooms, etc., to be available to Park visitors on handheld devices that can be carried into the Park. Campbell Webb of Yale University has already developed interactive key software (PalmKey) that operates on handheld PalmPilots.

Science

The benefits to taxonomy and systematics are myriad. Many of our most species-diverse taxa are not investigated and remain almost completely unknown because investigating them on a cosmopolitan basis is an undertaking that is simply too large. This is especially true for those taxa that do not have an obvious influence on our economic activities. In the systematic studies of most organisms it is now normal procedure to "revise" monophyletic taxa. (Monophyletic taxa are groups of organisms that exclusively share a common ancestor, i.e., an ancestral species and all of its descendants.). This practice allows the researcher to construct cladograms, with which hypotheses of phylogenetic relationship can be posed and tested. In biodiversity studies, such as the ATBI, this is difficult because usually we are not dealing with monophyletic taxa but with subsets of monophyletic taxa. Nonetheless, a great amount of information on character state distributions is obtained, and preliminary hypotheses of monophyly can be postulated and tested with more extensive collections. The ATBI of the Great Smokies will deal with many megadiverse taxa for the first time in the modern era of systematics. The results of these studies will provide a stepping-stone for studies of some of these taxa on a larger geographic scale, perhaps the Nearctic region or perhaps the world. In many cases, the number of species found in the Smokies for any monophyletic group will allow us to have an educated guess at the number of species found in the United States, or even worldwide.

The identification tools generated by the ATBI will directly service the entire eastern United States north of Florida and much of southeastern Canada. Only a small percentage of the species that occur in this vast area do not also occur in the Park. We expect that the database and identification keys will be augmented to offer biotic information to a much larger geographical area that will have an even greater audience than that of the ATBI. Though the inventory is restricted to the Park, the products will have far reaching utility for a much greater geographic area.

Any biologist conducting whole organism research can imagine that having available any biodiverse area of the world where all of the species are named and all are relatively easy to identify would be a great bonus to their research. It would be the ideal place to study natural biological interactions, an unprecedented living laboratory.

There is a comprehensive Geographical Information System (GIS) in the Park with which all of our sampling and locality data will be associated. This facilitates community structure studies and those on species distributions and interactions. The information will be available for extrapolation far beyond the Park boundaries.

Economic and other Societal Benefits

In their draft report to NSF on the feasibility of an ATBI in the tropics, Janzen and Hallwachs (1994) listed numerous benefits. Since the societal benefits are made succinctly in their text I have selected a few and present them here almost verbatim.

- Enormous opportunity to gather biodiversity samples, as an add-on process, for biodiversity prospecting of genes, chemicals, structures, and behavior.
- Enormous opportunity to gather living samples with which to stock seed banks, gene banks, tissue banks, sperm banks, culture collections, botanical gardens, zoos, etc.
- A major injection of actual wildland specimens and genes into the national and global pool from which all sectors of society can draw for their needs.
- A major step forward in the evolution of scientific and computer technology that can accept, manage, manipulate, and package large masses of highly particulate and diverse biological information.
- A major step forward in the evolution of the administration of a highly interdisciplinary, cross-society project.
- A major injection of funds, motivation and experience into the Taxasphere (Taxa-

sphere refers to all of those people involved in taxonomic study and industry).
- A major increase in appreciation of the Taxasphere as a crucial social element.
- A major social event for the region in terms of employment, local opportunities for learning and training, commercial enterprise, and income generation through development of the information that will be forthcoming.
- A high profile biological effort that will generate considerable positive press, educate the public about diversity, and stimulate greater interest in and support of taxonomy and systematics.
- A world-class project for the processes that generate all of these products.

How To Do It

Administration: Discover Life in America (DLIA)

Shortly after our meeting in December of 1997, where we first discussed the idea of the ATBI, a group of us established Discover Life in America, a not for profit, public benefit organization, under the auspices of which the ATBI would be administered. This organization allows us to accept tax-exempt donations and interact in a coordinated manner with the Park administration. Our current president is Frank Harris of the University of Tennessee. A blue-ribbon Science Advisory Panel to DLIA has been organized to provide advice on the conduct of the ATBI. The panel consists of Daniel Janzen (University of Pennsylvania), Thomas Lovejoy (The World Bank), Ronald Pulliam (University of Georgia), Peter Raven (Missouri Botanical Garden), and Edward O. Wilson (Harvard University).

One of the committees appointed by the board of directors of DLIA was the Science Committee co-chaired by Peter White of The University of North Carolina and John Morse of Clemson University. Their most important task, to date, was to compile a science plan (White et al. 2000, available at http://atbi.biosci.ohio-state.edu:898/atbi/sciplan2000.pdf.). The interested reader can refer to that document for details. We wish to complete the inventory in 10-15 years, understanding that we will never find every species in the Park, even with enormous resources. Biodiversity is a dynamic process and what is found in one year will not be the same as the next.

Database

Our first and most important charge was to develop a central database to organize all of the information that would be forthcoming. It was clear from the beginning that this was the core of the inventory and in time it would become the inventory. With the help of a NSF grant, Norman Johnson and colleagues at Ohio State University have completed the development of the database. Now all that is left is to fill it with the information that we gather for the 100,000 species of life in the Park, and this process is well underway.

Taxonomic Working Groups (TWiGS)

As an organizational tool we have adopted the Taxonomic Working Group (TWiG) structure originally developed by Daniel Janzen for his ATBI in Costa Rica. We have divided life into approximately 20 units. A systematist has been assigned to develop a team for each of these TWiGS. The TWiGS are not necessarily organized around monophyletic taxa. Rather, practical considerations like the size of the organisms and their life histories are considered. For example, we have a Hymenoptera TWiG that is investigating a monophyletic taxon and an aquatic insects TWiG that is studying fresh water insects, a non-monophyletic assemblage.

Collecting organisms for the ATBI is very taxon dependent and consists of a mixture of organized repeated sampling and ad hoc collecting. As an example of how the TWiG structure works I will use the Hymenoptera TWiG. We have identified 19 terrestrial life zones in the Park that range from lowland cove hardwood to high altitude spruce-fir forests. In each of these we have established biodiversity reference points that are one hectare in area (Fig. 4). These serve as the primary sites for structured sampling. Currently we have 11 of these sites being sampled by Chuck Parker (Biological Resources Division) and his team. Every two weeks samples from Malaise and pitfall traps and Lindgren funnels are collected and sent to a primary sorting center in the Park. The samples are processed in a sorting pool in the Park where they are divided into TWiG taxa. One of these is the Hymenoptera. The Hymenoptera samples are sent to my lab at the University of Kentucky where they are sorted to the family level and sent out to the members of the Hymenoptera TWiG.

As an example of what happens at this next level I will use the Braconidae. Most braconid specimens are mounted, labeled, and given a unique identifying code. All braconids are identified to genus. There are a number of braconid genera that have hundreds of species, the majority of which are not described, and these are not mounted now but placed in vials of alcohol and stored in a freezer. I identify to species members of those genera that are sufficiently well known taxonomically. For braconid subfamilies for which I have colleagues with more expertise, the specimens are shipped to them for identification. The identified specimens are eventually returned to me and the specimen data are then entered into the ATBI database at Ohio State University. Im-

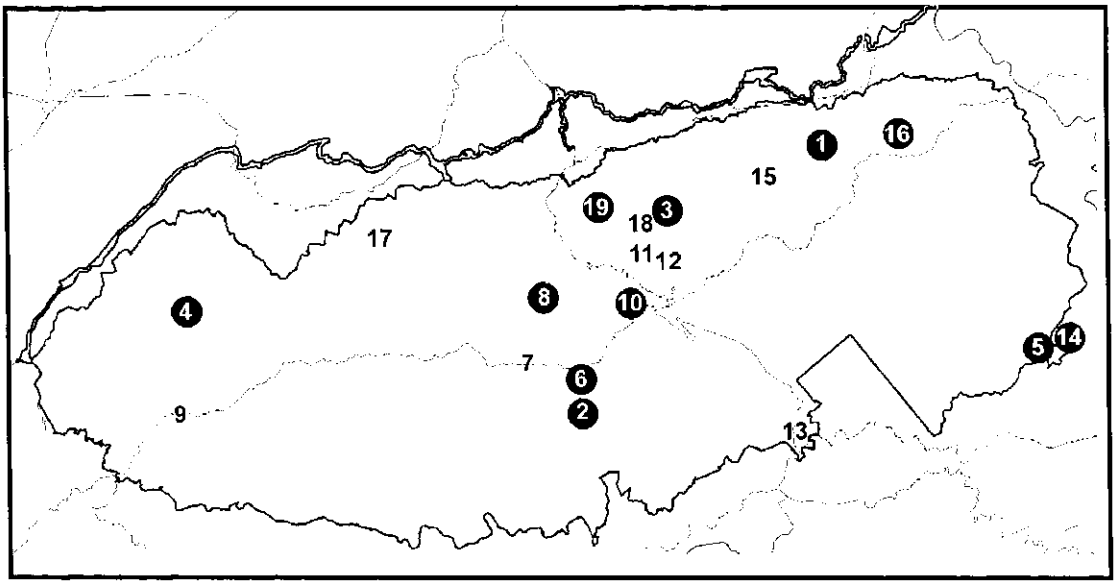


Fig. 4. The 19 localities where repeated long-term sampling will be conducted for the ATBI. The localities represented with black circles are currently being sampled with pit-fall traps, Malaise traps and other arthropod sampling methods.

Plot #	ATBI Plot Name	Elevation	Vegetation Type
1	Albright Cove	3,390'	Montane Cove
2	Andrews Bald	5,760'	Grassy Bald
3	Brushy Mountain	4,810'	Heath Bald
4	Cades Cove Old Field	1,710'	Treeless
5	Cataloochee	4,530'	Mesic Oak
6	Clingmans Dome	6,380'	Spruce—Fir
7	Double Springs	5,600'	Beech gap
8	Goshen Prong	2,940'	Cove Hardwood
9	Gregory Bald	4,940'	Grassy Bald
10	Indian Gap	5,490'	Beech Gap
11	Mt. LeConte Blvd.	6,010'	Spruce—Fir
12	Mt. LeConte 2	6,430'	Spruce—Fir
13	Oconaluftee	2,010'	Bottomland Hardwood
14	Purchase Knob	5,020'	Northern Hardwood
15	Ramsey Cascade	2,950'	Xeric Oak
16	Snakeden Ridge	3,260	Hemlock
17	Tremont	1,500'	Tulip Poplar
18	Trillium Gap	4,600'	Beech Gap
19	Twin Creeks	1,950'	Tulip Poplar—Hemlock

ages of each species are captured in my lab and interactive keys and species homepages are developed. Identified specimens are deposited in the Park collection, the University of Kentucky collection, and duplicate specimens are returned to collaborating braconologists. Because there are many replicates of each species, each collaborator builds a very complete collection of all common species of Braconidae. To augment the collections of Braconidae, numerous trips will be taken and different collecting methods, such as sweeping and pan traps, will be employed. Illustrated, interactive keys, to the braconid subfamilies and genera that are likely to occur in the Park are now available on my web site (www.uky.edu/~mjshar0).

At this point we still have all of those big nasty unknown taxa of braconids in the freezer. These constitute about 30% of the species of Braconidae and they represent our greatest challenge. Similar challenges will be found in most of the species-diverse taxa that inhabit the Park. Previously, I described the magnitude of our task and inferred the length of time and amount of money that it would take to complete treatments for 90,000-

100,000 species. Clearly, something has to be done to accelerate the process and reduce the cost. The taxa that are in the freezer represent the biggest bottleneck in our endeavor. There are several suggestions to describe and otherwise treat the species for these largely unknown groups. The one that I like is referred to as Accelerated Research for Taxonomic Systems (ARTS). When the state of knowledge for a group is particularly poor, for example for the stink bugs (Pentatomidae), we might refer to this process as fundamental accelerated research for taxonomic systems. Either way the process and its rationalization, described below, are much the same.

The mechanics of conducting taxonomic research have not changed appreciably over the last generation. Most taxonomists do all of the work themselves. At best, they have a technician to do some repetitive work such as taking measurements or recording locality data. Taxonomists collect specimens, prepare and label the specimens, discover useful morphological characters to group the specimens into species, write dichotomous keys to allow others to distinguish the species, check type specimens and published articles to apply names to previously undescribed species, write detailed descriptions, prepare line drawings, and take photographs, including scanning electron micrographs, to illustrate characters and species. The tasks that require a systematist's expertise are few and much of our work is repetitive and technical in nature. The systematist's skills are best employed to find distinguishing characteristics to separate species and to wade through the sometimes complex literature and collections to identify previously described species. Most of the rest of the work can be automated with tools that are available today.

The DELTA/INTKEY system is one such technology. Given a list of characters and character states for each species, this combination of applications can generate diagnoses, descriptions, dichotomous keys, and interactive keys. I do not suggest that all collaborating taxonomists learn how to use these tools. On the contrary, we will train technicians to assist taxonomists. This is far more efficient and inexpensive and it will leave the taxonomists free to treat more species. Given a little direction, technicians can also be trained to acquire most of the illustrations using digital cameras attached to stereomicroscopes. New photographic technology that captures images in multiple layers allows us to illustrate structures that previously had to be drawn by hand because of depth of field limitations. I have used DELTA and INTKEY for numerous revisionary publications (Sharkey 1996, 1997, 1998) and computerized keys (see these on my web site www.uky.edu/~mjshar0); much time is saved with these applications and data are organized in such a way that it is simple to add species to the revision as new discoveries are made.

Given the financial resources, when a taxonomist agrees to tackle a megadiverse group for the Park, we will assist him/her by offering technical support described above. The products would complete what is needed for the ATBI but the data would be available to facilitate more extensive revisionary studies.

Another method of organized collecting and adding to the database of the ATBI is the bioblitz. In July of 2000 David Wagner and collaborating Lepidopterists visited the Park to see how many species of Lepidoptera they could find in one 24-hour period. They discovered 706 species of moths, including 301 species that had never been recorded in the Park and 25 undescribed species. The informal Park list included 800 species before the bioblitz. From these results Wagner and his group estimated that there are at least 3,000 moths and butterflies in the Park. We have also had a fly blitz and a beetle blitz.

Why The Great Smoky Mountain National Park?

The Park encompasses the richest natural area in eastern North America. It is the home of more than 1,570 species of vascular plants including 130 species of native trees. It boasts a diversity of salamanders that may be unmatched anywhere else in the world. The elevational range in the rugged ancient mountains (270 m-2025 m) endows the region with an array of climates comparable to a 1,250 mile north-south transect through the eastern United States and Canada. The diversity of the region is the main reason it has been added to the list of International Biosphere Reserves and World Heritage Sites recognized by the United Nations. While biodiversity may mean wild plants and animals to much of the general public, the Great Smoky Mountains literally brings this to their backyard. Over 4.8 million people live within a radius of 500 miles of the Park (1990 census data). It is the most visited national park in the New World, and it hosted over 9 million visitors in 1999.

The Park covers approximately 2,200 square kilometers (521,621 acres) in the southern Appalachian Mountains in the states of Tennessee and North Carolina (Fig. 4). Some 95% of this area is forested, but much was subjected to a range of disturbances in the past. Nevertheless, the Park contains some of the most extensive tracts of virgin forest remaining in the eastern U.S. The bedrock is heterogeneous consisting of igneous rocks, acidic phyllites, sandstones, shales, and carbonate rocks. The carbonates have produced various karst features, including the deepest cave in Tennessee. Precipitation levels vary from 1,650 mm per year at low elevations to over 2,500 mm at the highest elevations. Fog is an additional source of

precipitation and occurs about 73-100 days per year at Noland Divide. There are 3,400 km of permanent streams within the Park, and all major streams originate within its boundaries.

The choice of the GSMNP as an ATBI site is exemplary because: 1. It is the most species-diverse area in temperate North America. 2. It is federal land protected by the National Park Service. 3. It is in close proximity to millions of citizens who will benefit directly from the biodiversity research when visiting the Park and through their direct participation as volunteers. 4. The Park Service passionately supports and encourages the ATBI. 5. It is located in close proximity to one of the world's greatest concentrations of taxonomists and many important biological collections. 6. The Park is located in the United States of America, a country whose citizens have the political, economic, and intellectual will to accomplish great things.

The Future

The broad range of interest and participation in the ATBI is demonstrated by the fact that our planning meetings have included representatives from 37 colleges and universities in the United States and Canada, 17 private organizations, and officials from the National Park Service, the Smithsonian Institution, the USDA Systematic Entomology Laboratory, Biological Resources Division, USDA Natural Resource Conservation Service, USDA Forest Service, the U.S. Fish & Wildlife Service, the Environmental Protection Agency, the Oak Ridge National Laboratory, and the President's Office of Science and Technology Policy. More so than any other taxonomic endeavor, we have been widely covered by the popular press with articles in magazines such as Audubon, Science, and Newsweek.

If successful, the ATBI will require a lot of resources but, by and large, these will not be resources that would have otherwise gone towards taxonomic research. Presently, we have some funding from the National Science Foundation and other national scientific organizations but most of our support comes from private organizations such as the "Friends of the Park" which raises money for Park activities. We expect greater contributions from private sources as our products become more visible.

Due to the great public interest in the ATBI, the endeavor has become a rallying point that promotes the sciences of taxonomy and systematics. We present them to the public in such a way that they are appreciated. This sort of interest is certain to have a positive influence on the public perception of our research and therefore on the amount of money that public institutions are willing spend on taxonomy and natural history. Scientists involved in all aspects of biodiversity research, including those doing revisionary studies of monophyletic taxa, can expect to profit from the education and promotion components of the Great Smoky Mountains ATBI.

Acknowledgments

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THE EVOLUTION OF BIOLUMINESCENCE IN CANTHAROIDS (COLEOPTERA: ELATEROIDEA)

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ABSTRACT

We present the first cladistic analysis of genera in the family Lampyridae and other closely related beetles. A monophyletic concept of Lampyridae is established. The phylogenetic positions of the luminous cantharoid families [Omalisidae, Rhagophthalmidae and Phengodidae] in relation to Lampyridae are discussed, as well as the implications of the evolution of bioluminescence and photic signaling in this group of beetles. The Rhagophthalmidae appears to include *Dioptoma* and *Diplocladon* (formerly located in Phengodidae) and the Phengodidae apparently includes *Stenocladius* (formerly of Lampyridae). *Harmatelia, Drilaster* and *Pterotus* are transferred to Elateroidea *insertae sedis* and not included in Lampyridae where they were sometimes placed.

Key Words: Bioluminescence, Lampyridae, Omalisidae, Phengodidae, Rhagophthalmidae, Harmatelia, Drilaster, Pterotus

RESUMEN

Presentamos el primer análisis cladístico de los géneros en la familia Lampyridae y otros escarabajos muy relacionados. Se establece un concepto monofilético de Lampyridae. Se discuten las posiciones filogenéticas de las familias luminosas "cantharoid" [Omalisidae, Rhagophthalmidae y Phengodidae], y su relación con Lampyridae es discutida, al igual que las implicaciones de la evolución de la bioluminiscencia y señalamiento de luz en este grupo de escarabajos. La familia Rhagophthalmidae parece incluir *Dioptoma* y *Diplocladon* (antes localizados en Phengodidae) y la Phengodidae aparentemente incluye *Stenocladius* (anteriormente de Lampyridae). *Harmatelia*, *Drilaster* y *Pterotus* son transferidos *insertae sedis* a Elateroidea y no se incluyen en Lampyridae donde a veces han sido colocados.

The common and conspicuous bioluminescent displays of adult fireflies have been marveled at by man throughout history and have long been recognized, as displays of courtship. In 1647, Thomas Bartholin related an observation of Carolus Vintimillia that "nature had endowed them [female fireflies] with a vigorous light in order that they could call the males at night with their shine" (Harvey 1957). Bishop Heber in his *Tour through Ceylon* remarks: "Before beside us and above, the firefly lights his torch of love" (Harvey 1940). However, the less conspicuous bioluminescent emissions of less well-known beetles seem to have escaped notice by most. This phylogenetic analysis focuses on the origin of luminous habit and the evolution of luminescence. Therefore, the taxa chosen for this analysis most heavily represent the breadth of Lampyridae with an equal number of luminous and non-luminous genera in the cantharoid lineage. This analysis establishes the limits of a monophyletic Lampyridae, places other luminous taxa that are thought to be closely related to fireflies, and investigates possible origins and losses of luminescence in taxa related to Lampyridae.

The superfamily Cantharoidea was combined into the Elateroidea when Lawrence (1988) redefined Elateriformia. Our analysis includes most of the families that formerly composed the Cantharoidea of Crowson (1955, 1972) (his included Brachypsectridae, Omalisidae (= Omalysidae, Homa-lisidae), Karumiidae, Drilidae, Phengodidae, Telegeusidae, Lampyridae, Cantharidae, Lycidae, Cneoglossidae, Plastoceridae and Omethidae). We refer loosely to the taxa used in this analysis as "cantharoids," as they have been treated historically as a monophyletic group within the Elateroidea (Lawrence 1988).

MATERIALS AND METHODS

Eighty-five exemplar taxa were selected to represent a diversity of Lampyridae and outgroup families. Selection of taxa included as many subfamilies and tribes as possible within Lampyridae, based on the classification schemes of Crowson (1972) and Lawrence & Newton (1995), and 11 subfamilies within 9 other families, based on Lawrence & Newton (1995) (Appendix 1). We did not include any members of Elateridae in this analysis as they are too distantly related to the taxa considered here (Lawrence 1988). Seventy four male morphological characters with a total of

212 character states were used in the analysis. Inapplicable characters were coded as "-", while missing characters were coded as "?". All characters were analyzed under equal weights with 20 multistate characters as additive (see Appendix 2, 3). Plastoceridae was designated as the root of the tree based on Lawrence's (1988) phylogenetic analysis of the Elateriformia. The parsimony ratchet (Nixon 1999) (consisting of 100 iterations, weighting 12% of the characters) was implemented in Nona (Goloboff 1993), run within Winclada (Nixon 2000). The most parsimonious trees discovered were used as the starting place for a more exhaustive search using the "max*" command within NONA. The "best" command was then used to eliminate sub-optimal trees. A strict consensus tree was then calculated from these most parsimonious trees. Bremer support (Bremer 1988, 1994) was calculated using NONA, and the search was set to a Bremer support level of 5, with four runs, each with a buffer of 5000 trees.

RESULTS

The parsimony ratchet returned trees of 818 steps. Starting from these 52 trees, "max*" and "best" gave 280 most parsimonious trees of 818 steps. A strict consensus (Fig. 1) of these 280 trees collapsed 13 nodes and produced a consensus tree of 848 steps (ci = 0.16, ri = 0.57). Bremer values listed in Figure 2 indicate the number of steps that are required, up to 5, to find the closest tree that does not contain that particular node. Lampyridae is monophyletic with the exception of a few taxa that have been of controversial affinity (*Harmatelia, Drilaster, Pterotus,* and *Stenocladius*.) Two genera currently classified as phengodids (*Dioptoma* and *Diplocladon*) were placed with rhagophthalmids in this phylogenetic analysis. The families Drilidae, Omalisidae, Lycidae, Omethidae, Teleguesidae and Phengodidae appear to be monophyletic. The monophyly of Cantharidae is not supported.

DISCUSSION

Testing the Monophyly of Existing Families

Lampyridae.

In view of our phylogeny, Lampyridae as defined by Crowson (1972) and Lawrence and Newton (1995) is not monophyletic. The three synapomorphies that define the base of Lampyridae are: covered head position, oblique attachment of trochanter to femora, and wing vein CuA1 intersecting MP above fork (Kukalova-Peck & Lawrence 1993). The genera *Harmatelia, Pterotus, Drilaster* (*Ototreta*) and *Stenocladius* are currently classified as lampyrids (Lawrence & Newton 1995; after Crowson 1972) though in our analysis they are clearly placed outside of the family Lampyridae. This is not entirely unexpected, as several previous authors (LeConte 1859; McDermott 1964; Crowson 1972) who have examined some of these taxa have viewed them as possessing questionable affinities to existing families. LeConte (1859) placed *Pterotus obscuripennis* in Drilidae and then later (1881) moved it to Phengodidae. Of the genus *Pterotus*, LeConte (1859) stated, "A singular genus, which I have described at length from my inability to place it properly. It seems to have a mixture of characters belonging to the Lampyrides, Telephorides and Drilids, but from the small size of the posterior coxae is probably better placed with the latter." McDermott (1964) also mentions the difficulty he encountered in trying to place some of these taxa, "Both *Pterotus* and *Harmatelia* share a large degree of similarity between some characters. Also neither fits strictly to the accepted lampyrid characteristics and both have some suggestion of phengodid affinities. Combining these two genera in the subfamily Pterotinae is admittedly arbitrary but nevertheless serves to bring them together as transitional forms." Crowson (1972) wrote that the genera *Pterotus* and *Ototretadrilus* were the most phengodid-like and probably the most primitive firefly genera he had studied. (Specimens of *Ototretadrilus* were not available to us.)

The genus *Drilaster* was originally described in the family Drilidae by (Kiesenwetter 1879), and *Ototreta* was originally described in the family Lampyridae. The synonymy between *Drilaster* and *Ototreta* was noticed by Nakane (1950) (see also Sato 1968). However, Asian workers continued to use the older name (*Drilaster*) but moved it to Lampyridae. American and European workers continued using *Ototreta* as it appeared to be the valid name in McDermott 1964 and 1966. Therefore, not only should American workers discontinue the use of the name "*Ototreta*," but these taxa should no longer be associated with the family Lampyridae. For a short history of the taxonomic placement of *Drilaster* and *Ototreta,* see Table 1.

According to our phylogeny (Fig. 1), if *Harmatelia*, *Pterotus, Drilaster* and *Stenocladius* continue to be considered fireflies, the families Lycidae, Cantharidae, Phengodidae, Omethidae and Teleguesidae would need to be synonymized with Lampyridae. This seems drastic given the peripheral significance of the genera and the traditional affection for the families. *Harmatelia*, *Pterotus*, and *Drilaster* should be removed from Lampyridae and given the taxonomic label of "Elateroidea *incertae sedis*" awaiting further study to place them properly. *Drilaster* may not be monophyletic. Our analysis clearly places *Stenocladius* sp. in the family Phengodidae. Ohba et al. (1996) studied the external morphology of *Stenocladius* larvae and found that they did not posses an epicranial suture on the dorsal surface of the

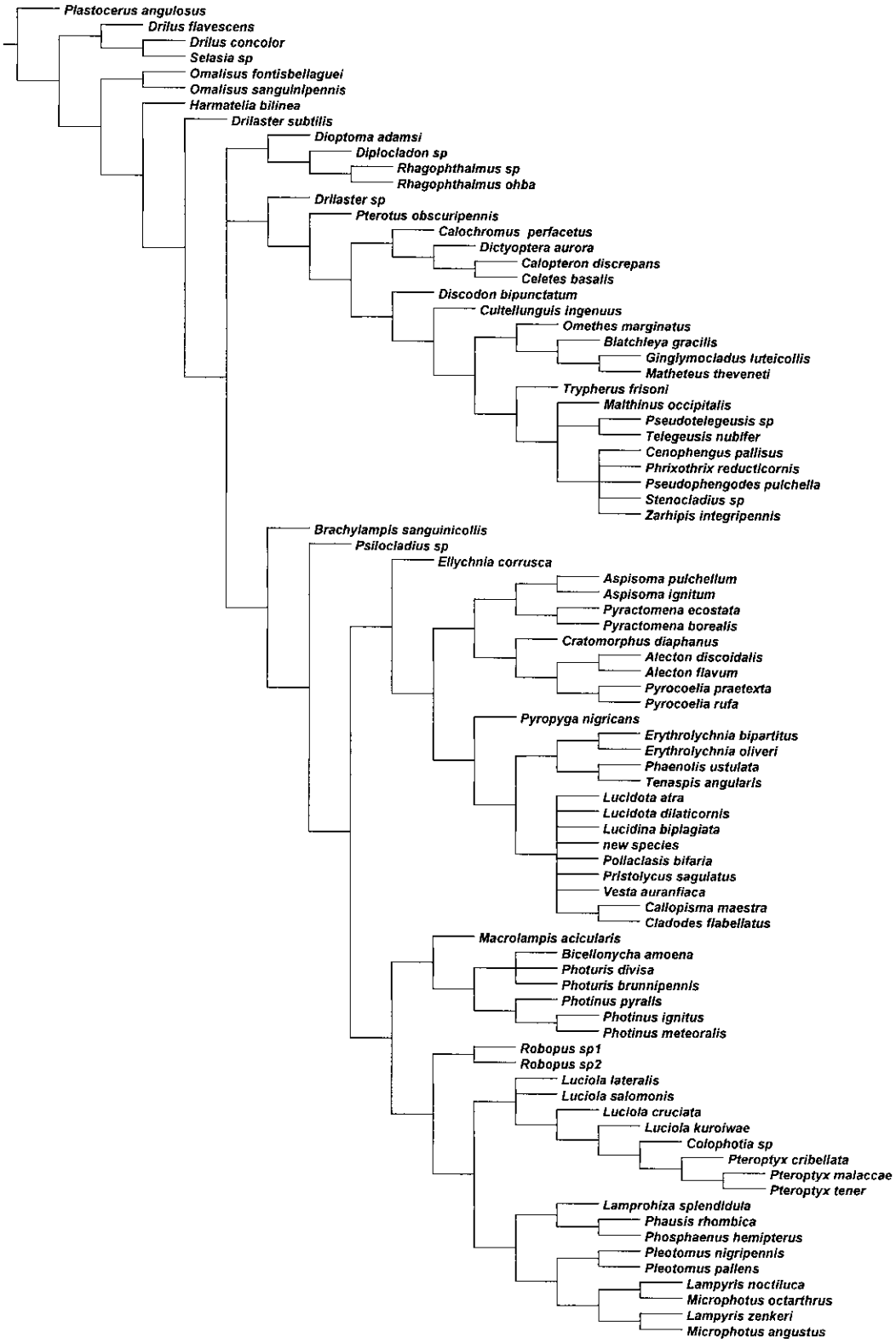

Fig. 1. Strict consensus of 280 most parsimonious trees (848 steps, C.I. 0.16, R.I. 0.57). The node at which *Brachylampis sanguinicollis* is the basal defines the base of the lampyrid clade.

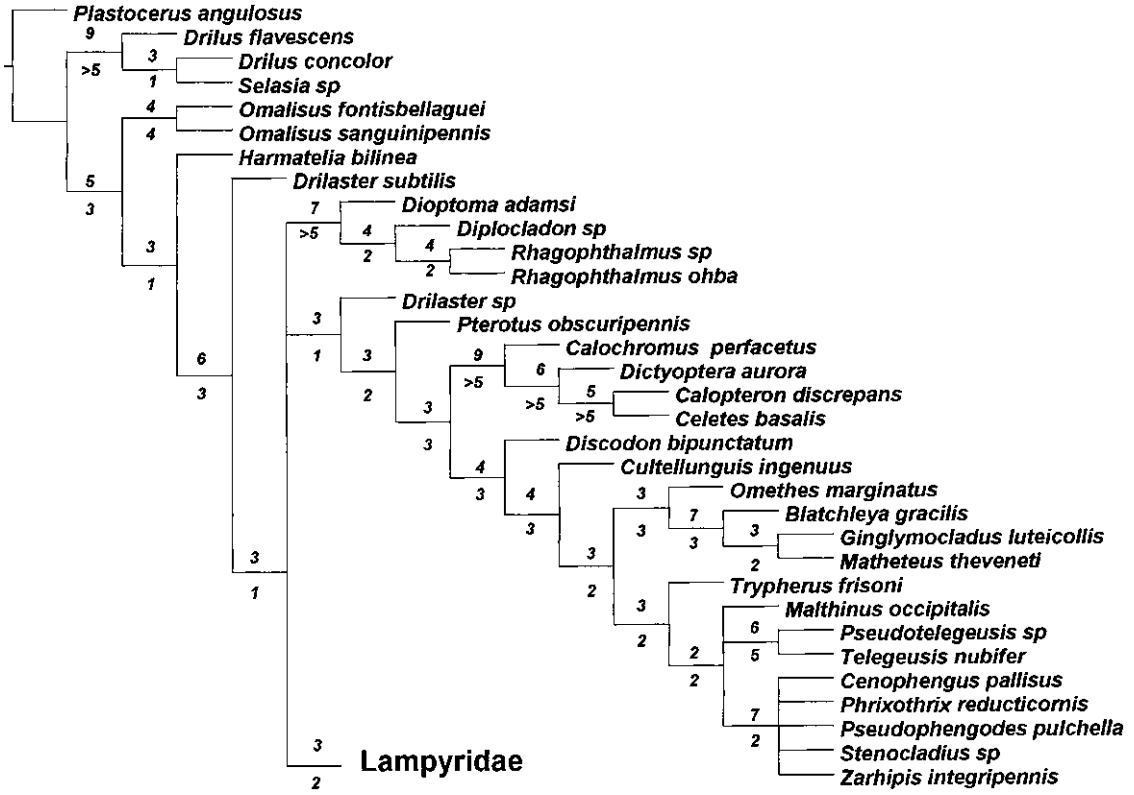

Fig. 2. The strict consensus with the lampyrid clade collapsed and represented by Lampyridae. Numbers located under the nodes are Bremer Support values (set at a max. Bremer value of 5.) Numbers located above the nodes present the number of synapomorphic characters at that node.

larval head. This suture is well developed in larvae of Lampyridae. They hypothesized that the fused dorsal surface of the larval head in *Stenocladius* is more closely allied with Phengodidae than Lampyridae. Our analysis supports this association. Because the clade containing these taxa in our analysis is unresolved, there is no information concerning which subfamily of Phengodidae *Stenocladius* should be placed within (Fig. 2).

Other Cantharoid families.

The families Plastoceridae, Drilidae, Omalisidae, Rhagophthalmidae, Lycidae, Omethidae, and Teleguesidae are supported as being monophyletic in our analysis including very few representatives. Phengodidae and Cantharidae are not supported as being monophyletic. With the exception of *Dioptoma adamsi* and *Diplocladon* sp., the four other phengodid taxa used in this analysis are a monophyletic clade. Our analysis placed *Dioptoma* and *Diplocladon* at the base of the clade containing the family Rhagophthalmidae. The Bremer support value for the base of this clade (Fig. 2) is high (>5), indicating strong support. The seven synapomorphies that define this clade are: twelve antennomeres in male antennae, third antennomere long, basal antennal flagellomeres not symmetrical with apical flagellomeres, mandible apices acute (inside angle < 90 degrees), emarginate eyes, eyes posteriorventrally approximated, and wing vein MP3 not contacting MP1+2. Therefore, we propose moving the genera *Dioptoma* and *Diplocladon* out of Phengodidae and into Rhagophthalmidae. On the other hand, Cantharidae does not seem to be supported as monophyletic in this analysis, and none of the four cantharid taxa included in the analysis form a clade. Cantharidae needs to be further examined in relation to other taxa and sampled more thoroughly within a phylogenetic context before a taxonomic change is made.

Phylogenetic Relationship Between Lampyridae and Phengodidae

The family Phengodidae is composed of bioluminescent species that commonly resemble fireflies in their general appearance and are usually also found to be sympatric with many firefly species. Even though phengodid beetles share aspects of their biology with lampyrids (larviform

TABLE 1. SOME NOTABLE PAPERS SHOWING THE PREVIOUS TAXONOMIC PLACEMENT OF TAXA THAT THIS STUDY RELEGATES TO "*INCERTAE SEDIS*" STATUS.

Early Work	E. Oliver (1910) a, b	F. McDermott (1964) (1966)	Lawrence & Newton (1995) (after Crowson 1972)	Branham & Wenzel (this analysis)
Lampyridae	Lampyridae (a)	Lampyridae	Lampyridae	Elateriodea
Ototreta	Luciolinae	Ototretinae (1964) and Luciolinae (1966)	Ototretinae	Incertae Sedis
{E. Olivier 1900}	*Ototreta*		*Ototreta* (= *Drilaster*)*	*Drilaster**
Stenocladius	Megalophthalminae	*Ototreta* (= Drilaster)*	*Harmatelia*	*Harmatelia*
{Fairmaire 1878}	*Harmatelia*	Pterotinae (1964,1966)	*Stenocladius*	*Pterotus*
		Pterotus	Pterotinae	Phengodidae
		Harmatelia	*Pterotus*	Stenocladius
Drilidae	Drilidae (b)	Rhagophthalminae (1964, 1966)	Phengodidae	Rhagophthalmidae
Drilaster	*Drilaster*	*Dioptoma*	Rhagophthalminae	*Dioptoma*
{Kiesenwetter 1879}	*Stenocladius*	{Pascoe 1860}	*Dioptoma*	Diplocladon
Pterotus			*Diplocladon*	
{LeConte 1859}			{Gorham 1883}	
Elateridae				
Harmatelia				
{Walker 1858}				

*McDermott (1964,1966) synonymized *Drilaster* and *Ototreta*, retaining the name *Ototreta*. Sato (1968) confirmed this synonymy while pointing out that *Drilaster* has priority over *Ototreta*. Crowson (1972) as well as Lawrence and Newton (1995) retained McDermott's use of "*Ototreta* (= *Drilaster*)". The varied use of these generic names has led to some confusion: the genus *Drilaster* is used in Asia without reference to *Ototreta*, while "*Ototreta* (= *Drilaster*)" is used in Europe and the United States. We refer to this genus as *Drilaster* based on the priority of the name *Drilaster* and to eliminate further confusion. Additionally, we propose that *Drilaster* be removed from Lampyridae and be given Elateriodea *Incertae Sedis* status.

females, the use of pheromones and luminescence), phengodids have historically been seen as a group taxonomically distinct from Lampyridae. However, it is probably the similarities between Lampyridae and Phengodidae, with bioluminescence being one of the most obvious, which have linked them as closely related taxa in the eyes of many cantharoid workers. "Within Cantharoidea, Phengodidae and Lampyridae appear to be directly related, so that the luminosity of both groups can plausibly be attributed to inheritance from a common ancestor . . ." (Crowson 1972). Our phylogeny provides evidence that Phengodidae is not sister to, or basal to, Lampyridae. In addition, it shows that Rhagophthalmidae and Omalisidae are the bioluminescent families that are sister, or basal to Lampyridae, respectively (Fig. 3).

The Evolution of Bioluminescence in Non-lampyrid Cantharoids

Bioluminescence in the order Coleoptera is known to occur in Elateridae, Staphilinidae (Costa et al. 1986) and four cantharoid families: Omalisidae, Rhagophthalmidae, Phengodidae and Lampyridae (Lloyd 1978). Several recent studies have provided hypotheses concerning the evolutionary relationships within or around Cantharoidea (Crowson 1972; Potatskaja 1983; Beutel 1995) using a variety of techniques, characters and explemplar taxa. Plotting luminescence (larval or adult) onto these different trees, supports interpretations ranging from three origins, to one origin and three loses. However, these studies treat families as single units. Therefore, if luminescence arises only once in each of the three luminescent families, (Omalisidae, Phengodidae, and Lampyridae, with *Rhagophthalmus* species treated as phengodids), three separate origins would be the maximum number of steps. Conversely, a single origin would be the minimum number of steps if all families were treated as being monophyletic. Crowson (1972) proposed a dendrogram for the relationships between the cantharoid families (Omethidae, Cantharidae, Plastoceridae, Lycidae, Omalisidae, Drilidae, Telegeusidae, Phengodidae, and Lampyridae). This scheme predicts two character optimizations of three steps each. One optimization poses three origins for bioluminescence, while the second poses two origins and one loss of bioluminescence. Potatskaja (1983) proposed a dendrogram for the relationships between the cantharoid families (Brachyspectridae, Cantharidae, Phengodidae, Drilidae, Omalisidae, Lycidae and Lampyridae) based on larval mouthpart characters. Potatskaja

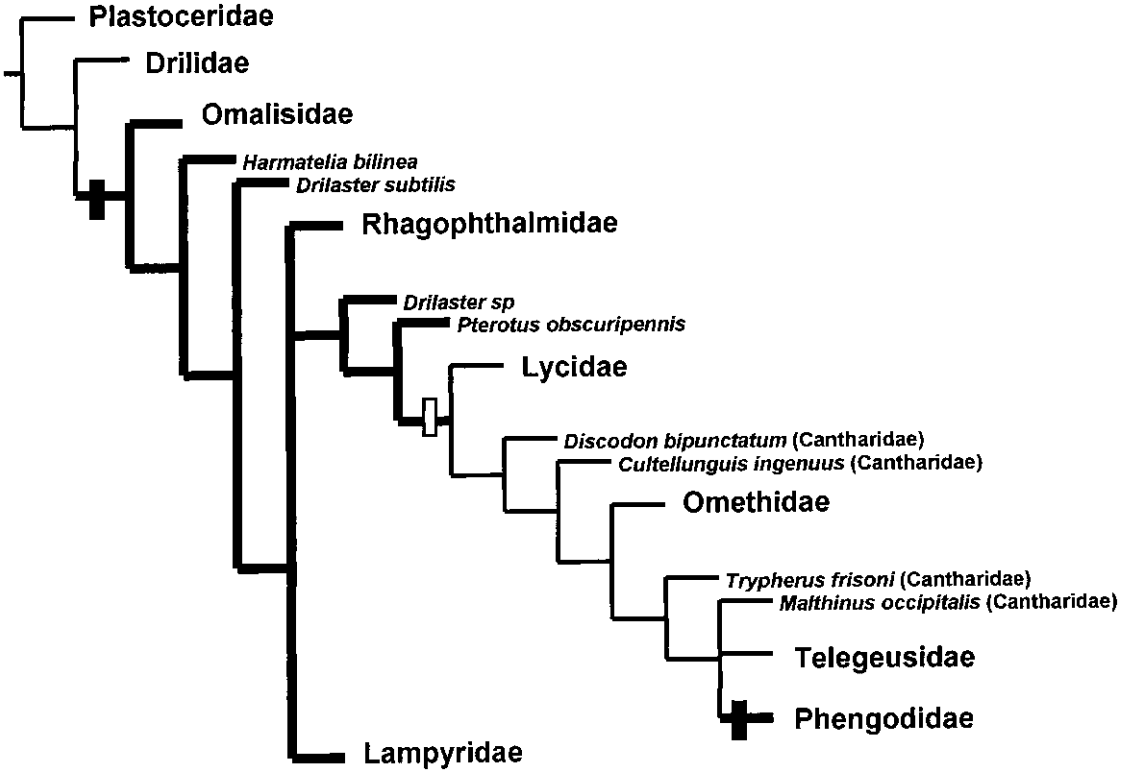

Fig. 3. The evolution of bioluminescence in cantharoids. The condensed strict consensus tree with two origins of luminescence and one loss plotted.

concluded that two lineages, one termed "cantharid" (composed of Phengodidae, Drilidae, Omalisidae, Brachyspectridae, and Cantharidae) and the other "lycid" (composed of Lampyridae and Lycidae) originated from a phengodid ancestral form. No specific taxon was designated as the root. In reference to the origin of bioluminescence, this topology predicts two optimizations of three steps each: three separate origins, or two origins and one loss. In 1995, Beutel proposed a phylogenetic analysis of Elateriformia based on 27 larval characters (33 states). Within this analysis Cantharoidea was represented by seven taxa, one species per each of Brachyspectridae, Cantharidae, Drilidae, Omalisidae, Phengodidae, Lampyridae, and Lycidae. All of the cantharoid taxa were placed in the same clade except for Cantharidae, which was placed close to Elateridae, rather than with the rest of the cantharoids. The clade containing the bioluminescent cantharoid taxa was poorly resolved in the consensus tree and predicts a single topology of one origin and three losses.

Our analysis suggests a single solution, considering a taxon to be luminescent if any life stage is luminescent. There are two origins of bioluminescence with one loss: luminescence arose once basally, early in the evolutionary history of the cantharoid clade, and was subsequently lost and then later regained in the phengodids, see Fig. 3. Taxa in which luminescence was regained under this scenario are currently classified as belonging to the family Phengodidae, (*Cenophengus pallisus, Phrixothrix reducticornis, Pseudophengodes pulchella,* and *Zarhipis integripennis*), as well as *Stenocladius* sp. which we consider to be a phengodid and propose its inclusion in this family. The seven synapomorphies that define Phengodidae are: tibial spurs are absent, bipectinate antennae, distal margin of antennal flagellomeres approximating proximal margin in width, antennal lobes produced from basal region of flagellomere, two elongated antennal lobes per flagellomere, narrow juncture between flagellomere and antennal lobe, and juncture between lateral and hind margins of pronotum are truncate (= 90 degrees). Therefore, all luminescence in the cantharoid lineage is homologous except for that of Phengodidae, which is a reversal to luminous habit. Additionally, all known luminescent cantharoid taxa have luminous larvae, and in Omalisidae the larvae are luminous, but not either adult (Crowson 1972). The fact that Omalisidae is the most basal of all the bioluminescent cantharoids indicates that luminescence arose first in the larvae and then subsequently in the adults (Fig. 4).

Photic Organ Evolution in Non-lampyrid Cantharoids

Larvae.

Only the larval photic organs of Phengodidae and Lampyridae have been studied in detail. The larvae of Omalisidae have never been studied, and the larvae of Rhagophthalmidae have been studied and described only recently (Wittmer & Ohba 1994), though no morphological, physiological or histological work has been published on this group. Therefore, from what is currently known from evidence scattered among the taxa, the pattern of two luminous spots per segment on larvae is the most ancient and common larval photic organ pattern in the cantharoid lineage (Fig. 4). The number of luminous segments varies, but all known luminous cantharoid larvae bear pairs of luminous photic organs. While most lampyrid larvae bear only a single pair of photic organs on the eighth abdominal segment, larvae of the other taxa generally posses a pair of photic organs on each abdominal segment with additional pairs sometimes present on the larval thorax (Table 2). While the larvae of many genera of luminous cantharoids are not yet known, all species known to be luminous as adults are also luminous as larvae. Therefore, while only some larvae are known from the families Omalisidae, Rhagophthalmidae, Phengodidae and Lampyridae, the larvae of all species in these families are hypothesized to be luminous (Fig. 4). Crowson (1972) hypothesized that Barber's (1908) luminous larva from Guatemala, described as *Astraptor* sp., could have been a large female larva or a larviform female of *Telegeusis.* Sivinski (1981) points out that in a later unpublished manuscript Schwarz and Barber identified the single specimen as the phengodid *Microphenus gorhami.* Therefore, as far as is known, the family Teleguesidae does not contain any luminous taxa. Barber (1908) mentions that there was a single photic organ in the head which produced a red light that was thrown directly forward and hence was not easily seen from above. This specimen seemed to have no other photic organs, though it was observed in the daytime and not for long. A red head-light is known only in other phengodid larvae (Viviani & Bechara 1997).

Adult Females.

Females of luminous cantharoid taxa, excluding Lampyridae, generally posses the same photic organ morphology as their larvae, which is generally paired, luminous spots on the post-lateral margins on some of the thoracic and each of the abdominal segments (Table 2). Females, and males of the family Lampyridae vary in photic organ morphology (Lloyd 1978), perhaps due to sexual selection as the females of many firefly species attract mates via a luminescent sexual signal system (McDermott 1917; Schwalb 1960; Lloyd 1978 and 1979; Branham & Greenfield 1996;Vencl & Carlson 1998). While the luminescent sexual signals of fireflies have received considerable attention, pheromones are the dominant sexual signals used in courtship in most cantharoids, including

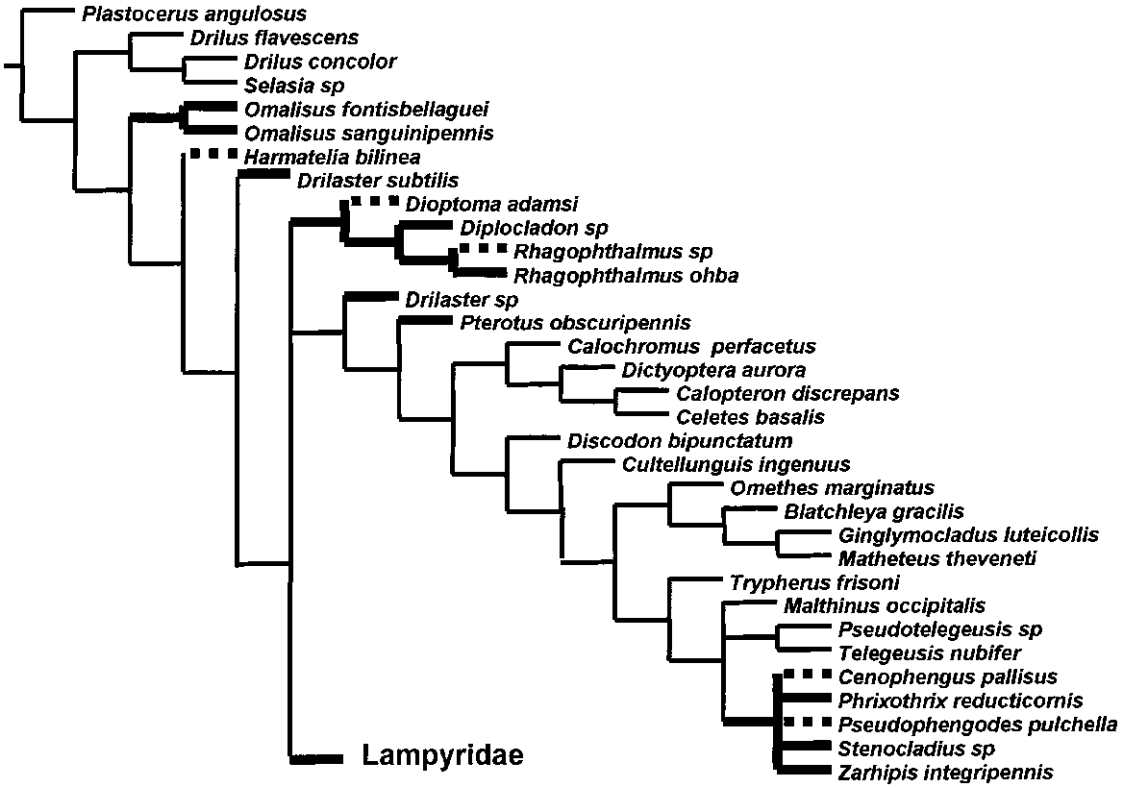

Fig. 4. The evolution of larval bioluminescence in cantharoids. The strict consensus tree with the lampyrid clade collapsed. The known presence of larval luminescence is indicated by bold branches, with the hypothesized presence of larval luminescence indicated by dotted branches.

Phengodidae, and are also used by many lampyrids (McDermott 1964; Lloyd 1971). Therefore, (with the exception of the family Omalisidae and the genus *Drilaster*), the pattern of bioluminescent evolution in the larvae (Fig. 4) and the pattern found in the females of luminous taxa (Fig. 5) is very similar. The fact that Omalisidae is the basal-most luminous cantharoid taxon and both adult males and females are not bioluminescent suggests that bioluminescence first arose in larvae and later in adults.

Rhagophthalmus ohbai females, in addition to retaining the larval pattern of photic organs, also possess a novel photic organ on the eighth ventrite, which is used in courtship, see Table 2 (Ohba et al. 1996a). After using the ventral photic organ on the eighth ventrite for courtship, females curl around their eggs and glow from ten sets of paired photic organs located at the lateral margins of the ten luminous body segments, (see Table 2), which serve as an aposematic warning display (Ohba et al. 1996a; Chen 1999). Rhagopthalmidae appears to be the sister of Lampyridae, which is the only other cantharoid family known to contain females that employ photic signals in courtship. In addition, based on the presence of extremely well developed eyes in rhagopthalmid males and the lack of greatly elaborate bipectinate antennae, such as those found in Phengodidae, we believe that photic signals are the primary mode of sexual signaling.

Crowson (1972) incorrectly cited Green (1912) as reporting that the female of *Harmatelia* is apterous and larviform. Green (1912) states that, "I have not yet succeeded in determining the female of this beetle, and it remains uncertain whether the other sex is an apterous grub-like creature, or whether it is in the form of another beetle."

Adult Males.

All known bioluminescent adult cantharoid males are restricted to the families Lampyridae, Rhagophthalmidae (as defined here) and Phengodidae (as defined here) as well as the genus *Harmatelia*. While the exact number and position of the photic organs varies, they are generally found in pairs on one or more of the thoracic segments, and on each of the first eight abdominal segments. Male photic organs, like those of larvae and females, are found near the lateral margins of these body segments (Table 2). The more dorsal

TABLE 2. A COMPARISON OF CANTHAROID TAXA INCLUDED IN THIS ANALYSIS WITH SPECIAL REFERENCE TO PHOTIC ORGAN MORPHOLOGY ACROSS LIFE STAGES AND THE PRESENCE OF NEOTENIC CHARACTERISTICS IN ADULT FEMALES.

	Larvae: Photic Organ Morphology	*Females*: Larviform or Alate	*Female*: Photic Organ Morphology	*Males*: Photic Organ Morphology
Plastoceridae	Unknown	Wingless, elytra shorter than abdomen (Crowson 1972)	None	None
Drilidae	None	Wingless, elytra shorter than abdomen (Lawrence 1991a). Females of Selasia unicolor are "larviform" (Barker 1969)	None	None
Omalisidae	Paired p. organs on sides of abdomen (Lawrence 1991b)	Wingless, elytra shorter than abdomen (Crowson 1972)	None	None
Rhagophtalmidae	Unknown			
Dioptoma		Neotenic: larviform with the exception of adult antennae and legs (tarsi subdivided into tarsomeres and claws) (Lawrence & Newton 1995)	Roundly quadrate p. organ, almost completely occupying the venter of penultimate abd. segment (Green 1912)	4 p. organs along dorsal hind margin of prothorax. One pair on lateral margins of all 8 abd. segments, and one pair of dorsal organs on each abd. seg.5-7 (Green 1912)
Diplocladon	A medial dorsal and two lateral p. organs on each body segment except head and last body segment (Halverson et al. 1973)	Larviform: possessing larval antennae and legs (Lawrence & Newton 1995)	A medial dorsal and two lateral p. organs on each body segment except head and last body segment (Haneda 1950)	None
Rhagophthalmus	A median dorsal and two postlateral p. organs on each segment: from mesothorax to 8th abdominal segment (10 sets total) (Ohba et al. 1996a)	Neotenic: larviform with the exception of 8-seg. antennae, tarsi subdivided into tarsomeres and claws (Costa et al. 1986)	Ten sets of paired p. organs on postlateral margins of mesothorax and abdomen; single p. organ on ventrite of abd. seg. 8 (Wittmer et al. 1996a)	Weak light visible from sets of paired p. organs on lateral margins of each abd. seg. and pronotum with an additional central organ on mesonotum (Chen 1999)
Lycidae	None	Nearly always alate	None	None
Cantharidae	None	Alate	None	None
Omethidae	Unknown	Alate, occasionally reduced wings (Lawrence 1991)	None	None
Teleguesidae	Unknown	Unknown	Unknown	None
Phengodidae				
Cenophengus	Unknown	Larviform	???	None
Phrixothrix	Two medial organs on head and eleven pairs of p. organs in the posterolateral margins of 2nd thoracic through the 9th abd. segment (Viviani & Bechara 1997; Halverson et al. 1973; Harvey 1952)	Larviform	Two medial organs on head and eleven pairs of p. organs in the posterolateral margins of 2nd thoracic through the 9th abd. segment (Halverson et al. 1973; Harvey 1952)	A single dorsomedian p.organ on prothorax and paired p. organs located dorsolaterally on thorasic and abd. segments (Viviani & Bechara 1997)

TABLE 2. (CONTINUED) A COMPARISON OF CANTHAROID TAXA INCLUDED IN THIS ANALYSIS WITH SPECIAL REFERENCE TO PHOTIC ORGAN MORPHOLOGY ACROSS LIFE STAGES AND THE PRESENCE OF NEOTENIC CHARACTERISTICS IN ADULT FEMALES.

	Larvae: Photic Organ Morphology	*Females*: Larviform or Alate	*Female*: Photic Organ Morphology	*Males*: Photic Organ Morphology
Pseudophengodes	Unknown	Unknown	Unknown	Large p. organs on ventral surface of 8th abd. segment (Viviani & Bechara 1997; M. Branham, pers. obs.)
Zarhipis	11 luminous bands: 1 each at base of meso- and metathroax, and on all but the last abd. tergites. Paired p. organs (1 spot per side): on upper lateral surfaces of abd. segs. 1-9 (Tiemann 1967)	Larviform	11 luminous bands: 1 each at base of meso- and metathroax, and on all but the last abd. tergites. Paired p. organs (1 spot per side): on upper lateral surfaces of abd. segs. 1-9. Also, 1-3 luminous spots on abd. sterna 2-9 (Tiemann 1967; Rivers 1886)	None
Stenocladius	Paired p. organ on 7th abd. segment (Ohba et al. 1996b)	Neotenic: larviform with the exception of tarsi subdivided into tarsomeres and claws (Ohba et al. 1997)	A diffuse glow emitted from entire body—no specific photic organs present (Ohba et al. 1997)	When present, paired p. organs on 6th abd. segment (Ohba et al. 1997)
"Incertae Sedis" *Harmatelia*	Unknown	Unknown	Unknown	One p. organ on each side of mesothorax with 1 pair of p. organs on dorsum of each of 8 abd. seg. (One each near posterolateral margin) (Green 1912; McDermott 1965)
Drilaster	Paired p. organs on 8th abd. seg. (Ohba 1983)	Alate (some larviform?)	None	None
Pterotus	Paired p. organ on 7th abd. segment (Dean 1979)	Larviform? Dean (1979) states that females are fully larviform. However, his Plate II indicates the presence of compound eyes, adult antennae and paired claws on each leg.	Paired p. organ on 7th abd. segment (Dean 1979)	None

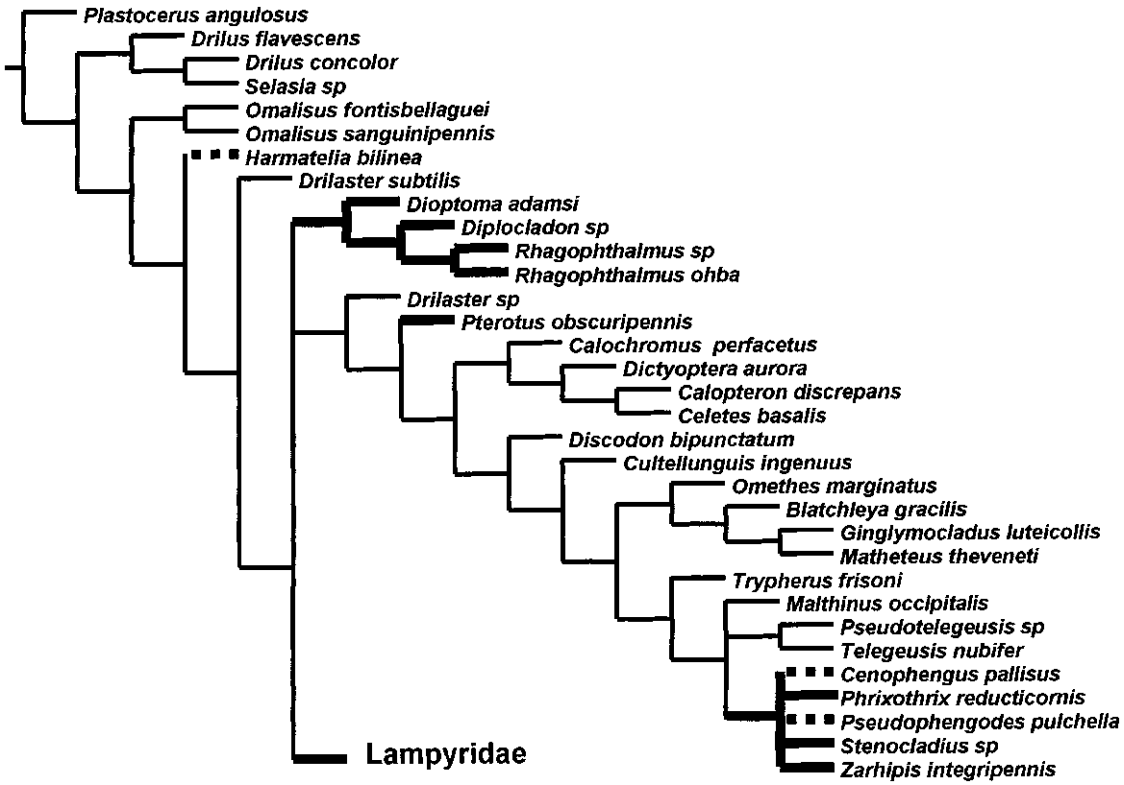

Fig. 5. The evolution of bioluminescence in female cantharoids. The strict consensus tree with the lampyrid clade collapsed. The known presence of luminescence in females is indicated by bold branches, with the hypothesized presence of luminescence in females indicated by dotted branches.

position of these lateral photic organs in the adult males versus larval males is probably due to the lateral tergites, found as plates in the dorsal region on the side of the larval abdomen, becoming fused to the larval tergites to form a single large plate covering the entire dorsal surface of the adult male abdomen. One exception is *Pseudophengodes pulchella*, which bears a large photic organ on the ventral surface of the eighth ventrite that seems to be used in courtship. Until recently, the only phengodid genus that was known to contain adult luminescent males was *Pseudophengodes*. However, Viviani and Bechara (1997) discovered through rearing experiments that phengodid males in the tribe Mastinocerini (*Brasilocerus*, *Euryopa, Mastinocerus*, *Mastinomorphus*, *Phrixothrix*, *Stenophrixothrix*, and *Taxinomastinocerus*) are luminous throughout the adult stage and that the luminescent emissions seem to serve a defensive rather than courtship function. No adult phengodid males in the North American tribe Phengodini (*Phengodes* and *Zarhipis*) are known to be continuously luminescent through the entire stage. Even though there is little variation found in male photic organs outside of Lampyridae, the scattered occurrence of photic organs in males clearly seems to indicate multiple origins (Fig. 6).

J. W. Green's first published observations (1911) of live *Harmatelia bilinea* males did not include any notice of luminescence, even though Green was specifically looking for evidence that this insect was luminescent. The following year (1912), Green published that he had observed two specimens that "exhibited a distinct light when examined in a dark room." The fact that Green had examined many *Harmatelia* specimens without noticing any photic emission may be an indication that these males are not luminescent throughout their entire adult life. It is well known (McDermott 1965; Lloyd 1978;Vivani & Bechara 1997; Branham & Archangelsky 2000) that some lampyrid species which are not luminescent as adults retain the ability to glow via larval photic organs for a short time after they have eclosed and are still teneral. McDermott (1965) hypothesized that the males of both *Pterotus* and *Harmatelia* might have the ability to produce light only briefly after eclosion as does the firefly *Lucidota atra*. McDermott also mentioned in this same work that H. S. Barber (unpublished observation, confirmed by J. E. Lloyd) observed that

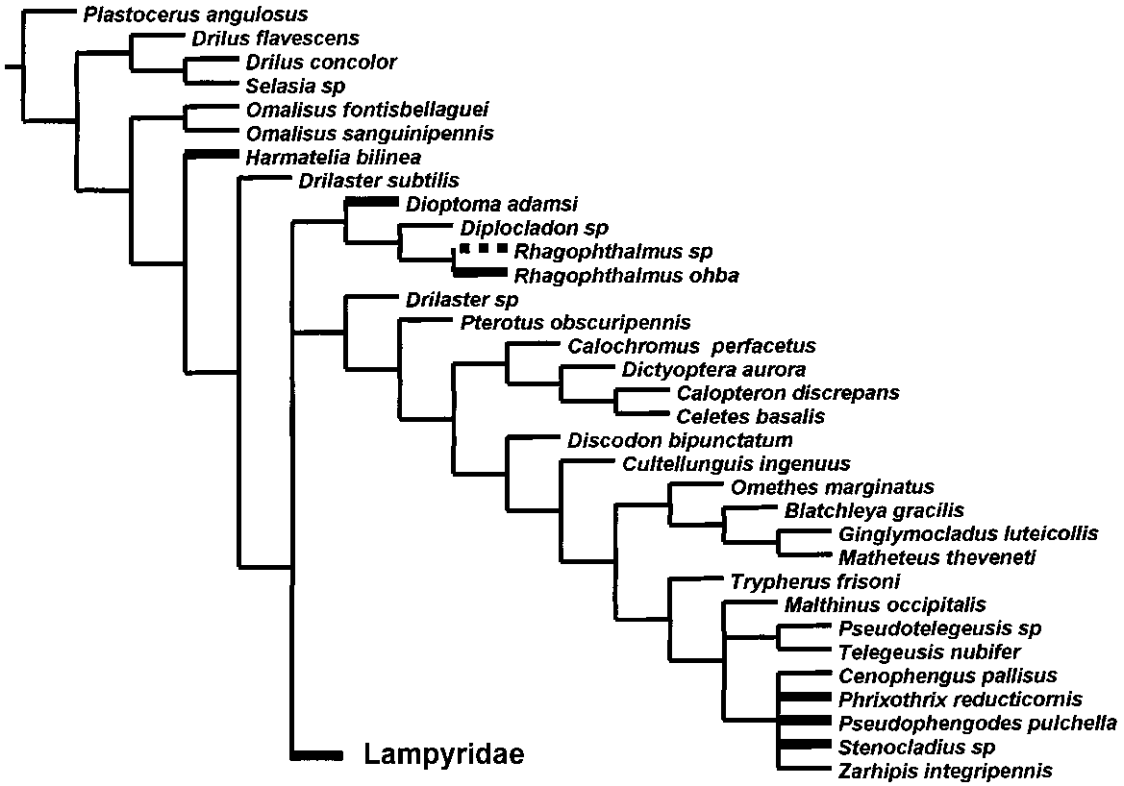

Fig. 6. The evolution of bioluminescence in male cantharoids. The strict consensus tree with the lampyrid clade collapsed. The known presence of luminescence in males is indicated by bold branches, with the hypothesized presence of luminescence in males indicated by dotted branches.

Phengodes males also have the ability to produce light shortly after eclosion. This photic carry-over into the adult, while only temporary in some taxa, is suggestive of a larval origin of the photic organ and its carry over into the adult.

Some *Rhagophthalmus ohbai* males are known to be luminous from paired spots along the lateral edges of ten body segments, (see Table 2). These males are weakly luminous (Chen 1999) and evidently are not always observed (Ohba et al. 1996a). It seems likely that *Rhagophthalmus* males have only a temporary ability to produce light immediately following eclosion and luminescence is not used in courtship (Ohba et al. 1996a).

Luminesence and Life Stages.

The phengodid genus *Phrixothrix* is the only luminous non-lampyrid cantharoid in which larvae, adult males, and adult females are known to be luminescent throughout all life stages (Table 2). Luminescence throughout all life stages of *Phrixothrix hirtus* is essentially the same. The photic organ morphology appears to be identical between all life stages with the exception that the head lantern is lacking in the adult males. Therefore the lateral lanterns of all stages appear identical and the head lanterns of the larvae and females are identical. In addition, the photic emission spectra is essentially the same for each type of photic organ regardless of life stage (Costa et al. 1999). An additional example of similarity in the emission spectra and a possible connection between larval and adult luminescence was found by Viviani and Bechara (1997) who argued that, "Continuance of the same bioluminescent color in the lateral lanterns of larval, pupal, and adult stages of *Mastinomorphus* sp.1 and *P. heydeni* suggests conservation of the same luciferase iso-form throughout its life cycle." The pattern of photic organ morphology appearing more or less identical across life stages along with similar photic emission spectra being emitted from these organs supports the hypothesis by Crowson (1972) that luminescence first evolved in larvae and was then "carried over into adults."

Evolution of Photic Signaling in Non-firefly Cantharoids

Sivinski (1981) provides a detailed synopsis of the various theories that have been proposed for the function of larval luminescence and the evi-

dence supporting each. While it is now generally accepted that lampyrids are chemically defended and larval photic emissions probably function as aposematic displays (Lloyd 1973; Sydow & Lloyd 1975; Eisner et al. 1978, Belt 1985, Underwood et al. 1997; Knight et al. 1999; De Cock 2000), there exists much less information concerning whether other larval cantharoids are distasteful as well, though it appears that at least some phengodids are chemically defended (Burmeister 1873; Harvey 1952; Sivinski 1981). It is interesting that almost all larval photic organs are paired and are located on the sides of the abdomen or on the eighth abdominal ventrite where the photic emissions are readily seen from the side or from above. This is most consistent with the aposematic warning display hypothesis. The exception to this rule is the pair of medial photic organs on the head of some phengodid larvae such as *Phrixothrix* (Table 1). The photic emissions from these organs were measured by Viviani and Bechara (1997) and were found to be in the range of 574-636nm, well into the red range. Electroretinograms of *Phrixothrix* larvae showed that these larvae have a spectral sensitivity shifted to the red (V. R. Viviani, E. J. H. Bechara, D. Ventura and A. Lall unpublished data; Viviani & Bechara 1997). Viviani and Bechara (1997) hypothesize that these red-emitting head-mounted photic organs provide an illumination function, which may help in locating prey that do not posses spectral sensitivity shifted to the red, and that the lateral photic organs serve an aposematic defensive function.

As the basal luminescent taxa only possess lateral photic organs, it is probable that the first function of larval luminescence was as an aposematic warning display. Larval photic organs where then lost in Lycidae, Omethidae and Cantharidae, and then reappear in Phengodidae. In some phengodids, a photic organ arose on the head and produced red light which was used for illuminating prey (Viviani & Bechara 1997).

The function of luminescence in the adult phengodids is not well understood. Available data suggest that bioluminescence produced by the lateral organs of the adult males and females in this family, seems to serve an aposematic defensive role rather than mate attraction (Rivers 1886, Tiemann 1967, Sivinski 1981). However, the continuous glow produced by the ventral photic organ on the eight abdominal ventrite in *Pseudophengodes* is also consistent with use as either illumination of the surroundings during flight or intersexual communication (Viviani & Bechara 1997).

The function of luminescence in *Rhagophthalmus ohbai* was studied by Ohba et al. (1996a) who provide evidence that the emissions of the lateral photic organs in females serve an aposematic warning function, illumination while the females guards her eggs, while the ventral photic organ on the eighth abdominal segment seems to function exclusively in a courtship context. Hence, in this family the paired lateral and the ventral photic organs are used independently in separate contexts: defense and courtship. Across all luminescent cantharoid taxa, photic organs used to produce sexual signals seem to be exclusively restricted to the ventral regions of the body. It is also interesting to note that the eighth abdominal segment is consistently associated with the location of such photic organs. The reason for this association remains unknown.

Conclusion

Our phylogenetic analysis suggests that bioluminescence arose twice within the cantharoid lineage and was lost once. The first origin of luminescence in the lineage was ancient and luminescence first arose in larvae where it served as an aposematic warning display. Luminescence was retained in the larvae of the Rhagophthalmidae and Lampyridae and was likely carried over through the pupae into the adult stage where it became functional in some taxa and not in others. While photic signals are used in mate attraction in the Rhagophthalmidae, adult photic signals reached their greatest sophistication in the adults of the family Lampyridae, where photic signals are used in intraspecific communication and both photic organs and photic signals became greatly elaborated under the context of sexual selection. The second origin of luminescence occurred in the family Phengodidae where its function in both larvae and adults is as an aposematic warning display. In some phengodid taxa, luminescence has become elaborated to serve possibly as an illumination device for locating prey. In addition, males of the genus *Pseudophengodes* possess a lampyrid-like photic organ on the eighth abdominal ventrite, which glows continuously and likely serves to either illuminate potential landing sites or functions in courtship. While some researchers have previously hypothesized that the families Lampyridae and Phengodidae were close relatives and shared the charismatic ability to produce bioluminescent signals, these two families are perhaps more interesting than previously thought because they are not closely related and their bioluminescence is convergent.

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APPENDIX 1. LIST OF TAXA USED IN THE ANALYSIS.

Material studied was borrowed from the following institutions: California Academy of Sciences, San Francisco, CA [CASC]; Field Museum of Natural History, Chicago, IL [FMNH]; Florida State Collection of Arthropods, Gainesville, FL [FSCA]; Collection of author [MABC]; Museum of Comparative Zoology, Harvard University, Cambridge, MA [MCZC]; Ohio State University Collection, The Ohio State University, Columbus, OH [OSUC]; Snow Entomological Museum Collection, University of Kansas, Lawrence, KS [SEMC]; Museum of Zoology, University of Michigan, Ann Arbor, MI [UMMZ]; National Museum of Natural History, Smithsonian Institution, Washington, D.C. [USNM].

List of Species Studied: The higher classification used here is based on Lawrence & Newton (1995), and in the case of Rhagophthalmidae, Wittmer and Ohba (1994).

Plastoceridae	
	Plastocerus (=Ceroplatus) angulosus (Germar) [FMNH]
Omalisidae	
	Omalisus (= Omalysus, Homalisus) fontisbellaguei (Fourar.) 1785 [FMNH]
	O. sanguinipennis Cast. 1840 [FMNH]
Drilidae	
	Drilus concolor Ahr. 1812 [FMNH]
	D. flavescens G.A. Olivier 1790 [USNM]
	Selasia sp. [FMNH]
Omethidae	
Matheteinae	*Matheteus theveneti* LeConte 1874 [CASC]
	Ginglymocladus luteicollis Van Dyke 1918 [CASC]
Omethinae	*Omethes marginatus* LeConte 1861 [CASC]
	Blatchleya gracilis Blatchley 1910 [OSUC]
Phengodidae	
Phengodinae	*Cenophengus pallidus* Schaeffer 1904 [FSCA]
	Phrixothrix reducticornis Wittmer 1963 [UMMZ]
	Zarhipis integripennis LeConte 1874 [MABC], [UMMZ]
Rhagophthalminae	*Dioptoma adamsi* Pascoe 1860 [USNM]
	Diplocladon sp. [CASC]
Rhagophthalmidae	
	Rhagophthalmus ohbai Wittmer and Ohba 1994 [MABC]
	Rhagophthalmus sp. [SEMC], [CASC]
Telegusidae	
	Pseudotelegeusis sp. [SEMC]
	Telegeusis nubifer Martin 1931 [SEMC]
Lycidae	
Calochrominae	*Calochromus perfacetus* (Say) 1825 [OSUC]
Lycinae	*Calopteron discrepans* (Newman) 1838 [OSUC]
	Celetes basalis LeConte 1851 [OSUC]
Erotinae	*Dictyoptera aurora* (Herbst) 1789 [OSUC]
Cantharidae	
Cantharinae	*Cultellunguis ingenuus* LeConte 1881 [OSUC]
Silinae	*Discodon bipunctatum* Schaeffer 1908 [OSUC]
Malthininae	*Malthinus occipitalis* LeConte 1851 [OSUC]
Chauliognathinae	*Trypherus frisoni* Fender 1960 [OSUC]
Lampyridae	
Pterotinae	*Pterotus obscuripennis* LeConte 1859 [UMMZ]
Cyphonocerinae	*Pollaclasis bifaria* (Say) 1835 [MCZC], [FSCA]
Ototretinae	*Brachylampis sanguinicollis* Van Dyke 1939 [CASC]
	Drilaster subtilis (E. Olivier) 1908 [CASC]
	Driliaster sp. [MABC]
	Harmatelia bilinea Walker 1858 [CASC]
	Stenocladius sp. [MABC]
Amydetinae	*Cladodes flabellatus* Solier 1849 [CASC]
	Psilocladus sp. [MABC]

APPENDIX 1. (CONTINUED) LIST OF TAXA USED IN THE ANALYSIS.

Material studied was borrowed from the following institutions: California Academy of Sciences, San Francisco, CA [CASC]; Field Museum of Natural History, Chicago, IL [FMNH]; Florida State Collection of Arthropods, Gainesville, FL [FSCA]; Collection of author [MABC]; Museum of Comparative Zoology, Harvard University, Cambridge, MA [MCZC]; Ohio State University Collection, The Ohio State University, Columbus, OH [OSUC]; Snow Entomological Museum Collection, University of Kansas, Lawrence, KS [SEMC]; Museum of Zoology, University of Michigan, Ann Arbor, MI [UMMZ]; National Museum of Natural History, Smithsonian Institution, Washington, D.C. [USNM].
List of Species Studied: The higher classification used here is based on Lawrence & Newton (1995), and in the case of Rhagophthalmidae, Wittmer and Ohba (1994).

	Vesta aurantiaca E. Olivier 1886 [USNM]
Lampyrinae	*Alecton discoidalis* Laporte 1833 [MCZC]
	A. flavum Leng et Mutch. 1922 [MCZC]
	Aspisoma ignitum (Linnaeus) 1767 [OSUC]
	A. pulchellum (Gorham) 1880 [FSCA]
	Callopisma maestra Mutch. 1923 [CASC]
	Cratomorphus diaphanus (Germar) 1824 [USNM]
	Ellychnia corrusca (Linnaeus) 1767 [MABC]
	Erythrolychnia bipartitus (E. Olivier) 1912 [FSCA]
	E. olivieri Leng et Mutch. 1922 [FSCA]
	Lamprohiza splendidula (Linnaeus) 1767 [CASC]
	Lampyris noctiluca Linnaeus 1767 [CASC], [FSCA]
	L. zenkeri Germar 1817 [FMNH]
	Lucidina biplagiata (Motsch.) 1866 [MABC]
	Lucidota atra (G. A. Olivier) 1790 [MABC]
	L. dilaticornis (Motschulsky) 1854 [FMNH]
	Macrolampis acicularis (E. Olivier) 1907 [CASC]
	Microphotus angustus LeConte 1874 [FMNH]
	M. octarthrus Fall 1912 [MABC]
	New Species [MABC]
	Phaenolis ustulata Gorham 1880 [FSCA]
	Phausis rhombica Fender 1962 [MABC]
	Photinus ignitus Fall 1927 [OSUC]
	P. meteoralis (Gorham) 1881 [CASC]
	P. pyralis (Linnaeus) 1767 [MABC]
	Phosphaenus hemipterus (Fourcroy) 1785 [CASC]
	Pleotomus nigripennis LeConte 1885
	P. pallens LeConte 1866 [MABC]
	Pristolycus sagulatus Gorham 1883 [CASC]
	Pyractomena ecostata (LeConte) 1878 [FSCA], [UMMZ]
	P. borealis (Randall) 1828 [MABC]
	Pyrocoelia praetexta E. Olivier 1911 [MABC]
	P. rufa E. Olivier 1886 [MABC]
	Pyropyga nigricans (Say) 1823 [MABC], [CASC]
	Robopus sp. *#1* [MABC]
	Robopus sp. *#2* [MABC]
	Tenaspis angularis (Gorham) 1880 [CASC], [MCZC]
Luciolinae	*Colophotia* sp. [MABC]
	Luciola cruciata Motschulsky 1854 [MABC]
	L. kuroiwae Matsumura 1918 [MABC]
	L. lateralis Motschulsky 1860 [CASC]
	L. salomonis (E. Olivier) 1911 [CASC]
	Pteroptyx cribellata (E. Olivier) 1891 [MABC], [UMMZ]
	P. malaccae (Gorham) 1880 [MABC]
	P. tener E. Olivier 1907 [MABC]
Photurinae	*Bicellonycha amoena* Gorham 1880 [FSCA]
	Photuris brunnipennis Jacq.-Duv. 1856 [OSUC]
	P. divisa LeConte 1852 [MABC]

APPENDIX 2. CHARACTERS AND CHARACTER STATES.

Multistate characters treated as ordered are specified below. Values for Consistency Index (C.I.) and Retention Index (R.I.) for each character in the analysis as they appear on the consensus tree are indicated after the last character state (C.I., R.I.). The character-taxon matrix is presented in Appendix 3. The morphological terminology of Lawrence & Britton (1991) and Snodgrass (1993) was used. Wing veination scheme follows that used in Kukalova-Peck & Lawrence (1993).

0. *Head position*: 0-exposed; 1-partially exposed; 2-covered. (C.I. 0.18, R.I. 0.72)
1. *Head shape*: 0-deflexed between eyes; 1-partially deflexed; 2-not deflexed. (C.I. 0.8, R.I. 0.52)
2. *Antennal insertions* (ordered): 0-widely separated; 1-moderately approximated; 2-approximated. (C.I. 0.8, R.I. 0.61)
3. *Antennal sockets*: 0-prominent; 1-flush. (C.I. 0.5, R.I. 0.33)
4. *Number segments (antennomeres) in male antennae* (ordered): 0-eight; 1-ten; 2-eleven; 3-twelve; 4-thirteen. (C.I. 0.44, R.I. 0.50)
5. *Antennal seg. #3 (flagellomere #1)* (ordered): 0-short, 1-same as #4; 2-long. (C.I. 0.7, R.I. 0.52)
6. *Antennal features (general)*: 0-filiform; 1-serrate; 2-flabellate; 3-pectinate; 4-bipectinate. (C.I. 0.25, R.I. 0.63)
7. *Distal antennal flagellomeres* (ordered): 0-longer than wide; 1-about as long as wide; 2-much wider than long. (C.I. 0.14, R.I. 0.29)
8. *Basal antennal flagellomere/s*: 0-not symmetrical with apical flagellomeres; 1-symetrical with apical flagellomeres. (C.I. 0.14, R.I. 0.53)
9. *Distal margins of flagellomeres*: 0-straight; 1-concave. (C.I. 0.11, R.I. 0.46)
10. *Distal margin of antennal flagellomeres*: 0-approximating proximal margin in width; 2-wider than proximal margin. (C.I. 0.7, R.I. 0.38)
11. *Antennal flagellomere #2* (ordered): 0-not compressed; 1-slightly compressed; 2-greatly compressed (C.I. 0.8, R.I. 0.60)
12. *Lateral margins of the distal antennal flagellomeres*: 0-parallel; 1-non-parallel. (C.I. 0.5, R.I. 0.52)
13. *Antennal lobes produced from* (ordered): 0-basal region of flagellomere; 1-medial region of flagellomere; 2-apical region of flagellomere. (C.I. 0.25, R.I. 0.62)
14. *Number of elongated antennal lobes per segment*: 0-one lobe; 1-two lobes. (C.I. 0.25, R.I. 0.62)
15. *Antennal lobes*: 0-compressed; 1-not compressed. (C.I. 0.20, R.I. 0.33)
16. *Length of antennal lobes* (ordered): 0-less than length of flagellomere; 1-approximating length of flagellomere; 2-greater than length of flagellomere. (C.I. 0.50, R.I. 0.66)
17. *Antennal lobe/flagellomere juncture*: 0-broad; 1-narrow (C.I. 0.16, R.I. 0.44)
18. *Antennal lobes*: 0-not bearing a sensory depression at apex; 1-bearing a sensory depression at apex (C.I. 1.0, R.I. 1.0)
19. *Mandibles* (ordered): 0-prominent; 1-normal sized; 2-reduced; 3-very reduced. (C.I. 0.14, R.I. 0.68)
20. *Mandible tooth*: 0-absent; 1-present. (C.I. 1.0, R.I. 1.0)
21. *Mandible width*: 0-stout; 1-slender. (C.I. 0.12, R.I. 0.68)
22. *Mandible shape*: 0-apices acute (inside angle <90 degrees); 1-apices non-acute(inside angle near 180 degrees). (C.I. 0.5, R.I. 0.56)
23. *Mandible type*: 0-normal type (arcuate, regularly narrowing to tips); 1-specialized type (tips slender and glaborous with discontinuous curvature). (C.I. 0.25, R.I. 0.84)
24. *Hypomera*: 0-not extending to anterior edge of pronotal shield; 1-narrowly extending to anterior edge of pronotal shield; 2-broadly extending to anterior edge of pronotal shield; 3-lacking. (C.I. 0.30, R.I. 0.82)
25. *Hypomera space around head (side view)*: 0-head (eyes) not able to retract between hypomera; 1-head (eyes) partially enclosed (up to half width of eyes); 2-head (eyes) retractable (less than half eye width exposed). (C.I. 0.11, R.I. 0.65)
26. *Maxillary palpi*: 0-filiform; 1-clavate compressed; 2-clavate; 3-modified. (C.I. 0.12, R.I. 0.57)
27. *Maxillary palp apical seg*: 0-filiform; 1-securiform; 2-elongate; 3-greatly elongate and flattened; 4-conical. (C.I. 0.4, R.I. 0.5)
28. *Labial palpi*: 0-filiform; 1-clavate compressed; 2-clavate; 3-modified. (C.I. 0.16, R.I. 0.44)
29. *Labial palp apical seg*: 0-filiform; 1-securiform; 2-elongate; 3-greatly elongate and flattened. (C.I. 0.20, R.I. 0.52)
30. *Eyes*: 0-oval; 1-emarginate. (C.I. 1.0, R.I. 1.0)
31. *Eyes posterior-ventrally* (ordered): 0-seperated; 1-approximated; 2-contiguous. (C.I. 0.25, R.I. 0.66)
32. *Pronotum border*: 0-smooth; 1-margined; 2-explanate. (C.I. 0.22, R.I. 0.46)
33. *Hind angles of pronotum*: 0-truncate (juncture between lateral and hind margin = 90 degrees); 1-acute (juncture < 90 degrees); 2-lateraly expanded (juncture > 90 degrees); 3-notched (juncture <9 0 degrees due to deep notch in hind margin). (C.I. 0.13, R.I. 0.58)
34. *Overall surface area of hypomeron* (ordered): 0-absent; 1-small; 2-large/broad. (C.I. 0.22, R.I. 0.58)
35. *Scutellum shape*: 0-distinct; 1-poorly developed. (C.I. 0.25, R.I. 0.40)
36. *Scutellum*: 0-membranous, 1-sclerotized. (C.I. 1.0, R.I. 1.0)

APPENDIX 2. (CONTINUED) CHARACTERS AND CHARACTER STATES.

Multistate characters treated as ordered are specified below. Values for Consistency Index (C.I.) and Retention Index (R.I.) for each character in the analysis as they appear on the consensus tree are indicated after the last character state (C.I., R.I.). The character-taxon matrix is presented in Appendix 3. The morphological terminology of Lawrence & Britton (1991) and Snodgrass (1993) was used. Wing veination scheme follows that used in Kukalova-Peck & Lawrence (1993).

37. *Prosternum* (ordered): 0-small; 1-medium; 2-large. (C.I. 0.22, R.I. 0.53)
38. *Mesosternum (ant. margin)*: 0-straight; 1-emarginate. (C.I. 0.50, R.I. 0.75)
39. *Mesal margins of metepisterna*: 0-sigmoid; 1-straight or nearly so. (C.I. 0.33, R.I. 0.83)
40. *Anterior coxae* (ordered): 0-contigous; 1-nearly contiguous; 2-separate at base. (C.I. 0.33, R.I. 0.42)
41. *Anterior coxal shape*: 0-conical; 1-subconical; 2-triangular; 3-broad; 4-bulbous. (C.I. 0.19, R.I. 0.54)
42. *Middle coxae* (ordered): 0-contiguous; 1-nearly contiguous; 2-separate. (C.I. 0.22, R.I. 0.63)
43. *Hind coxae* (ordered): 0-contiguous; 1-nearly contiguous; 2-separate. (C.I. 0.09, R.I. 0.33)
44. *Hind coxae/femoral plates* (ordered): 0-plates obsolete; 1-< length of coxae; 2-entire length of coxae. (C.I. 0.16, R.I. 0.74)
45. *Trochanter attachment to femora*: 0-oblique; 1-very oblique; 2-interstitial. (C.I. 0.22, R.I. 0.82)
46. *Middle trochantins*: 0-setiferous; 1-glabrous. (C.I. 0.10, R.I. 0.47)
47. *Femora*: 0-slender; 1-normal; 2-flattened; 3-swollen. (C.I. 0.22, R.I. 0.56)
48. *Tibiae*: 0-slender; 1-normal; 2-flattened; 3-swollen. (C.I. 0.14, R.I. 0.50)
49. *Tibial spurs* (ordered): 0-absent; 1-small; 2-well developed. (C.I. 0.06, R.I. 0.42)
50. *Hind tarsal segment one*: 0-normal; 1-elongate. (C.I. 0.22, R.I. 0.53)
51. *Tarsal segment three*: 0-simple; 1-lobed beneath. (C.I. 0.25, R.I. 0.66)
52. *Tarsal segment four*: 0-simple; 1-lobed beneath. (C.I. 0.25, R.I. 0.0)
53. *Claws*: 0-simple; 1-cleft. (C.I. 0.50, R.I. 0.66)
54. *Male elytra* (ordered): 0-fully covering abdomen; 1-somewhat reduced; 2-greatly reduced. (C.I. 0.28, R.I. 0.54)
55. *Elytra surface*: 0-slight punctures with no costae; 1-slight punctures with longitudinal costae; 2-deep window-shaped punctures with longitudinal costae; 3-coarse punctures with no costae; 4-slightly coarse punctures with longitudinal costae. (C.I. 0.26, R.I. 0.54)
56. *Elytral epipleural fold* (ordered): 0-absent; 1-narrow; 2-broad at base. (C.I. 0.22, R.I. 0.84)
57. *Abdominal ventrite # (including pygidium)* (ordered): 0-six visible; 1-seven visible; 2-eight visible. (C.I. 0.20, R.I. 0.72)
58. *Male ninth abdominal tergite*: 0-not emarginated behind; 1-emarginate behind. (C.I. 0.11, R.I. 0.75)
59. *Setae on claws*: 0-absent; 1-present. (C.I. 0.50, R.I. 0.85)
60. *Abdominal segment 6, shape of photic organ/s*: 0-two spots; 1-one spot; 2-all; 3-center strip; 4-none. (C.I. 0.57, R.I. 0.85)
61. *Abdominal segment 7, shape of photic organ/s*: 0-two spots; 2-strip; 3-all; 4-none. (C.I. 0.37, R.I. 0.73)
62. *Abdominal segment 8, photic organ's*: 0-absent; 1-present. (C.I. 0.08, R.I. 0.47)
63. *Paired photic organs on segments 1-7*: 0-absent; 1-present. (C.I. 0.50, R.I. 0.0)
64. *Wing vein r3*: 0-absent; 1-present. (C.I. 0.08, R.I. 0.26)
65. *Wing vein r4* (ordered): 0-absent; 1-partial; 2-complete. (C.I. 0.09, R.I. 0.42)
66. *Wing Radial Cell*: 0-open; 1-closed; 2-not present. (C.I. 0.13, R.I. 0.23)
67. *Wing vein MP3*: 0-contacting MP1+2; 1-not contacting MP1+2. (C.I. 0.07, R.I. 0.27)
68. *Wing 1*st *Cubito-Anal Cell*: 0-absent; 1-present. (C.I. 0.16, R.I. 0.54)
69. *Wing 2*nd *Cubito-Anal Cell*: 0-absent; 1-present. (C.I. 0.05, R.I. 0.55)
70. *Wing CuA1(cross-vein)*: 0-absent; 1-partial; 2-complete. (C.I. 0.11, R.I. 0.30)
71. *Wing CuA1 vein intersecting MP vein*: 0-above fork (MP3a&MP3b); 1-at fork 2-below fork; 3-other (no fork present). (C.I. 0.16, R.I. 0.21)
72. *Wing CuA2(cross vein)*: 0-absent; 1-partial; 2-complete. (C.I. 0.23, R.I. 0.67)
73. *Wing AA3+4 vein*: 0-absent; 1-present. (C.I. 0.08, R.I. 0.5)

APPENDIX 3. MORPHOLOGICAL CHARACTER MATRIX.

Character Number (10)	1	2	3	4	5	6	7
Character Number	0123456789012345678901234567890123456789012345678901234567890123456789012345678901234567890123						
Plastocerus angulosus	02002130101012002100?000100000001220120114202111111000031 1-143000211112221						
Drilus flavescens	10002230001112002000001010000000222011110310211110011000120143001 00-100-00						
Drilus concolor	1200221201111---------0000010000000222011110110211210001000 22?14300100-000-00						
Selasia sp.	11012221000001002100?000100100001220111101102101100010002201430010 0-000-00						
Omalisus fontisbellaguei	1210200010101---------1?0101001010012201211011121122010100311-043001111112031						
Omalisus sanguinipennis	1210200010101---------1?0101021210012201211011121122010100311-043001210102000						
Harmatelia bilinea	1100203010100200210000101001010012201111020020121010100112 00----10211112221						
Drilaster subtilis	1201200010010---------1001010210100222010110100210221101001120043?01210112221						
Dioptoma adamsi	1211321200110---------0010011011111222010110200211220101000120 0----11211112321						
Diplocladon sp.	1201321100011201101001001104001122101011000001022210100112004300021110220 1						
Rhagophthalmus sp.	1011321000010201001001001104001222201011000021022210100122004300020111222 0						
Rhagophthalmus ohba	1011321000011201001001001004001122201011101121022101100122004300121111222 0						
Drilaster sp.	1201201010121---------0011001210100222010110111211202101001120043001110112221						
Pterotus obscuripennis	1200223010000100200001001100000021201 0?1011121122210100112004300121010220 1						
Calochromus perfacetus	2201211010111---------0011010010100211110010321021222011001020043000001100-01						
Dictyoptera aurora	2220201000111---------0011010212100212010011321020222011002020043001100102101						
Calopteron discrepans	2220201010121---------1010010111100211110012321020221011002020043001210102001						
Celetes basalis	1220201011121---------1010010212100212110012322020220011002020043000111100-00						
Discodon bipunctatum	1201210010110---------0011000010100212010100100010111110100102-043001210102001						
Cultellunguis ingenuus	0200210010100---------0011010010100001010100002010112101001 02-043001210100-00						
Omethes marginatus	0200200010101---------0110010010100231010100200210112111000 01-043001110012200						
Blatchleya gracilis	1101200000101---------0101010000000231010110000010001111000 01?043001110102201						
Ginglymocladus luteicollis	1100203000000200110110110110100131010100200210202110010 1-043001110112221						
Matheteus theveneti	2100203000010100100010100001010023211010020001000021110011004300121011222 1						
Trypherus frisoni	0111200010100---------0010030010100131010100101010111101010 02-043000010100-00						
Malthinus occipitalis	0201200010101---------1010010000000131010100001010111101013 02-043000100100-00						
Pseudotelegeusis sp.	0200211010101101100001002002000013010 0?000000101011??010020043000 03-000-00						
Telegeusis nubifer	0101200010101---------0?1002033330013010010000001010210101002004300000-000-00						
Cenophengus pallisus	0221304001101010210001002001010000001110000001010010102002004300111 0000-00						
Phrixothrix reducticornis	0200314001000010210000101000000010201010200101011210002002004300023110 2300						
Pseudophengodes pulchella	0200205010000011210001001000000013101 0?000001020000101002004310010 0100-00						
Stenocladius sp.	1211203010000000210100101100000000101011002111000010000012004300013010 0-00						
Zarhipis integripennis	0200304001001011210001001000000021101010020001011010101112104300121011222 1						
Brachylampis sanguinicollis	2200210010110---------0011012210000222010110200201221101000220043001110102021						
Psilocladius sp.	2211204010000011210101101121000021201011020020022010100112004300121011202 1						
Ellychnia corrusca	2211211010110---------1001001111100212010110200200221101001221043001210111021						

APPENDIX 3. (CONTINUED) MORPHOLOGICAL CHARACTER MATRIX.

Character Number (10)	1	2	3	4	5	6	7
Character Number	01234567890123456789012345678901234567890123456789012345678901234567890123						
Pyractomena ecostata	2211210010110---------2011102111100202010110200201220001001221122001210112221						
Pyractomena borealis	2111210010110---------2011102111100202010110200201221001001221122001210112221						
Aspisoma pulchellum	2121210010010---------2011101211100212010110200100221001001220122101210102221						
Aspisoma ignitum	2211210010110---------2010102111100212011110200200221001001220122101210102021						
Cratomorphus diaphanus	2021211010110---------201110210?10121201011021120022110100122100000121011222l						
Pyrocoelia praetexta	2121201011121---------2011102111100212010110401200220101001221031001211112221						
Pyrocoelia rufa	2021211111121---------2011101111100212010110401200220101001221031001210112221						
Alecton discoidalis	2121211210101---------2010102111100212010110101200221101001220043001210112221						
Alecton flavum	2121211210111---------2010102111100212010110201200221101001220043001210112221						
Pyropyga nigricans	2201211010120---------1010002111100212010110200200221100001221043001210112221						
Phaenolis ustulata	2221204010120210200001110211010020201111010120022010100121104300120010202l						
Tenaspis angularis	2211201011121---------1011102210100212010110100200221001001211043101210112021						
Erythrolychnia bipartitus	2021211010121---------1010102212100202010110200200221101001211013001210012220						
Erythrolychnia oliveri	2021201010121---------1010102112100202010110200200221101001211013001211112220						
Lucidota atra	2121201011121---------1010002210100212010110200100220101001221043101210112221						
Lucidota dilaticornis	2121201011121---------0010001210100212010110201200221101001220043101201112221						
Lucidina biplagiata	2211201011121---------0010001212100212010110400200220101001221043001100112221						
new species	2221211011121---------0010001112100212010110200200220101000220043101210112221						
Pollaclasis bifaria	2111214011101010210001001201010021201011020121021010100122104310021011222l						
Pristolycus sagulatus	2211201011121---------2010012112100221010110301210220101004101043001011112221						
Vesta auranfiaca	2221?01011121---------0010001110100222010110200200221101001221043101111112021						
Callopisma maestra	2220201010120---------0011001212100212010110200200220101001221043001210100-01						
Cladodes flabellatus	2221202011021200210001100221210021201011020120022010100122104310210110-21						
Macrolampis acicularis	2011210010110---------0001001111210020201011020120022110100122004300121011202l						
Photinus pyralis	2111210010020---------0001001210100202010110100200222101001220022001210101011						
Photinus ignitus	2101220010010---------1001001110100212010110100200221101001221022101210112121						
Photinus meteoralis	2201210010020---------1001001211100212011110101200222101001221022101210112121						
Bicellonycha amoena	2021200010100---------0001001110100222010110200210222101101220022001110101321						
Photuris divisa	1020200010100---------0000000112100212010110200210222101100220022001210110-20						
Photuris brunnipennis	2021200010100---------0001000010100212010110200210222101101220022101210102201						
Robopus sp1	2121210010020---------1011001110100202010110200200220101001220043101210110-11						
Robopus sp2	2121210010020---------0011001110100202010110200200220101001220043101210111221						
Luciola lateralis	2011210010111---------1011011010101222010110200201211101001200021-01210112220						
Luciola salomonis	2021220010111---------1011011210101212010110200200211101000200021-01210112221						
Luciola cruciata	1220210010111---------0001011112101222010110200210220101001200022-01210112221						
Luciola kuroiwae	1021220110101---------1011011112101202010110200?2201010012000022-01211002200						

APPENDIX 3. (CONTINUED) MORPHOLOGICAL CHARACTER MATRIX.

Character Number (10)	1	2	3	4	5	6	7
Character Number	01234567890123456789012345678901234567890123456789012345678901234567890123						
Colophotia sp.	2111200010000---------1000011112100232010110200211110101001201022-00211000-00						
Pteroptyx cribellata	1001220010100---------0010011110100232010110200200220101001201022-01211002100						
Pteroptyx malaccae	1010210010111---------0010011110100232010110200210220101000201020-01210000-00						
Pteroptyx tener	1011210010101---------0010011110100232010110200210110101001201020-01210002200						
Lamprohiza splendidula	2021210010101---------2011001010101212010110200201222101001211031001100102201						
Phausis rhombica	2110210110010---------1010102210100212010110400201220101001221043 00-100101001						
Phosphaenus hemipterus	2020220110100---------101000221??00202010 1?02012012200010202210431 0----------						
Pleotomus nigripennis	2021402010100210200101110211010121201111020020022110100121104310121011 2221						
Pleotomus pallens	2021402010100210200101110221010121201011010120022100100122104310121011 2221						
Lampyris zenkeri	2021200010110---------3011101110102212011110200100221101001221043101000110-21						
Microphotus angustus	2021110210100---------301?101210102212011110200100220101001221043101001102020						
Lampyris noctiluca	2021210110110---------301?101212101202010110101100221101001221043101210112221						
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ON RESEARCH AND ENTOMOLOGICAL EDUCATION V: A SPECIES (C)ONCEPT FOR FIREFLYERS, AT THE BENCH AND IN OLD FIELDS, AND BACK TO THE WISCONSIAN GLACIER

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ABSTRACT

There is no lack of species concepts available for consideration, nor of discussion and speculation about what a species concept should be and do, but nothing seen in recent literature is suitable nor adequately clear and descriptive for firefly naturalist/taxonomists as they begin their studies. A reasonable ad hoc solution combines the now-classical and practical omnispective view of the phenotype for pragmatic utility, with a composite of early 20th-century elements and theoretical (notional) fragments from various nominal "Concepts," particularly the Biological Species Concept, and places natural selection and inevitable population divergence into foremost consideration, to provide a microevolutionary expectation of firefly populations in nature. A short history of about 18,000 years is introduced because of the possible existence of geologically dated, clear evidence of population changes that may be recognizable in fireflies living in regions that came under the influence of the last major NA glacier.

Key Words: Lampyridae, fireflies, taxonomy, species concepts, species problem

RESUMEN

Para los naturalistas/taxonomistas de luciérnagas que comienzan sus estudios, no se ha visto nada en la literatura reciente que sea apropiado o adecuadamente claro o descriptivo, ya que no se carece de conceptos de especies para la consideración o discusión y especulación sobre lo que un concepto de especie debe ser y hacer. Una solución razonable para este caso combina la perspectiva práctica y ahora clásica de fenotipo para el uso pragmático, con una composición de elementos de comienzo del siglo 20 y fragmentos teóricos (hipotéticos) de varios "Conceptos" nominales, en particular el Concepto de Especie Biológico, y coloca a la selección natural y a la inevitable divergencia de población bajo la consideración mas destacada, para proveer una esperanza microevolucionaria de las poblaciones de luciérnagas en la naturaleza. Se introduce una corta historia de alrededor de 18,000 años debido a la posible existencia de evidencia clara, con fecha geológica, de cambios de población que pueden ser reconocibles en luciérnagas que viven en regiones que estuvieron bajo la influencia del último glaciar importante de NA.

"Among the diverse aspects of the so-called species problem, there is none that has received more unsatisfactory treatment than the study of species. . . . comparative studies of species, first-hand contacts with thousands of individuals of hundreds of related species, the careful examination of these individuals with modern laboratory facilities, and the correlation of such studies with the findings of genetics . . . has only occasionally been accomplished." (Alfred Kinsey 1930)

"a variety of species concepts is necessary to adequately capture the complexity of variation patterns in nature. To subsume this variation under the rubric of any one concept leads to confusion and tends to obscure important evolutionary questions." (Mishler & Donoghue 1982)

NATURALIST'S INTRODUCTION

"What is a species?" Does not this question presume too much? Could there possibly be anything real in nature such as preDarwinians created and saw, and almost everyone until recently has expected? Should not Darwin's "Origin" have put an end to obsession or flirtation with any form of essentialism?—should it not have quickly led to realization that an expectation of *species* as a universal in the living world was quite unrealistic? Today among professional systematists the question can often mean, "what arbitrary, utilitarian definition for your personal research subjects do you wish to refer to, want to write about, when you use the word 'species'." But a half-century ago when Ernst Mayr, Theodosius Dobzhansky and others taught us about what has come to be known as the Biological Species Concept (BSC), a very good seed, they seemed to focus and guide us

toward an intrinsically defined taxonomic unit, toward making a truly definable "natural species" a scientific reality for the first time. For a brief and golden moment, a Camelot looking back on it, the naturalist had his species and could go back and forth easily and comfortably between the morphology under the microscope and the flashing of populations of his biological species in the field. We remember this as a good time, we were modernized, and we thought it would never end.

It is important that educators remember that before the BSC there was some very good thinking too, by naturalists, taxonomists, and phylogeneticists who got the century off to an admirable start. For those who were paying attention to the species question, there were sound perspectives and ideas to help them in research and teaching. Gordon Ferris' text "The Principles of Systematic Entomology" (1928) taught a generation of insect taxonomists, and at the end of the second chapter, "The Scope of Systematic Biology," he wrote, in italics: "Systematic biology should include in proper proportion all those activities which arise from or are connected with the study of those *aggregates of organisms we call species* [jel emphasis]. It is in its broad implications essentially synonymous with the study of organic evolution." A quotation Ferris used in his consideration of species that is particularly relevant for fireflyers was from Harvey Hall and Frederick Clements' "The Phylogenetic Method in Taxonomy" (1923): "The evolutionary view of the species is that it is a definite phylogenetic stock, sprung from and related to similar stocks, and itself undergoing modification into a number of variads. As they have recently come from the same stock, these variads are more nearly related to each other than they are to those of any other species, and they represent a definite phylogenetic unit, the species, *at the same time they mark its further differentiation* [jel emphasis]." For a comprehensive statement about species and speciation, yet economy of words, it is difficult to do better than that!

When we learn about species from field work, and at the same time, consider the pragmatic responsibilities of species taxonomists and naturalists, we should not forget Alfred Kinsey—who later became famous as a pioneer sexologist—and his monograph "The gall wasp genus *Cynips*: a study in the origin of species" (1930): "If taxonomy has been in ill repute, it is because we have considered as our chief function the solution of something other than biologic problems. . . . The older definition of a species as a group of similar (implying nearly identical) individuals fails because of the amount of variation actually found in nature. . . . if [instead] species are defined as populations with common heredity, we obtain a concept which seems genetically sound and which, we will try to show, is a reality in nature. . . . after such field experience, one comes to feel there is a reality summed up in the word 'species' which is more than a few cabinet specimens or a bottle full of experimental material or a Latin binomial in a textbook." Kinsey noted, as reminder or for those who were not of the taxonomist's cloth, that there were two often confused uses of the term "species" in taxonomy: "It must be pointed out that there is a biologic concept called species and a taxonomic category called species, and that the two are not always synonymous. The concept we have developed is the biologic concept to which all except the taxonomist must refer whenever they consider the problem of species. This is the sense in which even taxonomists, including ourselves, intend the word when it is used in most biologic connections."

Returning to the mid-century developers of the BSC, they went on to discuss "reproductive isolating mechanisms" and saw them as population adaptations that prevented genetic pollution from other species. It was eventually realized that this view needed rethinking. Selectionists argued the importance of carefully identifying the actors, the so-called selected entities, and led BSC advocates to focus their attention on reproductive individuals making up their biological populations. Mate selection became apparent as a reasonable self-defining element of a biological species, at least ideally, making this BSC even more different from other Species Concepts. In this revised edition, individual members of a species themselves set the boundaries of their species, and for (soft) evidence of this a fireflyer saw individual fireflies flash communicate, antennate, then copulate.

This BSC2, envisioning a mutual gene pool of self-defining individuals as a theoretical description of reality might seem to have it all, for we would not necessarily require that a theoretical model be verifiable—we cannot usually know whether copulations produce successful fertilizations, or fertilizations produce surviving, competitive offspring. But in a good theory reach will exceed grasp: "a concept cannot be completely operational and still be useful for the growth of science" (D. Hull, seen in Mishler & Donoghue 1982). But BSC2 embodied another, long-recognized imperfection for fireflyers. Mate choice and gene flow cannot easily be presumed to maintain a mega-population's unit integrity across half a continent, or when a presumptive gene pool is fragmented into small and variably-isolated local populations. As Mayr has pointed out, when they are separated across space we cannot know the *relational* status of local "conspecific" populations—that is, know whether they are independent units, have diverged a little, significantly, or too much to be in fact the same species. Likewise, when experimentally transported individuals from distant regions of a "continuous" mega-population communicate and copulate, what can we find or should we read into the results? (But some

might view this experiment as an in-vivo molecular technique and make some use of it.)

What this means is that many of our "good" operational (cabinet) firefly species with such distributions, e.g. *Photinus pyralis* (L.) and *Photinus cookii* Green (Figs. 1-3), should only be thought of as bookkeeping (formally named, operational, working) species. We can imagine that once there was a gene-pool unity about each of them, and in the simplest of models and however spaced out they occur now, that each originally derived from a single, local population, a real and true biological species. But it is obvious that when we conceptualize about such species as these two, that we have a relativity problem, a riddle in space and time. Nevertheless, it is axiomatic that knowledge of the genetics of contemporary species-designates, and the tenuous and recent-past interconnections of their local populations are necessary for understanding what we seek to know about the existence of the things we call firefly species. Whatever notional fragments he eventually adopts into a mental construct, the fireflyer can never abandon the fertile seed present in the BSC.

What fireflyers could use is a simple but explicit conceptual framework, one which would include first an operational plan, and second, a comprehensible, somewhat theoretical overview and expectation of such "biological-species-gone-apart-too-far-too-long"—something as understood by Hall and Clements in their quotation given above. Fireflies, with their lights that identify not only them but their mating seasons, their micro-locale and -spreeing hot-spots, and even their

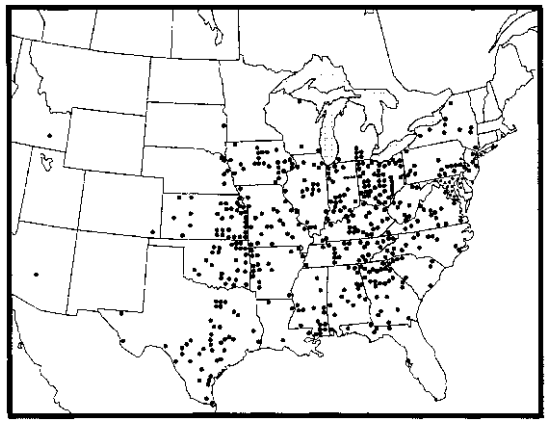

Fig. 2. Known geographic distribution of working species *Photinus pyralis* (L.), a seeming mega-population spread over a vast region. Locality records shown are from the examination of extensive museum and other archival holdings, and personal observations since 1963.

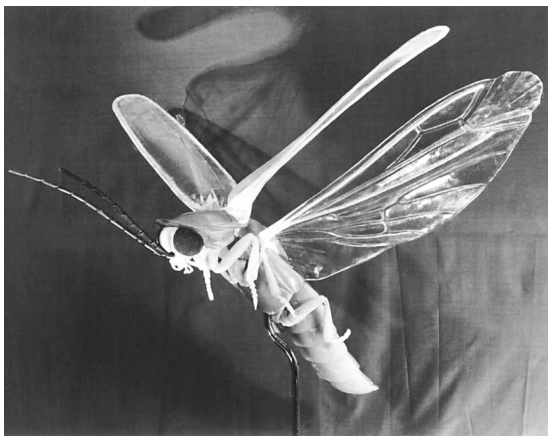

Fig. 1. A model of a male *Photinus pyralis* (L.) in flight. The "Big Dipper Firefly" is probably the best known and most widely distributed firefly in North America, and should be celebrated on a cereal box or in a book of records for having raced more children across lawns at twilight than any other species. This early-plastic sculpture was probably made in the 1950s and may be "lost" in a museum somewhere in northeastern U.S. It was made from a photograph taken by Frank McDermott which was published in a beetle journal in 1954. An article about it and the artist may have been published in the popular press, though this reference with the details has long been mislaid. This print was made from one found in McDermott's files after his death.

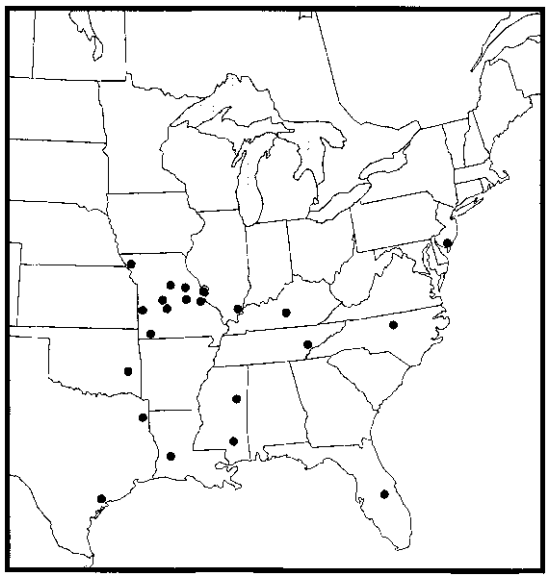

Fig. 3. Known geographic locations of (working) *Photinus cookii* Green, a seldom collected firefly with a fragmented distribution, based on examination of extensive museum and other archival holdings, and personal observations since 1963. There may be hundreds of local populations of this rarely collected species, and those represented here should be viewed in a comparative way, and understood as evidence for the occurrence of a relatively uncommon firefly.

wanderings, including travels among local active sites (demes), seem ideal for such study. And, incidentally, flashed patterns represent neurological hence soft parts of the phenotype, and maybe they sometimes evolve more rapidly than hard parts, and are more quickly tuned by selection to the exigencies of life, than characters that are usually available for such study and comparison? A useful image would also project us back in time just a little, for this reason: local populations in sites across the US and Canada may still reveal recognizable evidence of genetic population developments that occurred as a consequence of the Wisconsian glacier—North America's recent, omnipotent, geography-, climate-, and habitat-altering presence. What is more, geologists may be able to tell us how long ago these events took place!

One of the most significant intellectual moments I recall having as a graduate student was when my mentor explained that what I had discovered about the biology and distribution of a firefly—suggesting that it had started from west of the Mississippi River and moved eastward—was a pattern observed in several other organisms from orthops to snakes. I could imagine millions of flashes in the twilights of a few thousand summers, gradually moving eastward through a new prairie-like grassland across what is now Illinois, northern Indiana and Ohio, and into the corridor of the Mohawk Valley of New York. It was quite a "kick" to realize that I had found descendants of this little firefly, flourishing after generations of interbreeding with a "closest relative" in the Valley all the way to the Hudson River, and in particular, on the lawn of my boyhood home among glacial hills just south of the Valley.

Systematist's Introduction

In their Preface to "Species Concepts and Phylogenetic Theory: A Debate," editors Wheeler and Meier observe: "Surprisingly, and in spite of literally thousands of scientific papers relevant to the subject, there are more species concepts in popular usage today than at any point in the past century, and the consensus in zoology about the Biological Species Concept has begun to unravel. An aggressive search for a species concept that is consistent with phylogenetic theory has begun." I am truly glad for their progress . . . but a phylogenetic concept will not help fireflyers answer the questions they ask. After 38 years of chasing and trying to understand the species of flashing fireflies I see in the field—having taken up the flash-focused taxonomy begun by pioneers F. A. McDermott and H. S. Barber early in the 20th century—I would find no more comfort in phylogenetic species than in the metaphysical musings and promises of celestial guides. Fireflyers have a pretty good operational program for sorting, describing, and naming; what they need is to have this made a part of a comprehensive view that addresses the apparent, or "seemingly likely" genetic circumstances and reality of firefly populations in nature, in the here and now, and fairly recent past.

Here I must step to the front of the stage for a moment, and tell any outsider onlookers in the balcony that when working taxonomists and systematists, such as phylogeneticists, bacteriologists, virologists and fireflyers offer different points of view and come up with different so-called Species Concepts, we are wrestling the problems of how best to define or specify what we will term "species" for our own research needs and taxons' peculiarities. I suppose you might consider this a "lower case" species problem, and though there may be a connection with the species problem that philosophers of science have pondered—and led one to say, regarding "species":

> "It should be a matter of considerable embarrassment to biology that one of its central notions—indeed, one of its oldest concepts—should remain to this day the subject of heated intratheoretical controversy. No definition of the term has found universal adoption; indeed, some responsible biologists dispute its intelligibility altogether. Despite its apparently crucial role in the most imposing of biological achievements, the theory of 'On the Origin of Species,' the term is still without clear meaning." (Rosenberg 1985)

—it is the difference between a can of worms and Pandora's Box. (I think it should be a matter of considerable embarrassment to philosophy that after all of this time they still have not been able answer to some satisfaction, the most important question from their domain, "Why all of this?")

Our species problem has been with entomologists since Darwin, and a survey of the literature on the subject should convince nearly anyone except an end-timer that it is not likely to go away. There are numerous treatments of or around the subject, with titles that catch the attention and raise hopes of attentive and confused biologists: species, "the units of evolution" and "the units of biodiversity", their "concepts and phylogenetic theory", "as individuals", and the "metaphysics of"! One title in particular caught my attention—"Species: New Interdisciplinary Essays"—and am I glad I read a review first!: "More species concepts! I opened the book with a sense of foreboding. Its authors are anthropologists, philosophers and psychologists, as well as systematists. We biologists can't solve the species problem, so call in the shrinks, eh?" (Mallet 2000). The authors, the reviewer went on, and here I freely paraphrase his survey, lay out questions about whether there is more than one type of species, whether species are real or human constructs, whether species definitions are useful and to what extent are they

are influenced by the history of human thought rather than biological reality, and whence our psychological need to classify organisms as species? Mallet suggests that "most authors were more interested in species concepts as a way of studying how we think." Such is not the view, review, or overview that a working virologist, botanist, phylogeneticist, or fireflyer will be looking for, at least until he permanently reaches some "higher and gray retirement of the museum and library."

Now, to address the species problem at the operational level, whence most nominal Species Concepts arise, along with the difficulties of cross-communication. When I get to it, I will use for comparison with natural history what may be the most dynamic though acerbic discipline of the bunch. But first, as prelude and predicate, consider this, from a book entitled "Why People Believe Weird Things": "'what there is depends upon what paradigm you hold. For Priestly, there literally was no such thing as oxygen. . . . In the case of Lavoisier, he not only believed in oxygen: oxygen existed' [P. Ruse]. . . . Similarly, for Georges Buffon and Charles Lyell, varieties in a population were merely degenerates from the originally created kind; nature eliminated them to preserve the essence of the species. For Charles Darwin and Alfred Russell Wallace, varieties were the key to evolutionary change. Each view depends on a different ontological paradigm: Buffon and Lyell could not see varieties as evolutionary engines because evolution did not exist for them; Darwin and Wallace did not view varieties as degenerates because degeneration is irrelevant to evolution." (Shermer 1997).

A Species Problem, 2001

cladists in our bio world
are electron quick; contention!
they will know a species is,
resolve, hot cold convention.
but chasing flashes as i do,
looking, seeking here and now,
i can't embrace mere digit bliss,
less kiss a sacred cow.
i follow little lights at night,
cross Boone's mounts and streams,
far from madding, clicking plight,
pc-peeps and ranting dreams.
alone, i hear "whose cooking?" owls,
Carr's "bean'n-bacon" frogs,
follow my own drinking gourd,
an odyssey in foggy bogs. (Fig. 4)

Now consider the unraveling of the BSC and the search for a concept that is consistent with phylogenetic theory. The long view into the past from a computer keyboard and detailed character matrix is not the same as the one fireflyers try to see. We peer across old fields through hedgerows and into the next old field, and beyond, and back to the northeastern forests and fire-maintained grasslands of the day before Europe arrived (see MacLeish 1994), to a summer after the Wisconsian Glacier. Perhaps biological species cannot exist for a phylogeneticist because in his much longer view, summers past with living populations are so compressed as to be but fragmented membranes of carbon between layers of shale. Consider what a fireflyer does within his membrane of time: he locates populations of flashed patterns in the field, makes electronic recordings of them, collects voucher specimens emitting them (to be examined under the microscope) and photographs them, and sends living vouchers to Johns Hopkins U. to have their bioluminescence spectra analyzed; he sees whether such pattern-flashers change their patterns through the evening, or in response to answering (female) flashes, or to different levels of male competition, or to variations in the vegetation they search, and whether any of their patterns match those of those of other species flashing at the same time and in the same space; and then, driving with head-lights off, the fireflyer finds other flash-conforming populations down the road, out of town, across the state, and over the mountain. If there is time, there is also consideration of cuticular hydrocarbons, mollecute and *Wolbachia* infections . . . and DNA. . . .

Fireflyers will be very interested in following developments in professional systematics' search for a phylogenetically useful definition/concept, because the data fireflyers collect may be organized, coded, ordered, and interpreted most objectively using the cladistic analysis procedures and perspectives developed in this arena, and with the kind help of phylogeneticists. We will view our tables of flash patterns with cladograms that are developed from their character matrices, for insight and interpretation, and then combine all of this with what we know about geographic and seasonal distributions. And then we will be able to look way, way back, long before the Wisconsian with the vision of the phylogeneticist. But this is not where we are now, and it is not to our point of light. We want to see each of our fireflies and flash patterns in the field and in as many populations as we can, and from this speculate and experiment with how flashed patterns and species may evolve (Lloyd 1984), and maybe even see something actually in progress among differentiating "conspecific" populations in the field, as Hall and Clements said we would. It's as simple, untechnical, unprofound, and myopic as that.

So that fireflyers will know where they might begin thinking about what we have called firefly species, and how early fireflyers thought, and how to explore the paths that fireflies have taken to be the way we find them, and to help students develop a conceptual framework that can carry them

Fig. 4. The tamarack swamp in Wisconsin where Eunice Myers, Herbert Barber's technician, and her student Bernard Boland on 8 July 1926 collected the *Photuris* specimens that Barber subsequently named *Photuris aureolucens*. Myers and Boland took me to this site in the summer of 1970 when I was learning Barber's species. Miss Myers noted that not much had changed in the years since they collected there, though when I visited the site in the 1990s the vegetation was much denser and the land was posted. This photo is from a Polaroid® print.

intelligently and heuristically from their bench to the field, and back, with a temporary shortcut through the long-accumulated literature, wisdom, confusion, dialogue, debate, frustration, and tension on the subject, here is a brief introduction.

Letter XXXX

The Firefly Species Problem, and
A concept With A View For Fireflyers

"'To be is to be experienced.'
. . . That which falls beyond the possibility
of being experienced is not real.'"
(Berkeley, seen in Sahakian
& Sahakian 1993)"?" (jel 2001)

Dear Fireflyers, In our discussions of fireflies and their biology, especially their species-specific flashing, we have up till now spoken as though each named species was a real and natural entity in nature, and that the mission of firefly taxonomy was to discover and name every one of them that lives in North America—maybe even the World—to make them all available for research and conservation. Once upon a time biologists thought this was possible, but after decades of collecting, comparing, analyzing, thinking, and theorizing, it now seems fairly certain to many biologists that specialize in the fields of taxonomy and evolution that not only is such a project impossible, as incredible as it may sound, there actually is no general and real class of species-things that exists in nature. Thus, one should not ask or develop an introductory lesson on "real firefly species" around the question, "What is a species" but instead, should address such questions as "why is the reality of species questioned?" and "what, then, is the real (i.e., scientific) nature of the species-like entities that we observe—that have seduced everyman and taxonomists into believing in them with so much conviction for so long?" The uncertainty thus identified may be termed the "firefly species problem." A practical question to be answered is, "how, then, do we determine those entities that we should formally recognize with scientific names?"

Historical synopsis: For a century and a half after Linnaeus first named fireflies (1758), firefly

taxonomists continued to name their species exclusively "on the pin" by their morphological distinctiveness, so judging their uniqueness, their "species-ness." Given prevailing beliefs until Darwin's "Origin" (1859), this seemed "theoretically logical," though today we could simply view it as "theologically ordained." Before Darwin it was presumed that each species of "Creation" had a unique and distinctive existence/character (≈ Essence), and representative specimens would not only fit their species' Pattern, each Pattern, which is to say each species would remain unchanged through time, for they were as Plato's circle and triangle, perfect and immortal. The work plan from this World View lingered for a long time after evolution was discovered, for although this Essentialist Concept of species was no longer carried in the mind, taxonomists at their bench continued with the same general methods for finding and naming new species—this is not a criticism, because when faced with millions of unidentified and unnamed pinned specimens, and the only information available about them is on their cuticle and labels, there is no alternative toward accomplishing mission impossible.

In the early and mid 1900s appeared two key contributions of significance for fireflyers: (1) Frank McDermott published a series of papers reporting that flashed mating signals were useful for species identification and reservedly used them to make a token but formal nomenclatural (name) change, and (2) Herbert Barber applied this thinking to show that the flash patterns of *Photuris* fireflies were useful taxonomic characters for the species-distinguishing problems this genus had long presented, aligning his approach with the best-informed evolutionary thinking of the time. These fireflies had given taxonomists fits for decades because their morphology seemed a hodge-podge of chaotic and relentless variation, never promising, always confusing, and beetle experts knew something fishy was going on—"some day somebody is going to split that thing up," said Barber's mentor E. A. Schwarz, of the catch-all *Photuris pennsylvanica*, in 1910.

Barber's studies resolved a few specific problems, but more importantly he identified key elements of the larger puzzle of *Photuris*, and provided invaluable guides, practical examples, and intellectual encouragement for his successors. Unfortunately, publication of Barber's work was suppressed until after his death and he never lived to see it receive the recognition it deserved. For one thing, it was deemed inappropriate for government employees to study insects that had no commercial or practical significance, and for another, museum taxonomists refused to accept the impractical notion that behavior should be used in classification (species "systematization"). They argued that one could not observe flash patterns on a pin, and as noted, virtually all of the specimens they processed were pinned or in vials of preservative. Barber's futile response to this was written shortly before his death in a 1949 letter to McDermott: "Taxonomy from old mummies which fill collections is a misguided concept. It leads to the misidentification of rotten old samples in collections. How these poor fireflies would resent being placed in such diverse company—among specimens of enemy species—if they were alive and intelligent! What contempt they would feel for the 'damned taxonomist.'" Long before this letter was written Barber had demonstrated that behavior could indeed be preserved on an insect pin (Fig. 5).

Barber was tuned to the old and legitimate understanding (<1700s) that members of a species could interbreed, with the emerging sophistication that members of a species formed a genetic population, and more to the point, he appreciated that his responsibility as a taxonomist was to work toward the discovery of such populations. He wrote in his notes in 1945: ". . . each species is an isolated self-perpetuating population, limitless in individuals by past and future generations, and . . . our taxonomy must correctly interpret these natural species which contrast so hopelessly with the customary 'taxonomic' species. . . . " You may recognize that Barber's view of species in 1945 was what one now learns

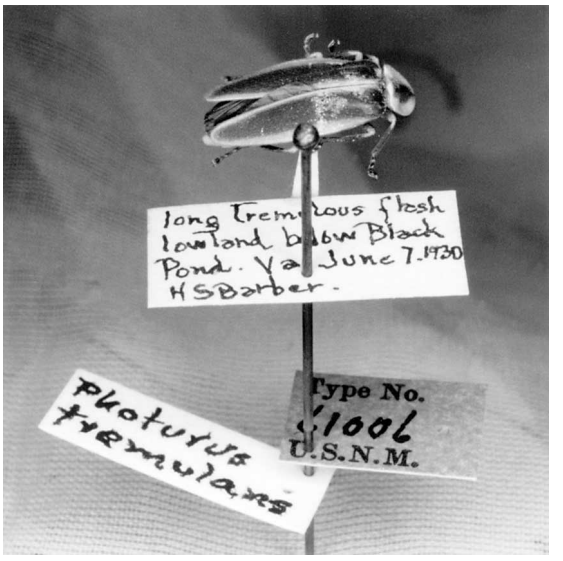

Fig. 5. One of Barber's specimens, the taxonomic Type specimen and flash pattern voucher specimen of *Photuris tremulans*, which he observed and then captured in the lowland below Black Pond, Virginia, on 7 June 1930. This firefly emitted a long tremulous flash, according to the label, demonstrating that flash pattern data also can be put on an insect pin. Barber discovered that males of this species emit two distinctive flash patterns, one of his especially significant discoveries for fireflyers that use flash patterns for taxonomy.

in biology texts, and is referred to as the "Biological Species Concept" (BSC), though Barber included "past and future generations" providing an historical dimension, as found in the slightly more recent "Evolutionary Species Concept," a view used by some systematists today. Actually there are many so-called "Species Concepts," most intended to satisfy working requirements presented by different groups of organisms and the interests and focus of researchers (Table 1).

The BSC was mainstream thinking on species for decades (1940-1990?) in zoology, though not in botany, and not without serious and sometimes acrimonious debate and criticism, and when progressive museum entomologists looked at unit trays of elderly and faded *Photinus pyralis* and other specimens that had been identified via morphology, in their minds they saw populations and gene pools, so easily and thoroughly could the apparent logic of the BSC meld with work-a-day taxonomic thinking. When you next look at the masterful 1950s generic revisions of *Photinus* and *Pyractomena* by John Wagoner Green you will see that they are based exclusively on dead-specimen morphology, but the spirit of the BSC is present and comes through. In the jargon of Species Concept addicts and purveyors, Green used the "Morphological Species Concept" for his bench work on firefly taxonomy but he thought with the BSC, or an antecedent of it.

Firefly species brought into question. Now, with the level of understanding made possible by Green's revision of *Photinus*, it is possible to move on and ask basic questions about "nature's reality" and its presumptive "evolutionary units" using examples from this genus. Consider specimens identified in Green's key as *P. pyralis* (Fig. 1). The map in Fig. 2 is based on label data from more than 1200 specimens sequestered in more than thirty museums and individual collections, fireflies caught during twilights on the veranda, family travels, Fourth of July weekends, picnics, camping, and camp meetings, and the netting, pinning, labeling, and unbroken responsible preservation by hundreds of entomologists, beginning with a specimen in the Cornell collection from Peoria, Illinois, summer of 1875; another from Spirit Lake, Iowa, June 1896; and another caught "flying around lawn at evening" in Birmingham, Alabama, 1904. (Be reminded that on these antique dates, twilight trips at such localities could expose collectors to malaria or yellow fever!)

Is it reasonable, in view of such vast real-estate, virtually a half a continent, and the uncertainty of the efficacy of gene flow to maintain a population's genetic integrity, to consider *P. pyralis* a real and true biological (genetic) population, a species of nature, or again, a unit of evolution, as species are repeatedly being called? Toward finding an answer to this I have observed *P. pyralis* flash patterns, twilight activity, and various other "*pyralis*-typical" behavior at more than 300 localities throughout this broad distribution, unsuccessfully seeking eye-catching differences. In spite of this, and though *P. pyralis* is (now especially) ubiquitous, occurring along highway and powerline grassways, in pastures, meadows, and croplands, in lawns, parks, cemetaries, and orchards, does it make sense to perfunctorily accept *P. pyralis* as a biological species, without consideration and examination of mechanisms and circumstances that would make this possible, or impossible? How quickly must genes flow and what else must occur to hold such a population all together? Perhaps there are hidden (i.e. sibling, cryptic) species, such as Barber found in *Photuris*, and subtly different flashed mating codes that have evolved locally and trick resident *Photuris* femmes fatales in their deceptive predations, that have been overlooked?

TABLE 1. A LIST OF SO-CALLED SPECIES CONCEPTS, FROM VARIOUS SOURCES INCLUDING THREE (2+1) NAMED FOR ILLUSTRATION HERE, SEVERAL FROM R. L. MAYDEN, IN CLARIDGE, DAWAH, AND WILSON 1997, AND OTHERS FROM MAYR 1991.

Species Concepts	
1. Nominalist Species Concept	14. Genetic Species Concept
2. Biological Species Concept	15. Non-Dimensional Species Concept
3. Recognition Species Concept	16. Phenetic Species Concept
4. Morphological Species Concept	17. Successional Species Concept
5. Evolutionary Species Concept	18. Hennegian Species Concept
6. Essentialist Species Concept	19. Cohesion Species Concept
7. Typological Species Concept	20. Composite Species Concept
8. Phylogenetic Species Concept	21. Geneological Concordance Concept
9. Taxonomic Species Concept	22. Internodal Species Concept
10. Agamospecies Concept	23. Polythetic Species Concept
11. Cladistic Species Concept	24. Omnispective Species Concept
12. Composite Species Concept	25. Extended-r Species Concept
13. Ecological Species Concept	26. [Ferris, Hall, Clements, and Barber's little-c Species (c)oncept]

With respect to gene flow serving as a glue to tie members of an overgrown population together as a species unit, studies on butterflies have shown that individuals do not necessarily move very far from their "birth(hatch)places" but we have no information about this for fireflies, and it could differ greatly among the various kinds of fireflies—a brachypterous female of *Photinus collustrans* LeConte is not going put her eggs far from her birth burrow. If *P. pyralis* is genetically connected across its broad span, perhaps the Mississippi River is enough of a barrier to retard flow such that differences can be detected in the DNA? Should it be that such huge and seemingly unmanageable populations are unitary, but certainly sluggish to change(?), does this result in detectable evolutionary stagnation for long periods of time? In the view I recommend, *P. pyralis* remains only a working species, one that invites us to learn more about and from it.

Another step into species/population uncertainty is illustrated by the firefly *Photinus cookii* Green. This is a daylight, dark firefly without a light, that is rarely found in museum collections, and seemingly occurs in relatively few, scattered localities (Fig. 3). Gene-flow connections are obviously tenuous, maybe stretched to the breaking point if not already broken at weakened joints in some places. (Remember, though, that there certainly are many, maybe even hundreds more local populations, and collections and map dots can only suggest relative abundance and site spacing.) When local populations are isolated what brings them to a speciation point—excessive time between contact, strongly differential selection pressures, narrow mate-selection criteria, local and idiosyncratic genetic disturbances (Table 2)? *P. cookii* too can correctly only be viewed as a working (morphological) species. At least in the case of *P. cookii* we can have some confidence that (individuals of) its local populations are reproductively isolated from all sympatric, closely related species—being lantern-less as it is—which is more than we can say about others in its species-group if they do not occur together (see below).

Florida's *Micronaspis floridana* Green (Fig. 6) illustrates the shoestring variation of this geographic isolation theme, because it is only known to occur at the edges of salt water marshes around the coast of the peninsula, between Volusia and Levy Counties (Fig. 7), and any gene flow among its populations must be linear and jumping, as on an island archipelago. Such distribution and spatial separation would be a common pattern in species whose suitable-habitat sites are isolated by inhospitable conditions, such as stream-bank (riparian) fireflies, especially those in the high and dry plains of west Texas, or species in the deep valleys of mountains in Colorado, and strand species along the shores of huge islands or bodies of water.

A more complex and instructional case of population isolation and the firefly species problem can be illustrated with two other species in Green's *Photinus* Division I—the species group to which *P. cookii* belongs. As you read the historical-fiction-based-on-fact account below, (1) note how these fireflies illustrate the occurrence of stochastic (long-shot, fortuitous) juxtaposition of re-

TABLE 2. POTENTIAL FACTORS IN THE EVOLUTIONARY COHESION AND DIVERGENCE OF LOCAL POPULATIONS. FLASHING FIREFLIES MAY LEND THEMSELVES TO GATHERING EMPIRICAL DATA AND THE QUANTIFICATION OF SOME OF THESE.

Factors In Deme Cohesion/Divergence	
Cohesion Enhancement	
1.	broad habitat utilization, generalists, little physical separation of inhabitable sites
2.	ecologically similar selection pressures
3.	extensive flight movement, local and emigration; winged females
4.	broad season of adult sexual activity
5.	synchronous mating of demes—astronomical cues?
6.	mate selection weak, tolerant
7.	female control of fertilization weak, mating system polyandrous
8.	internal (genomic) resistance to genetic variation, change
Divergence Enhancement	
1.	narrow habitat utilization, specialists, separation of inhabitable sites
2.	ecologically different and strong selection pressures
3.	little, weak flight movement; females flightless
4.	short season of adult mating activity
5.	mating among demes asynchronous—cues local conditions
6.	mate selection rigorous, narrow, progressive
7.	female control of fertilization strong, mating system monandrous
8.	weak internal genetic resistance to variation, "genetics in revolution"

Fig. 6. Habitus of *Micronaspis floridana* Green, the "Fiddler Crab Firefly." This firefly occurs around coastal marshes in Florida, and its larvae probably prey upon snails. See its known distribution in Fig. 7. Carbon-dust illustration by Laura Line.

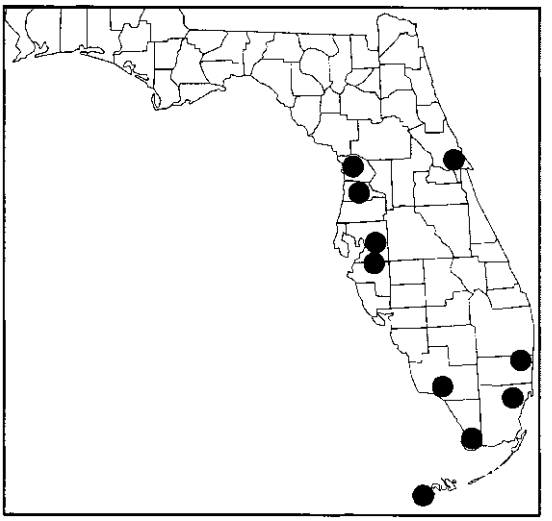

Fig. 7. Known geographic distribution of working species *Micronaspis floridana* Green, a shoestring distribution around the coast of Florida. The map is based on Green's data, my examination of museum and other archival holdings, and personal observations. Gene flow between Volusia County on the Atlantic and Levy County on the Gulf has probably been slow, even before the emergence of Ft. Lauderdale, Miami, and Tampa/St. Pete.

gional ecology and firefly population divergence in time and space, and then, (2) how they challenge us to think more about what we expect a "good and true natural species" is, or ought be, and the sometimes ephemeral nature of species, as well as of our own sound and well-reasoned conclusions in such matters!

Background: Known Division I fireflies, except for *P. cookii*, are generally twilight fireflies with yellow light and simple mating signals (male: single flash—female: "no" response delay, single-flash), each characterized and easily identified by distinctive male genitalia. These fireflies are "good species" by Morphological Concept standards, but we ask, if certain species combinations never occur together, if their geographic ranges do not overlap so that we can observe that they remain independent populations, are we justified in assuming any more about their "true" species status? This question broaches the issue of whether the "condition" of being a "natural" (real) species is something a population has unto (all by) itself, or is necessarily dependent upon its sexual/reproductive relationship to/with other such populations (correctly said: upon sexual relationships its members have with those of other such populations!).

Certainly a taxonomist would be justified in considering that a morphological species was more than mere working species if it occurred with (was sympatric with) a closely related species but there was no interbreeding. But, is this judgement for such a species only valid in respect (relationship) to this single other species? Sound silly?; think about it. Suppose distinctive morphological species never come into such contact; can morphology alone ever provide sufficient reason for considering them different natural (real) species? The species criterion in the first and simpler situation is the non-interbreeding relationship between the two sympatric populations; in the second, intrinsic features (e.g., distinctive morphology) of a population are accepted for making a nomenclatural decision. But, in this second case with no contact, real species-ness is only presumed, the decision arbitrary and untested, and unless the isolated populations are clearly, distantly related, we are only bookkeeping . . . aren't we? What would be a measure of "distantly related"? (I am not merely sandbagging here, i.e., tactically withholding "the answers" to these questions, being rhetorical for instructional purposes!)

We must return to basics for a suitable answer, like the losing football coach that on Monday holds up a ball and tells his team "this specimen is a football," we ask, to remind ourselves, what is

the fireflyer's real intent, purpose, goal, and main focus in chasing "real species of nature"? It is to discover and understand the genetic descent of populations through time and space and learn the kinds of things that happen to them in their passages through time and space. To do this we need to name recognizable working units so we can share, discuss, and store/retrieve information about them. And, we must expect to intercept different genetic lineages at different points and stages in their individual evolutions, in trivial and permanent divergences, and sometimes even convergences. Our taxonomy and species identifications must, as Barber understood, promote this. Now, with this as prelude, the following is a brief and only a partly fictional account in the history of two Division I fireflies, as a simple instructive exemplar:

A Species-Problem Case History: *P. marginellus* LeConte has an extensive distribution in eastern NA and its close relative *Photinus curtatus* Green occurs from Kansas and Oklahoma eastward, in a teardrop-shaped distribution that narrows as it reaches western New York State, whence its influence is seen all along the Mohawk Valley eastward to the Hudson River as it interbreeds with *P. marginellus* in a "hybrid swarm" (Fig. 8). Hybrid populations present an array of genitalic intermediates between the two parent species (Fig. 9). In contrast, only a few questionable hybrids have been found west of New York State, though there is broad and long-time geographic overlap with potential contact and intermingling. After the Wisconsian Glacier retreated, following its maximum 18,000 years before the present (B. P.) occurred a xerothermic (warm dry) period, and a prairie-like grassland extended from the Mississippi River eastward across midwestern states and connected with an east-west (steppe-like) corridor in (what became) New York State. Several western species of organisms moved eastward along this so-called Prairie Peninsula, and *P. curtatus* apparently was one of them, pushing eastward, further into the range of *P. marginellus*.

If we had a time-machine, and at the Glacial maximum about 18,000 B. P. observed and collected specimens of this pair in the west and in the east we would have found two morphologically distinct populations, and would appropriately have named them as "good" (working) species. On a similar trip, say at 10,000 B. P. we might have found the two together in "Illinois," northern "Indiana" and "Ohio" not interbreeding,

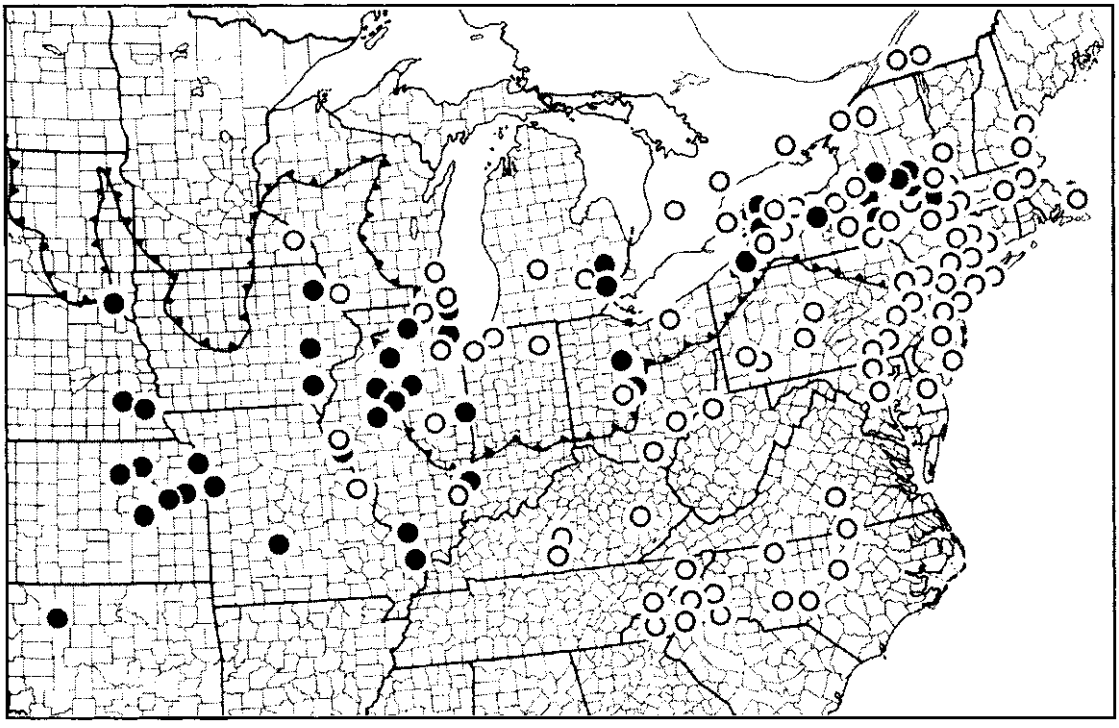

Fig. 8. Geographic distribution of *P. curtatus* Green (dots) and *P. marginellus* LeConte (circles). Where they overlap along the so-called steppe-corridor from Lake Erie east to the Hudson River occurs what could be termed a hybrid swarm, with an array of intermediates, based on the analysis of male genitalia. The toothed line shows the southernmost extent of the Wisconsian Glacier.

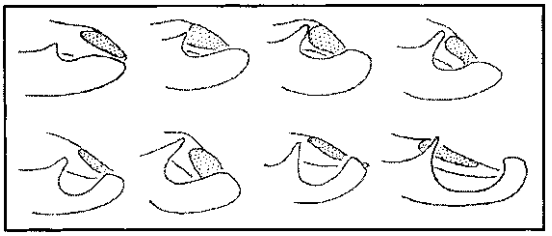

Fig. 9. Six examples of genitalic variation in the hybrid swarm of the Mohawk Valley, arranged between "pure" *P. curtatus* (upper left) and "pure" *P. marginellus* (lower right) from outside the region of sympatry. Each drawing shows a lateral lobe and the median lobe in a slightly dorso-lateral view.

and we could, with personal satisfaction, have recognized that our two working species were actually distinct evolutionary units, "real and natural" species. But, at 2,000 B. P. in apparent contradicton, we found the two hybridizing in the "Mohawk Valley." This is all reasonable, though unknowable, but at least possible. The point of this scenario for fireflyers: as we work today with living populations, we must expect to intercept firefly populations in obscure, mostly unknowable transitions, and recognize our species judiciously, with understanding and purpose, and in a manner that will disclose evolutionary questions and promote nomenclatural (bookkeeping) stability. (Can you develop another historical explanation for the data?; hint: would it help you to know where the questionable western hybrids were collected?—or how *P. marginellus* varies throughout its distribution?)

Postscript. The diurnal and lightless *P. cooki* occurs with several other Division I species, but there is no evidence that it interbreeds with any of them. Could mating interference and failed (e.g., sterile) hybridizations with close relatives with identical bioluminescent signals have been the reason for *cookii's* lantern loss and behavioral changes? Wouldn't it be neat if isolated local populations of working *P. cookii* reveal different degrees of divergence and lantern loss, and show us something of what has happened . . . is happening now? Also, note that in this Letter I have assumed that geographic isolation was the external factor responsible for the initial genetic isolation of the populations (the allopatric speciation model). This model is graphic, easily generating pictures in the mind, and is simple to grasp, but there is an alternative though too little is known about firefly biology to appreciate how it might work. This is the sympatric (same locality) speciation model as developed by Guy Bush from his studies on fruit fly host-plant preference. Perhaps a theoretical model could be invented for *Photuris* fireflies, say involving female aggressive mimicry and/or male flash pattern mimicry(?).

The bottom line of this section, in which I tried to bring the always-assumed, seemingly-obvious reality of firefly species into question and doubt, is spelled out in the next section where I will sketch a "work view with reminders" for seeking the reality of fireflies in nature.

Constructing a conceptual framework for chasing "real fireflies". According to a recent analysis there are 22 distinctively different nominal Species Concepts used in biology today (see R. L. Mayden, in Claridge et al. 1997). Table 1 lists several of these, and also some from the past that may now be extinct, and some I have invented here, but please, only for the moment! Though the term "concept" is confusing, because it should refer to a mental image or construct in the mind, it slipped into usage for non-formal, verbal definitions of species decades ago. With this usage a person may have more than one concept simultaneously—a working one for weekdays and a thinking one for Sundays perhaps! Concepts range between the operational, used for getting on with the sorting and naming bench work (e.g., the Morphological Species Concept), the philosophical, which address the learned/reflective nature of things (e.g., the Essentialist Species Concept, from Plato's supernatural world view), and the theoretical, an outline of what logically seems to be the hidden reality, the mystery of species, if we could only get to the bottom and crux of it scientifically, with observation and experimentation (the BSC in part).

A useful mental construct for fireflyers combines two elements: (A) a more inclusive alternative to the Morphological Concept, with (B) a theoretical stand-in for the BSC, made from fragments of Concepts listed in Table 1. The A part is self explanatory, and we use it when we inspect, organize, and describe our specimens, certainly with some thought to apparent genetic relationships, and make decisions about how the specimens and the populations they represent should be formally recognized or informally noted in the taxonomic literature. Part B is the theoretical and more difficult part of our mental construct, where we address the question raised at the beginning, "what, then, is the real nature of the species-like entities that we have observed?" I will develop these two notions, A and B:

(A) Working species recognition, characterization, and formal description can involve a variety of phenotypic attributes in addition to gross morphology, and were fireflyers to put a "Concept" name on it, we could call it the "Omnispective Concept," from the view that alpha taxonomy should be all-viewing in its search for species. According to the critical "Concept" analysis referred to, such a view is the equivalent of the Taxonomic Species Concept of botanists. Fireflyers in North America use a variety of characters including genitalia morphology, sclerite coloration, setal

patterns, and luminescent signal patterns, but eventually other features, perhaps cuticular hydrocarbons, chromosome structure, and DNA will be used too.

(B) We must abridge the original BSC to construct a more genetically correct, heuristic, and user friendly theoretical concept. There are two parts of the BSC I want to "mend": First, the BSC directed attention to gene pools and populations, and embodied (genetically illogical) group selection, failing to recognize that it was the competitively breeding individuals of these populations that were the actual operative (selected) elements of species. There are a couple of images (models) that may be helpful guides and reminders for applying the necessary, so-called "selection thinking" scalpel (the hallmark of sociobiology and behavioral ecology). Here are two mnemonic images that can be used as crutches to remind us that a species must first and foremost be presumed to be nothing more than the aggregate of its participating free agents.—*The Firefly Tree Image*: This model finds an analogy (homology?) with the firefly trees in Thailand, New Guinea, Malaysia, and other exotic places in this part of the world, where multitudes of male fireflies gather in various broad-leaved trees, often along waterways, and some species emit their flashes in precise and splendiferous rhythmic synchrony. These pulsing treefulls were long explained solely as beacons that benefited other members of their species, with no analytical thought to how each individual firefly that burned his time and luciferin flashing for others was promoting the perpetuation of his own genes, the ones responsible for his behavior and chemistry. Truly, couldn't you just as easily make a genetic argument that the "beacon tree" phenomenon evolved for the navigation of Thai boatman? Today most students can appreciate that the logical genetic explanation is that each male is interacting, even cooperating with near-neighbors to maintain the species-identifying rhythm of his local spot on the tree (Figs. 10-12), and when an attracted female lands within his group, he will compete with his former cooperators now-become rivals until she chooses one (maybe more?) of them, or flies off to inspect males at other hot-spots on the tree. A pulsing treeful, a conspicuous reality in nature, nevertheless is the net result of interconnecting selfish cooperations over its foliage, and though it is real (i.e., not an illusion) and spectacular, no evidence has yet come to light that it is more than an *epiphenomenon* like a "cloud" of gnats shaped like a cedar tree or an airborne fish. The object lesson: view a species as the (mere) consequence of sexually selfish individuals of similar phenotypes and genotypes seeking mates and breeding with others that fall within each individual's window of acceptability; do this until empirical evidence or a reasonable genetic model suggests otherwise.

Fig. 10. An individual male *Pteroptyx valida* E. Olivier firefly in a Thailand nipa-palm swamp with his lantern aimed outward, illustrating the true essence of a firefly tree. Males are surrounded by rivals competing for fertilizations. His genes provided the instructions during development for the neural and structural mechanisms that make it possible for him to aim his lantern outward and flash attractively in the direction of approaching potential mates, as he burns luciferin that his own genes have manufactured correctly, in a reaction catalyzed by enzyme products (luciferase) of another of his time-tested genes. His flashing may also warn rivals to keep clear of his private landing space—perhaps it is the leaf in front of him—for incoming females, to which he will deliver copies of these genes.

Ecological Niche Image: This model adds a dimension to the well-known ecological niche concept. Sometimes ecologists speak of the aggregate (totality) of requirements for bodily (somatic) survival of a species as its ecological niche. In their species' niche is where individuals find food, places to nest, and so on. Likewise, a mate can be viewed as a niche necessity/dimension for genetic survival. A female has eggs, and must join with a cooperator, an injector of sperm. She needs a cooperator with DNA and accessories that are within certain restricted limits of variation, two of which we oversimplify and abbreviate (to our own confusion) as "of the opposite sex." and "of the same species." When next you see male fireflies cruising over an old-field seeking females, see lone-operators pursuing a limited necessity in their reproduction niche, surrounded by blood-rivals and the worst kind of enemies, looking for the same thing. The species to which they belong is merely the aggregate of all of the selfish individuals that seek cooperators in the same reproductive niche.

The second part of the BSC I want to "adjust" for fireflyer purposes is the view of the isolated but similar populations that the BSC includes in its sometimes omitted but nevertheless implicit phrase "potentially interbreeding populations." This is ok theory, for even if we cannot easily test it we can at least know that there often will be

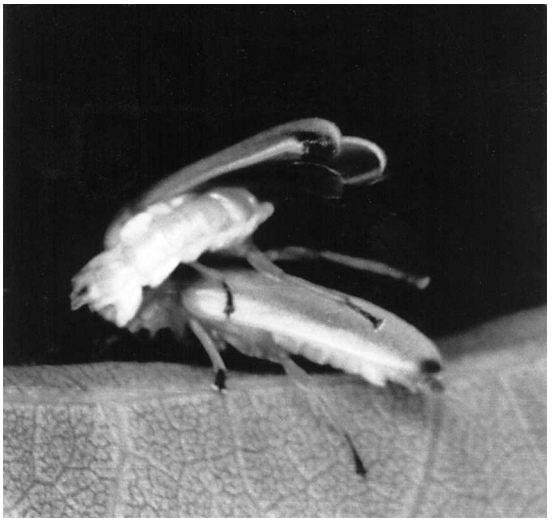

Fig. 11. A *P. valida* male atop a female, his back toward the camera and tail bent around in an "in your face" courtship, perhaps giving her a chemical message concerning his individual qualifications as a genetic cooperator in reproduction.

some isolated local populations that qualify. But, we want to emphasize our uncertainties about such populations, to promote suspicion, inspection, and analysis of them. We lump them all for bookkeeping convenience and out of ignorance, in the Omnispective (working species) part of our program, but we need to be reminded to think of such populations as an astronomer views other points of light in his expanding universe, as always moving away from his reference point where he sets up his telescope (the first local population we study), unless there is evidence to the contrary. There is a "definition" by Hall and Clements (1923) that makes this point very clearly, and I modify it only slightly here:—<A species is phylogenetic stock (breeding population), sprung from and related to similar stocks, and itself undergoing modification into a number of diverging branches. Because they have recently come from the same stock, these branches are more nearly related to each other than they are to those of any other species, and they represent a definite phylogenetic unit, the species, *and at the same time they mark its further differentiation.*>

Fig. 12. A *P. valida* male (left) has maneuvered his elytral tips under those of the female and his abdomen tip under her abdomen, these structures forming a clamp that hold her for sperm injection and probably against separation and genital intrusions by other males. See Wing et al. (1983) for details.

As a "Concept" term for this "Part B," if there must be one, there is a useful analogy from the genetics of nuclear and extended families, the latter being relatives of decreasing genetic affinity as they have departed from each other and their ancestral common connection—an "Extended-r Species Concept"—analogizing from kin considerations of sociobiology (recall, siblings and parent-offspring generally have an r of 0.5, first cousins, 0.25, and so on). Populations tentatively included under this concept would initially be those identified in the Omnispective Concept, but they would remain under suspicion until research gave reason to view them differently. Some isolated local populations we especially want to follow, like the uncle from the down the road that moves to California to pan gold and is never heard from again, they may evolve off in a new direction; another may start to break away, remain in limbo for a while, then move back, regain connections, and remain become part of the Extended-r species network. (note that this imagery merely analogizes non-genetic social connections)

A patch-work synthesis for an Extended-r notion would incorporate fragments from the Biological, Nominalist, Recognition, and Evolutionary Species Concepts (Table 1), focusing on competitive individuals, the mate-recognizing-choosing fireflies making up the populations, and seeing back about 18,000 years to the Wisconsian Glacier, because this amazing mountain range of ice and out-flowing frigid air will have had a significant influence on North America's climate and ecology, and some firefly populations today can be expected to yet show evidence of its larger-than-life, continental presence.

Now, fuse the Omnispective and Extended-r Concepts into a single mental construct—call it the "Ferris, Hall, Clements, and Barber's little-c Species (c)oncept" if you wish (the FHCBc!; Table 1, no. 26), because together these men combine ideas and practices we want to be certain to adopt: the first one emphasized species as aggre-

gates of individuals; the next two had a keen perception of populations (stocks) in nature in space and time; and the last was an omnispective firefly, careful in his field observations (and provided good voucher specimens), and theoretically aware, and he exercised farsighted yet conservative judgement in his use of zoological nomenclature—and was an intellectual and entomological inspiration to those who would next chase firefly species in field and lab, and he did it without electronic recording devices, a computer, or the approval of his politically sensitive bosses—who were never his superiors.

Acknowledgments

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CONSUMPTION AND OVIPOSITION RATES OF SIX PHYTOSEIID SPECIES FEEDING ON EGGS OF THE CASSAVA GREEN MITE *MONONYCHELLUS TANAJOA* (ACARI: TETRANYCHIDAE)

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ABSTRACT

In Africa the cassava green mite, *Mononychellus tanajoa,* is an important pest of cassava, *Manihot esculenta*. Phytoseiid mites from South America are being evaluated as potential biological control agents of this alien pest. We evaluated six phytoseiid (Acari: Phytoseiidae) species, collected in South America: *Euseius ho*, *Typhlodromalus aripo*, *Typhlodromalus tenuiscutus*, *Neoseiulus californicus*, *Neoseiulus idaeus*, and *Galendromus annectens*. Their effectiveness as a biological control agent was estimated by measuring rates of prey consumption and oviposition in relation to prey density under optimal laboratory conditions. Prey consumption by *E. ho*, *T. aripo* and *T. tenuiscutus* continued increasing linearly up to the highest density of prey evaluated (200 prey eggs) for a maximum of 93, 101 and 59 prey in 24 h. For the other predators, prey consumption levelled off at prey density of 30 or more. Maximum daily consumption was 40, 35 and 18 eggs for *N. californicus*, *N. idaeus* and *G. annectens*, respectively. Except for *T. tenuiscutus*, daily fecundity appeared to reach a plateau at the prey densities tested. Higher maximum daily oviposition rates were registered for *T. tenuiscutus*, *N. californicus*, *N. idaeus* and *G. annectens*, ovipositing 3.9, 3.6, 2.9 and 2.8 eggs, respectively; whereas *E. ho* and *T. aripo* oviposited a maximum of 2.2 and 1.4 eggs in 24 h, respectively. The ratio between oviposition and prey consumption rates was generally higher for *G. annectens*, *N. californicus* and *N. idaeus*. The high prey consumption rate of *E. ho*, *T. aripo* and *T. tenuiscutus* suggests that these species are the best agents in regard to the attack of pest eggs. The high fecundity rate and oviposition/consumption ratio especially at low prey densities (30 prey eggs) of *N. californicus*, *N. idaeus* and *G. annectens* suggests that these species may be able to multiply well at low prey densities.

Key Words: *Euseius ho*, *Typhlodromalus aripo*, *Typhlodromalus tenuiscutus*, *Neoseiulus californicus*, *Neoseiulus idaeus*, *Galendromus annectens*, biological control

RESUMEN

En Africa el ácaro verde de la yuca, *Mononychellus tanajoa*, es una plaga importante de la yuca *Manihot esculenta*. Se están evaluando ácaros fitoseidos de Sur América como agentes potenciales de control biológico de esta plaga. Se evaluarón seis especies de fitoseidos (Acari: Phytoseiidae), colectadas en Sur América: *Typhlodromalus aripo*, *Typhlodromalus tenuiscutus*, *Neoseiulus californicus*, *Neoseiulus idaeus*, y *Galendromus annectens*. Su efectividad como agentes de control biológico se estimó midiendo la tasa de consumo de presa y oviposición en relación con la densidad de presa bajo condiciones óptimas de laboratorio. El consumo de presa por *E. ho*, *T. aripo* y *T. tenuiscutus* continuó incrementando linealmente a la densidad de presa más alta evaluada (200 huevos de la presa) a un máximo de 93, 101 y 59 presas en 24 horas. Para los otros de predadores, el consumo de presa alcanzó un màximo a la densidad de 30 o màs. El consumo diario máximo fue 40, 35 y 18 huevos para *N. californicus*, *N. idaeus* y *G. annectens*, respectivamente. Con excepción de *T. tenuiscutus*, la fecundidad diaria pareció alcanzar una meseta a las densidades de presa probadas. La oviposición diaria máxima más alta se registró para *T. tenuiscutus*, *N. californicus*, *N. idaeus* y *G. annectens*, ovipositando 3.9, 3.6, 2.9 y 2.8 huevos, respectivamente; mientras que *E. ho* y *T. aripo* ovipositaron un máximo de 2.2 y 1.4 huevos en 24 horas, respectivamente. La relación entre la oviposición y la tasa de consumo de presa fue más alta generalmente para *G. annectens*, *N. californicus* y *N. idaeus*. La tasa alta de consumo de presa de *E. ho*, *T. aripo* y *T. tenuiscutus* sugiere que estas especies son los mejores agentes para atacar los huevos de la presa. La tasa de fecundidad alta y el ratio oviposición/consumo especialmente a bajas densidades de la presa (30 huevos de la presa) de *N. californicus*, *N. idaeus* y *G. annectens* sugiere que estas especies pueden ser capaces de multiplicarse bien a densidades bajas de la presa.

The cassava green mite, *Mononychellus tanajoa* Bondar (Acari: Tetranychidae) is an important pest of cassava, *Manihot esculenta* Crantz (Euphorbiaceae) in dry regions of South America (Farias et al. 1982; Byrne et al. 1983; Veiga 1985). In the early 1970s, this mite species was accidentally introduced into Africa, spreading rapidly across the Subsaharan zone in the absence of its natural enemies (Yaninek & Herren 1988) and causing severe yield losses (Yaninek et al. 1990; Bonato et al. 1994). Classical biological control (i.e., through the use of introduced natural enemies) was developed to control *M. tanajoa* in Africa (Mégevand et al. 1987, Yaninek & Herren 1988). Among ten phytoseiid species released in Africa from 1984 to 1993 three of them are now well established but only one is spreading well and affecting the green mite population (Bellotti et al. 1999). It is therefore necessary to release more phytoseiid species or strains from South America. Meanwhile, The International Center for Tropical Agriculture began exploration and evaluation of phytoseiids from coastal Colombia and Ecuador, which has a dry climate similar to target areas in Africa.

Two factors that affect the success of phytoseiid mites in controlling their mite prey are their functional and numerical responses (Sabelis 1985). These factors must be considered when the importance of the phytoseiid species is to be evaluated. First described by Solomon (1949), the functional and numerical responses were defined as follows. The functional response refers to the change in the number of prey consumed per unit time in relation to the change in prey density. The numerical response refers to the increase in numbers of predators in response to increases in prey density and is thus positively correlated with the ovipositional rate. A good candidate for controlling mite populations should have both increased prey consumption and oviposition rates in proportion to the available prey density. Furthermore, Sabelis (1985) theorized that the most efficient (i.e., most co-adapted) predator should be the most efficient at converting their prey into progeny. The ratio between the oviposition and the consumption rates reflects in a straightforward way this theorical efficiency.

The aim of this study was to evaluate, under optimal laboratory conditions, prey consumption and oviposition rates of six phytoseiid predatory mite species in relation to prey density. The objective was to estimate the maximum number of prey consumed and the maximum number of eggs laid as well as their maximum efficiency at converting food energy into egg production of six phytoseiid species.

Materials and Methods

Six phytoseiid mite species (Acari: Phytoseiidae) were collected from coastal areas of Colombia and Ecuador (Table 1). All predatory mite species were maintained in the laboratory on cassava leaves infested by *M. tanajoa* at 25 ± 1°C, 75 ± 5% RH and 12-h photoperiod. Immediately after emergence, individual females were placed with a male in the predation arena, described below, with an uncontrolled egg prey density (generally > 100) for 3 days. Gravid female predators from the predation arenas were then used for the experiments.

For several phytoseiid species, females consume more eggs than mobile stages of their prey (Sabelis 1985). This was also observed with the species used in this study (M. E. Cuellar, unpublished data). Moreover, egg prey is easier to manipulate and control than mobile stages. Consequently, subsequent studies were done with eggs of the prey.

M. tanajoa, the prey for the phytoseiid species, were reared on 2-month-old cassava plants, var. CMC-40, in a greenhouse under natural conditions of temperature and relative humidity and 12-h photoperiod in Palmira, Colombia.

All experiments were conducted under laboratory conditions at 25 ± 1°C, 75 ± 5% RH and 12-h photoperiod [optimal conditions to rear all phytoseiid species studied in laboratory (M. E. Cuellar, unpubl. data)]. The experiments were performed on 3.14 cm^2 greenhouse-collected cas-

Table 1. Origin of six Phytoseiid mite species used in the experiments and collected from different areas of South America.

Species	Country	Region	Location	Altitude (m)	Collection Date
Neoseiulus idaeus Denmark & Muma	Colombia	Guajira	Fonseca	180	2-97
Typhlodromalus aripo De León	Colombia	Magdalena	Pivijay	3	6-97
Galendromus annectens De León	Ecuador	Manabí	Crucita	—	12-95
Neoseiulus californicus McGregor	Ecuador	Manabí	Portoviejo	50	11-94
Typhlodromalus tenuiscutus McMurtry & Moraes	Ecuador	Manabí	Puerto Cayo	40	12-95
Euseius ho De León	Ecuador	Manabí	Rocafuerte	16	12-95

sava leaf discs of var. CMC-40, containing controlled egg densities of *M. tanajoa*. The leaf disc floated abaxially on water-saturated filter paper in plastic dishes (diam., 2 cm, height, 1.5 cm). Individual predatory mite females were placed on the leaf discs, and the predation arena was sealed with transparent plastic wrap.

The number of egg prey consumed per predatory mite female was counted at 24 hours. The same predatory mite female was then transferred to a new predation arena with the same egg density of prey as on previous day, and the number of eggs laid by the predatory female was counted after 24 hours. For each predator species, 14 to 18 predatory mite females were used at each egg prey density.

To obtain different egg densities, gravid *M. tanajoa* females were placed on cassava leaves and left to oviposit until the required egg density was obtained. The following egg densities were tested: 1, 3, 7, 15, 30, 105 or 200 eggs per leaf disc.

Statistical tests were performed with Statview software (Abacus Concept, USA). For two-way analyses of variance (2-way ANOVA), the factors "prey density" and "phytoseiid species" were considered as fixed factors. Homogeneity of variance and data normality were examined by the F-test and Kolmogorov-Smirnov method, respectively, before running the ANOVA. Only the number of eggs consumed was normalized by log (X + 1) transformation. The Fisher's PLSD (Protected Least Significant Difference) test following the ANOVA was used to compare means post-hoc.

Results

Prey density had a significant influence on the number of eggs consumed regardless of the phytoseiid species [result of 2-way ANOVA: F = 1177.7, df = (6, 616), $P < 0.05$ for the factor "prey density"]. There was a general increase in egg consumption with increasing prey density (Table 2). This indicated that all predator species responded functionally to *M. tanajoa* egg density and thus curves of functional responses can be plotted (Fig. 1). Prey consumption by *E. ho*, *T. aripo* and *T. tenuiscutus* continued increasing up to the highest density of prey evaluated (200 prey eggs per leaf disc). In fact, linear regression coefficients (r^2) between consumption and prey density were high for these species, about 0.99, 0.94 and 0.89, respectively. Furthermore, they presented the highest consumption rates, consuming a maximum of 93, 101 and 59 prey in 24 h, respectively. In contrast, lowest correlations were found for *N. californicus*, *N. idaeus* and *G. annectens* (linear regression coefficients: r^2= 0.79, 0.32 and 0.26 respectively). Nevertheless, at lowest prey densities (≤30 prey eggs per leaf disc), high correlations were also obtained (linear regression coefficient: r^2 = 0.94 to 0.99). This indicated that prey consumption by these species increased linearly up to 30 prey eggs offered and then leveled off at a plateau (Fig. 1). Consequently, they exhibited lower consumptions, consuming a maximum of 40, 35 and 18 eggs in 24 h, respectively.

Prey density also had a significant influence on the number of eggs laid by all phytoseiid species [result of 2-way ANOVA: F = 601.6, df = (6, 614), $P < 0.05$ for the factor "prey density"]. There was a general increase in eggs oviposited by female predator with increasing prey density, regardless of the phytoseiid species (Table 2). Nevertheless, little increase was generally noted at the highest densities evaluated, so daily fecundity appeared to reach a plateau for all species. Highest maximum oviposition rates were registered for *T. tenuiscutus*, *N. californicus*, *N. idaeus* and *G. annectens*, ovipositing a maximum of 3.9, 3.6, 2.9 and 2.8 eggs in 24 h; whereas *E. ho* and *T. aripo* oviposited no more than 2.2 and 1.4 eggs in 24 h, respectively.

The number of eggs laid per prey consumed was calculated (i.e. mean number of eggs oviposited/mean number of prey eggs consumed), and presented in Table 2. As mentioned above, this ratio reflects in a straightforward way the efficiency of a predator at converting their prey into progeny. In general highest ratios were obtained for *G. annectens, N. californicus* and *N. idaeus* showing a maximum of 35.6, 14.5 and 12.0, respectively, suggesting that these species presented highest efficiency at converting prey into progeny. In contrast, lowest ratios were generally registered for *T. aripo*, *T. tenuiscutus* and *E. ho* showing a maximum of 6.7, 9.9 and 11.6, respectively, indicating that these species were the least efficient. The ratio at the first density for *T. aripo* was not considered because this level was obtained only one time for this species and at the lowest prey density. Thus this value appeared to be aberrant.

Discussion

All predator species studied responded functionally to *M. tanajoa* egg density (Fig. 1). Holling (1959) proposed three types of functional response curves: Type 1, a linear rise to a plateau; Type 2, a curvilinear rise to an asymptote; and Type 3, a sigmoid curve rising to an asymptote. These curves, which have been extensively used in predator-prey interactions, are used to evaluate the effectiveness of a predator [see Sabelis (1985) for review]. At lowest prey densities (≤30 prey eggs per leaf disc), curves fitted well to a typical Holling Type-1 functional response for all phytoseiid species. Nevertheless, at higher densities, a flat response was clearly observed and can be regarded as a "plateau" for *N. californicus*, *N. idaeus* and *G. annectens.*

Various factors influence the plateau level of the functional response curve [see Sabelis (1985)

TABLE 2. INFLUENCE OF SEVEN LEVELS OF EGG PREY AVAILABILITY ON THE NUMBER OF EGGS CONSUMED AND NUMBER OF EGGS LAID PER PREDATOR (MEANS[1] + SE) IN 24 H BY FEMALES OF SIX PHYTOSEIID SPECIES AND ON EGGS LAID/PREY CONSUMED RATIO.

Species	Egg prey densities	Eggs consumed	Eggs laid	Ratio (×100)
Euseius ho	1	0.93 ± 0.07 a	0	0
	3	3.00	0.23 ± 0.12 a	7.8
	7	6.30 ± 0.34 b	0.73 ± 0.12 ab	11.6
	15	10.90 ± 0.70 c	1.25 ± 0.21 bc	11.5
	30	23.93 ± 1.30 d	1.60 ± 0.23 c	6.7
	105	52.80 ± 5.73 e	2.23 ± 0.25 d	4.2
	200	93.40 ± 9.84 f	2.07 ± 0.30 cd	2.2
Typhlodromalus aripo	1	0.93 ± 0.07 a	0.30 ± 0.12 a	32.2
	3	2.90 ± 0.08 b	0.20 ± 0.10 a	6.7
	7	6.83 ± 0.12 c	0.40 ± 0.12 a	5.8
	15	14.94 ± 0.06 d	0.62 ± 0.12 a	4.1
	30	28.60 ± 0.40 e	1.30 ± 0.13 b	4.5
	105	81.30 ± 3.40 f	1.22 ± 0.13 b	1.5
	200	101.31 ± 7.60 g	1.40 ± 0.20 b	1.4
Typhlodromalus tenuiscutus	1	0. 91 ± 0.09 a	0.09 ± 0.09 a	9.9
	3	3.00	0	0
	7	6.85 ± 0.11 b	0.30 ± 0.10 *a*	4.4
	15	14.53 ± 0.24 c	1.13 ± 0.21 b	7.8
	30	26.12 ± 1.80 d	2.40 ± 0.40 c	9.2
	105	48.22 ± 4.60 e	2.41 ± 0.30 c	5.0
	200	59.20 ± 5.90 f	3.93 ± 0.21 d	6.6
Neoseiulus californicus	1	1. 00	0	0
	3	3.00	0.07 ± 0.07 a	2.3
	7	6.90 ± 1.12 *a*	1.00 ± 0.09 b	14.5
	15	14.50 ± 0.35 b	1.90 ± 0.30 c	13.1
	30	24.80 ± 1.10 c	3.13 ± 0.32 d	12.6
	105	25.00 ± 1.60 c	3.10 ± 0.30 d	12.4
	200	39.72 ± 5.30 d	3.60 ± 0.20 d	9.1
Neoseiulus idaeus	1	0.92 ± 0.08 a	0	0
	3	3.00	0.25 ± 0.14 a	8.3
	7	6.73 ± 0.15 b	0.60 ± 0.13 a	8.9
	15	12.93 ± 0.93 c	1.40 ± 0.30 b	10.8
	30	24.53 ± 1.20 d	2.94 ± 0.22 d	12.0
	105	34.73 ± 3.61 e	2.90 ± 0.35 d	8.3
	200	18.60 ± 1.61 f	2.12 ± 0.15 c	11.4
Galendromus annectens	1	1. 00	0	0
	3	2.53 ± 0.30 a	0.90 ± 0.20 a	35.6
	7	6.20 ± 0.50 b	1.80 ± 0.20 b	29.0
	15	11.31 ± 0.90 c	2.31 ± 0.22 cd	20.4
	30	15.53 ± 1.40 d	2.80 ± 0.14 d	18.0
	105	18.10 ± 3.21 d	2.70 ± 0.20 cd	14.9
	200	11.50 ± 1.95 c	2.23 ± 0.20 bc	19.4

[1]Means followed by different letters are significantly different at 5% level using Fisher's PLDS test following the ANOVA (when means or SE = 0, no statistical test can be performed then no letter was given).

for review]. For example, it is well known that the plateau level depends to a major extent on the prey stage supplied and the age of the predator. In this study, the prey stage and the age of female predator were held constant. The single factor varying in the experiments was the phytoseiid species. Therefore, the differences in the plateau level of curve are mainly a consequence of differences in the phytoseiid species. The fact that the curves do not rise clearly to a plateau for *E. ho*,

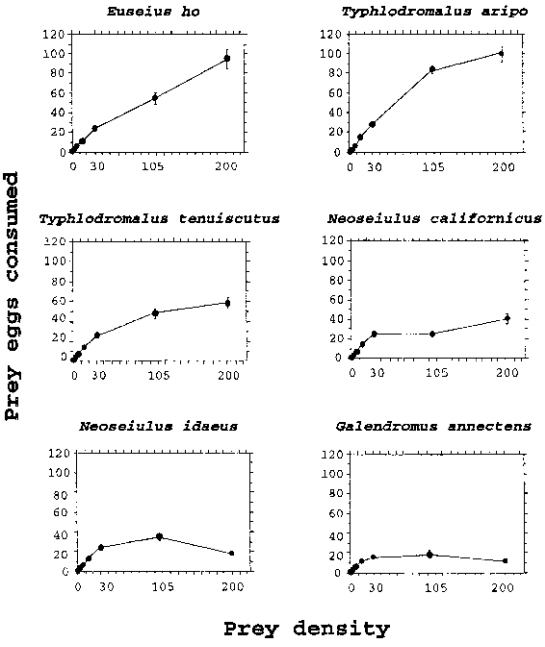

Fig. 1. Functional response of six phytoseiid species to increases in density of *M. tanajoa* eggs (curves were plotted with means ± SE).

T. aripo and *T. tenuiscutus* (Fig. 1) indicates that these species exhibit higher consumption in the range of high prey densities consuming a maximum of 93, 101 and 59 preys in 24 h, respectively. In contrast, *N. californicus*, *N. idaeus* and *G. annectens*, whose curves rose more clearly to a plateau at the density 30, have a low consumption capacity among the high egg densities tested, consuming no more than 40, 35 and 18 eggs in 24 h, respectively. These results suggested that when the prey population is high, *E. ho*, *T. aripo* and *T. tenuiscutus* will be more efficient in controlling *M. tanajoa*.

Nevertheless, among these phytoseiid species, *E. ho* and *T. aripo* had lower maximum daily oviposition rates than *T. tenuiscutus*, *N. californicus*, *N. idaeus* and *G. annectens*. Similar to Ball's (1980) results obtained on four phytoseiid species, the high consumption rate capacities of predators were not reflected in proportionately high reproductive rates. Furthermore, the differences in egg production obtained in our study seems not be correlated with the relative sizes of the predator species or their eggs but more due to the phytoseiid species characteristic. For example, *E. ho* and *G. annectens* had similar body and egg sizes (288 and 189.6 µm, 252 and 175.2 µm body and egg sizes, respectively) but different egg production. As evoked by Eveleigh & Chant (1981) for *Phytoseiulus persimilis* Athias-Henriot (Acari: Phytoseiidae) eating protonymphs of *Tetranychus pacificus* McGregor (Acari: Tetranychidae), the differences in oviposition rates in our study are more likely due to the fact some species such as *G. annectens* are more efficient in converting food energy into egg production. In fact, highest oviposition/consumption ratios were obtained for this species, regardless of the prey density (Table 2). In contrast, lowest ratios were obtained for *T. aripo*, suggesting that this species is the least efficient in converting food energy into egg production.

Daily fecundity rates at the prey density 30 (the density where functional response curves reached a plateau) were higher for *N. californicus*, *N. idaeus* and *G. annectens*. In fact, it was at 3.1, 2.9 and 2.8 eggs in 24 h for *N. californicus*, *N. idaeus* and *G. annectens*, respectively; whereas it was only at 1.6, 1.3 and 2.4 eggs in 24 h for *E. ho*, *T. aripo* and *T. tenuiscutus*, respectively. This suggests that *N. californicus*, *N. idaeus* and *G. annectens* may be able to multiply well at low prey densities. Furthermore, by their higher oviposition/consumption ratios at this prey density, these phytoseiid species converted prey to predator progeny efficiently at the lower levels of prey eggs availability. As emphasized by Friese & Gilstrap (1982) for three other phytoseiid species, predator species which require fewer prey should be better able to survive as an effective searching population at low prey density and therefore better able to maintain the population at low prey density.

In conclusion, it appeared that among the predatory species studied, when *M. tanajoa* population increases markedly or during at outbreak, the use of *E. ho*, *T. aripo* or *T. tenuiscutus* phytoseiid species should be recommended. In contrast, when the mite population is low on cassava, the use of *N. californicus*, *N. idaeus* or *G. annectens* should be better because they may be able to multiply well. The fact that all phytoseiid strains or populations used in this study came from semi-arid areas of South America suggests that they may establish well in semi-arid areas of Africa to help control cassava green mite populations.

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NUMERICAL RESPONSE OF *OLLA V-NIGRUM* (COLEOPTERA: COCCINELLIDAE) TO INFESTATIONS OF ASIAN CITRUS PSYLLID, (HEMIPTERA: PSYLLIDAE) IN FLORIDA

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ABSTRACT

Data are presented on the relative abundance of the coccinellid *Olla v-nigrum* (Mulsant) in Florida citrus, before and after invasion by the Asian citrus psyllid, *Diaphorina citri* Kuwayama. Adults and larvae of *O. v-nigrum* were observed preying on immature psyllids throughout their range in Florida. Immature psyllids were eliminated by predation from many flushed citrus terminals that exhibited damage symptoms; pupae of *O. v-nigrum* and *Harmonia axyridis* Pallas were recovered from adjacent leaves. *Olla v-nigrum*, a relatively rare species before the invasion by *D. citri*, is now a dominant species throughout Florida in citrus groves where the psyllid is present, but remains rare in regions where *D. citri* is absent. The strong numerical response of this native ladybeetle to *D. citri* populations indicates that it is assuming a key role in biological control of the psyllid.

Key Words: abundance, biological control, coccinellids, *Diaphorina citri*, *Harmonia axyridis*, *Olla v-nigrum*

RESUMEN

Se presentan datos sobre la abundancia relativa del coccinélido *Olla v-nigrum* (Mulsant) en cítricos en la Florida, antes y después de la invasión del psílido Asiático, *Diphorina citri* Kuwayama. Adultos y larvas de *Olla v-nigrum* fueron observados alimentándose de las formas inmaduras del psílido a través de la Florida. Se observaron muchos brotes terminales en los cítrcos con daños del psílido, pero estos fueron eliminados por depredación; pupas de *O. v-nigrum* y *Harmonia axyridis* Pallas fueron coleccionadas en hojas adyacentes. *Olla v-nigrum*, una especie relativamente escasa antes de la invasión de *D. citri*, ahora es dominante en los cítricos de Florida donde está presente el psílido, pero sigue siendo escasa donde *D. citri* está ausente. La fuerte respuesta numérica de este coccinélido en comparación con las poblaciones de *D. citri* indica que está asumiendo un papel clave en el control biológico del psílido.

The Asian citrus psyllid, *Diaphorina citri* Kuwayama, is the primary vector of citrus greening disease in Asia (Catling 1970) and was first reported in Stuart, Florida in 1998 (Halbert et al. 1998). Originally discovered on hedges of Jasmine Orange, *Murraya paniculata* (L.) Jack, the psyllid spread to infest commercial citrus plantings throughout St. Lucie, and Indian River counties, south to Miami-Dade, and eastward through Okeechobee in 1998. As of March 2001, it can be found throughout southwestern Florida (Lee, Collier, and Hendry Counties) and northward along the central ridge as far as southern Polk County (Alturas and Lake Wales). A relatively recent report on the range of *D. citri* in Florida can be found in Halbert et al. (2000). Efforts have been under way to release and establish two exotic parasitoids, *Tamarixia radiata* (Waterston) and *Diaphorencyrtus aligarhensis* (Shafee, Alam and Agaral) (Hoy & Nguyen 2001) that are reportedly specific for *D. citri* (Tang 1990). This paper reports observations on a native coccinellid species, *Olla v-nigrum* (Mulsant) (= *Olla abdominalis* (Say)), that, together with the Asian multicolored ladybeetle, *Harmonia axyridis* Pallas, can be found preying on *D. citri* throughout its range in Florida.

The ash-gray ladybeetle, *O. v-nigrum*, is an indigenous coccinellid species inhabiting arboreal habitats throughout most of the United States (Gordon 1985), Mexico (J. P. Michaud, unpublished), and through much of South America including Paraguay (Michel 1992), Argentina (Bado & Rodriguez 1997) and Brazil (Fraga et al. 1986). It occurs in light and dark forms, the dark form predominating in Florida where it can easily be mistaken for the twice-stabbed ladybeetle, *Chilocorus stigma* (Say). The latter is distinguishable from *O. v-nigrum* by its generally smaller size, a recurvature of the edge of the elytra, and the lack of a conspicuous white border along the edge of the pronotum. Although *O. v-nigrum* can be observed feeding on various aphid species (Tedders 1978, Edelson & Estes 1987) the ability of *O. v-nigrum* to develop and reproduce on these aphids has not often been examined. However, it is also renowned as a natural enemy of psyllids (Fraga et al. 1986) and can complete development on species such as *Heteropsylla cubana* Crawford that

are unsuitable food for many other generalist predators (Chazeau et al. 1991).

Although *O. v-nigrum* is attracted to colonies of *Toxoptera citricida* (Kirkaldy) and *Aphis spiraecola* Patch and will feed on them (Michaud & Browning 1999), it is known that these aphid species do not support larval development, despite the fact that viable eggs were produced by adult females fed *T. citricida* (Michaud 2000a). This inability to develop on the primary citrus aphids may partially explain why the species has been relatively rare in citrus until recently. Bado & Rodriguez (1997) reported life history data and prey preference of *O. v-nigrum* feeding on various aphid species including *Schizaphis graminum* (Rondoni), *Hyadaphis* sp., *Metopolophium dirhodum* (Walker), *Uroleucon* sp., *Brevicoryne brassicae* L.and *Myzus* sp. Chazeau et al. (1991) compiled a life table for *O. v-nigrum* feeding on *H. cubana* and concluded this psyllid was a highly suitable prey species. Developmental and behavioral aspects of *O. v-nigrum* feeding on *Psylla* sp. are described by Kato et al. (1999).

Preliminary observations in south Florida in 1999 identified various indigenous predator species attacking *D. citri*, including *O. v-nigrum*, and late instar larvae of this species collected from *D. citri* colonies pupated successfully in the laboratory and yielded viable adults (Michaud 2000b). More recent observations reveal that populations of *O. v-nigrum* have apparently exploded wherever psyllids are present in citrus. This paper reports on the increase in relative abundance of *O. v-nigrum* in apparent response to the availability of *D. citri* as a new food source.

Materials and Methods

From 1996 to 1998 the commercial citrus-growing regions of Florida were invaded by the brown citrus aphid, *Toxoptera citricida* (Kirkaldy) and, as part of a survey of predators attacking *T. citricida*, a series of observations was made on the relative abundance of coccinellid species in these regions. Flowering and flushing citrus trees are attractive to many coccinellid species. Adult beetles can be found feeding on pollen and nectar of citrus flowers in the spring. Many potential prey species, including aphids and leaf miners, attack newly expanding citrus terminals. Consequently, citrus groves were selected based on the presence of flowering and/or flushing trees and these trees were examined selectively. Relative coccinellid abundance was estimated by visual counts of adult beetles on whole trees. Observation periods ranged from 40 minutes to 2 hours at each site. Voucher specimens were collected and identified by M. Thomas, Florida Department of Agriculture and Consumer Affairs, Department of Plant Industry, Gainesville, FL, 32608. Exact observation dates for each location were as follows: Dade County (Homestead), 24-II-1997, 7-IV-1998, 13-V-1999; Collier County, 19-V-1997, 15-III-2001; Hendry County, 14-II-1998, 14-V-1998; St. Lucie County, 21-IV-1997, 9-VII-1997, 15-II-1998, 13-V-1998, 14-III-2001; Highlands County, 25-VII-1997, 21-III-1998, 21-III/2001; Polk County, 18-III-1998, 18-V-1998, 27-X-1998, 8-III-2001, 21-III-2001, 27-III-2001.

The data from years 1997 and 1998 reflect coccinellid abundance in Florida during a period when *T. citricida* and *A. spiraecola* were the primary prey available for aphidophagous coccinellids in citrus. Since 1999, population densities of both aphid species have been very low compared to levels observed in previous years, probably due to the numerical responses of predatory species such as *Cycloneda sanguinea* L. and *Harmonia axyridis* Pallas that successfully develop and reproduce on *T. citricida* (Michaud 2000a). Subsequent to the invasion of *D. citri*, I returned to many of the same groves to identify sources of mortality in psyllid colonies. In the course of these observations, data were again collected on the relative abundance of coccinellids by visual counts of adult beetles in the same manner as in previous years. The body of data collected before 1999 now form a historical reference point for the relative abundance of *O. v-nigrum* before invasion by the Asian citrus psyllid. Data on *O. v-nigrum* abundance in the presence and absence of *D. citri*, as a proportion of total coccinellids observed, were compared by means of a '2 × r' contingency table analysis (SAS Institute 1998).

Results and Discussion

The historical data on the abundance of *O. v-nigrum* relative to other coccinellids and thaose from recent observations are presented in Fig. 1. The data are representative of the four major citrus-producing regions of the state: south Florida (Dade County), southwestern Florida (Collier and Hendry Counties), the Indian River District (St. Lucie County) and the central ridge district (Highlands and Polk Counties). In all regions where psyllids are now present, *O. v-nigrum* has increased significantly as a proportion of total coccinellids (Dade County: $\chi^2 = 56.468$, 2df, $P < 0.001$; Collier County: $\chi^2 = 24.922$, 1df, $P < 0.001$; Hendry County: $\chi^2 = 15.923$, 2df, $P < 0.001$; St. Lucie County: $\chi^2 = 44.531$, 4df, $P < 0.001$; Highlands County: $\chi^2 = 80.415$, 2df, $P < 0.001$; Polk County: $\chi^2 = 116.944$, 5df, $P < 0.001$).

The data represented in Fig. 1 for Spring 2001 in Polk County were collected from a very recent psyllid infestation just south of Lake Wales. Two additional sites further north in Polk County (where *D. citri* is not yet present) were also sampled in spring 2001, one in Lake Alfred on 8-III-2001 and one in Polk City on 27-III-2001 (not shown in Fig. 1 because of graphical constraints).

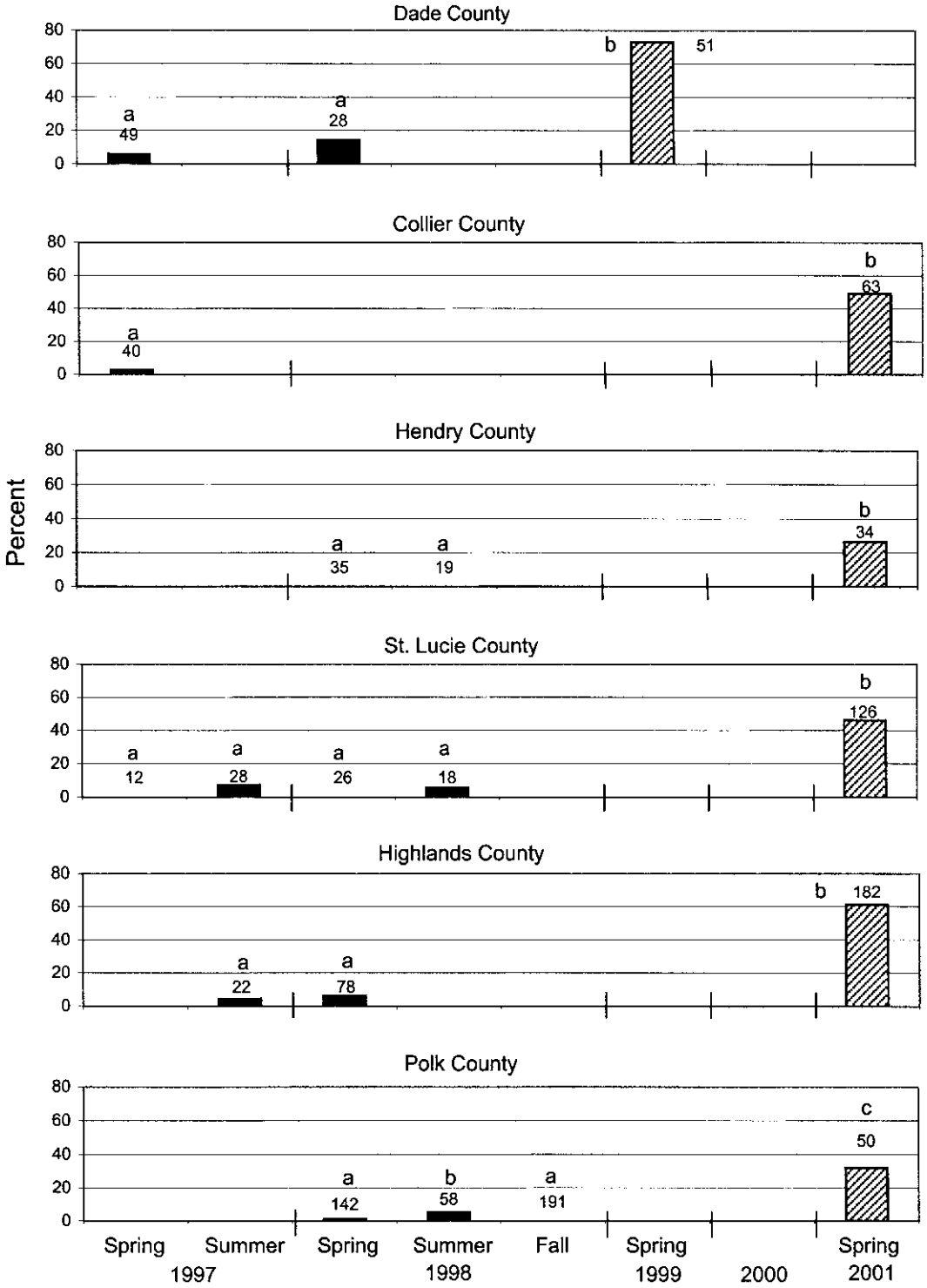

Fig. 1 Relative abundance of *O. v-nigrum* expressed as a percentage of total coccinellid adults observed on flowering and flushing citrus trees at various locations in Florida over a five year period. Solid bars: *D. citri* absent, shaded bars: *D. citri* present. Bars bearing the same letter were not significantly different in contingency table analyses within counties; all significant differences were $P < 0.001$ in a Chi-square test. Numbers represent sample sizes (n) and spaces associated with letters indicate '0' counts of *O. v-nigrum*; other spaces represent missing data. See text for exact sampling dates.

The total numbers of coccinellids observed at these sites were 131 and 75 respectively, *O. v-nigrum* comprising 3 (2.3%) and 6 (8.0%) individuals, respectively. The proportions of *O. v-nigrum* in samples at these two sites were not significantly different from one another in '2 × 2' contingency table $\chi^2 = 3.722$, 1df, $P = 0.054$, but both sites had significantly fewer *O. v-nigrum* as a proportion of total coccinellids than did the Lake Wales site ($\chi^2 = 11.915$, 1df, $P < 0.001$ and $\chi^2 = 33.998$, 1df, $P < 0.001$). Thus *O. v-nigrum* remains rare in sites where *D. citri* is not yet present, but has increased significantly in abundance at all sites where *D. citri* is present.

During the recent observations in spring 2001, larvae and adults of *O. v-nigrum* were often observed feeding on psyllid nymphs. Pupae collected from hardened leaves adjacent to extinct psyllid colonies gave rise to viable adults in the laboratory. Consumption of the adult stage by coccinellids has not yet been directly observed. Many young citrus terminals exhibited typical damage symptoms (characteristic twisting and distortion of expanding leaves) and retained residues of the waxy nymphal secretions, although no live psyllid nymphs remained. Most nymphs appeared to have been eliminated by predation from terminals with feeding damage and wax residues. Adults and larvae of *C. sanguinea* and *H. axyridis*, as well as larvae of *Ceraeochrysa* sp. and an unidentified syrphid, were other predators observed feeding on nymphs. Although the exotic parasitoid *Tamarixia radiata* is now apparently established in some of these regions (A. Chow[1] personal communication), no mummified or obviously parasitized nymphs were noticed during these observations. However, while adult psyllids were evident, immature stages were quite rare in most of the groves sampled, despite the presence of abundant new growth on some trees.

It is notable that *O. v-nigrum* has been imported to Asia from the new world as a biological control agent of psyllids, particularly for control of *H. cubana*, a pest of nitrogen-fixing trees and shrubs of the genus *Leucaena*. It was imported to Tahiti from tropical America in the 1980s where it gave good control of *H. cubana*, and subsequently to New Caledonia (Chazeau 1987a,b). Control of *H. cubana* by *O. v-nigrum* has not been as effective in New Caledonia as in Tahiti, partially because it is parasitized by *Phalacratophora quadrimaculata* Schmitz (Diptera: Phoridae) (Disney & Chazeau 1990). Another new world coccinellid, *Curinus coeruleus* Mulsant, was later released in New Caledonia to supplement the action of *O. v-nigrum* (Chazeau et al. 1992) and this species was also detected in the present survey, albeit in low numbers. Subsequently, *O. v-nigrum* was introduced to Reunion Island in 1992 (Vandeschricke et al. 1992) and in Hawaii increases in the populations of both *O. v-nigrum* and *C. coeruleus* were observed in response to invasion by *H. cubana* (Nitrogen Fixing Tree Association 1990). Although these coccinellid predators are considered generalists, they are known to express prey preferences (Dixon 2000) and have the potential to suppress pest populations as effectively as any specialist parasitoid. The ability to use alternative food sources when preferred prey are rare may actually buffer the population dynamics of a generalist species relative to the population of a specialist that inevitably crashes along with the pest population.

The response of *O. v-nigrum* to *D. citri* in Florida vividly illustrates the potential of certain native predators to respond to introduced pests. Although infestations of *D. citri* are still substantial in many groves, populations of indigenous natural enemies are still increasing and should ultimately provide good biological control of the psyllid. The situation is analogous to that of the brown citrus aphid, an invasive pest that was extremely abundant in Florida citrus for the first few years following its introduction. Although isolated outbreaks of *T. citricida* can occur when biological control is disrupted, populations are now relatively low in Florida, due largely to mortality inflicted by generalist predators, and despite the failure of any exotic parasitoid species to establish (Michaud 1999).

It could be argued that the association of abundant *O. v-nigrum* populations with *D. citri* infestations is merely circumstantial evidence and that correlation does not equal causation. However, the evidence is substantial and the trend is consistently significant, both temporally and spatially. Further work is warranted to determine the suitability of a diet of immature psyllids for the development and reproduction of *O. v-nigrum*, as well as *C. sanguinea* and *H. axyridis*. Given the apparent effect of *O. v-nigrum* on psyllid populations, any evaluation of classical biological control programs against *D. citri* must consider mortality contributed by this and other coccinellid species.

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A FURTHER CONTRIBUTION TO THE SYSTEMATICS OF THE TRIBE MEROPACHYINI (HETEROPTERA: COREIDAE: MEROPACHYINAE)

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ABSTRACT

Four new genera and three new species from Mexico, Belize, San Salvador, Honduras, Costa Rica, Brazil, Peru and Bolivia are described, illustrated and included in the tribe Meropachyini (Coreidae). *Flavius tristriatus* Kormilev is transferred to the new genus *Badilloniella*. A key to the 16 known genera of Meropachyini is given.

Key Words: Insecta, Heteroptera, Coreidae, Meropachyinae, new genera, new species, Neotropical

RESUMEN

Cuatro nuevos géneros y tres nuevas especies provenientes de México, Belize, San Salvador, Honduras, Costa Rica, Brasil, Peru y Bolivia son descritos, ilustrados, he incluidos en la tribu Meropachyini (Coreidae). *Flavius tristriatus* Kormilev es transferido a un nuevo género, *Badilloniella*, con la combinación *Badilloniella tristriatus* (Kormilev). Se incluye una clave para separar los 16 géneros conocidos de la tribu Meropachyini.

The knowledge of the tribe Meropachyini has been summarized recently by Brailovsky (1999), and Brailovsky and Luna (2000). Since then the senior author has accumulated further material of this tribe and from it has been compiled the present paper which includes the description of four new genera, and three new species collected in Mexico (1), Belize (1), San Salvador (1), Honduras (1), Costa Rica (1), Brasil (4), Peru (1) and Bolivia (2), as well as a modification in the generic position of *Flavius tristriatus* Kormilev (1951) which is transferred to the new genus *Badilloniella*, with the binomen *Badilloniella tristriatus* (Kormilev) new combination.

The tribe Meropachyini Stål, restricted to the Western Hemisphere, is recognized by the elongate scutellum which extends beyond the distal end of the clavus, hind acetabulae projecting laterally and visible in dorsal view, and hind tibiae broadly curved distally.

A key to the 16 genera included in Meropachyini is given.

All measurements are in millimeters.

Acronyms used are: AMNH (American Museum of Natural History, New York); BMNH (The Natural History Museum, London); CAS (California Academy of Sciences, San Francisco, CA); CMNH (Carnegie Museum of Natural History, Pittsburgh, PA); CNCI (Canadian National Collection of Insects, Ottawa, Ontario, Canada); FSCA (Florida State Collection of Arthropods, Gainesville, FL); INBIO (Instituto Nacional de Biodiversidad, Santo Domingo de Heredia, Costa Rica); TAMU (Texas A & M University Insect Collection, College Station, TX); UMRM (W. R. Enns Entomology Museum, University of Missouri, Columbia, MO); UNAM (Instituto de Biología, Universidad Nacional Autónoma de México); ZMUH (Zoologisches Institut und Museum, Universitat Hamburg, Germany).

FEATURES IN COMMON OF THE GENERA DESCRIBED

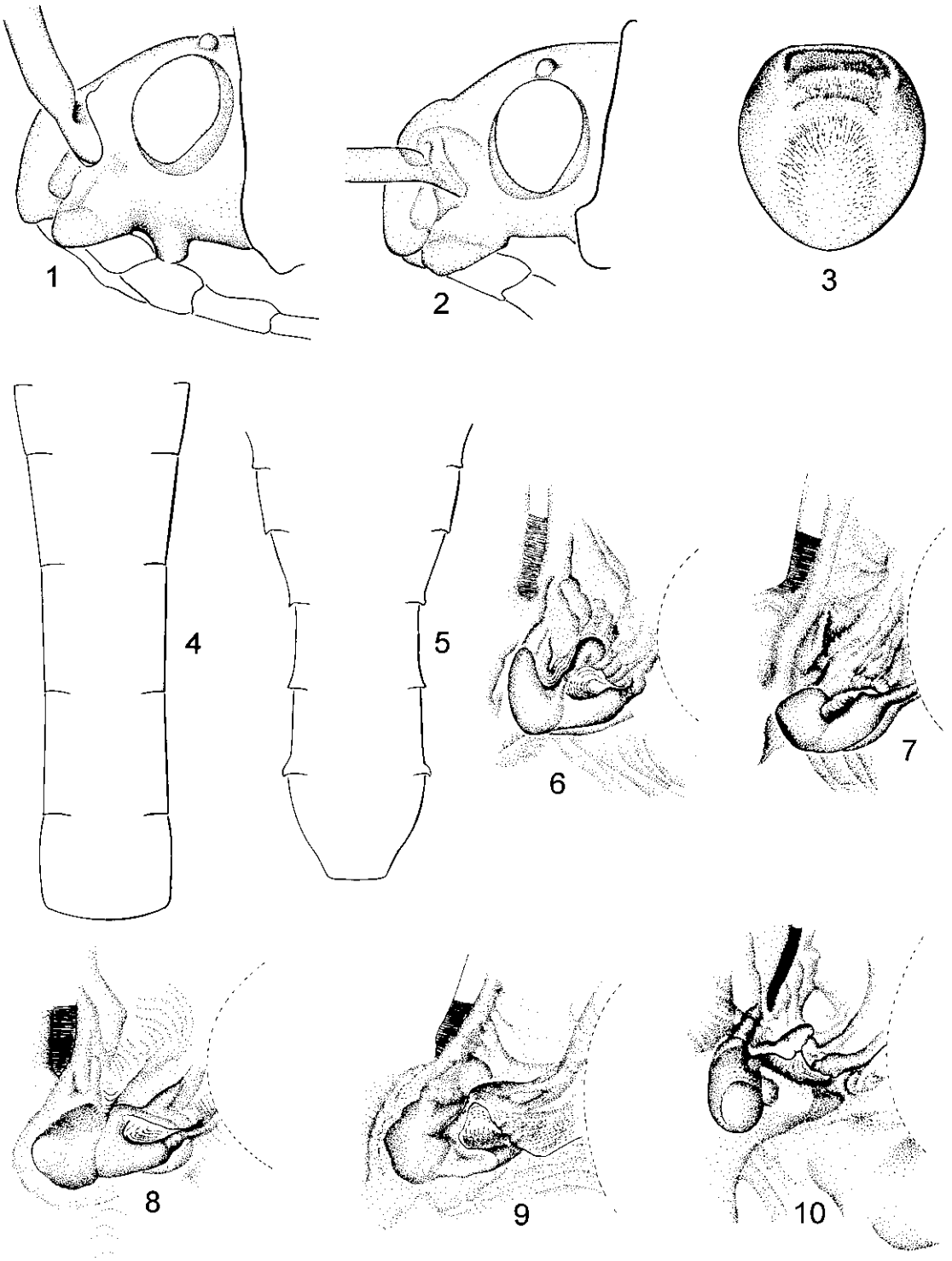
Head. Antenniferous tubercles unarmed; antennal segment IV the longest, III the shortest, or II and III subequal, and I longer than II and III; postocular tubercle absent; mandibular plate absent; head ventrally and posterior to the buccula with conical tubercle; rostrum short barely reaching anterior third of mesosternum; rostral segment III the shortest, IV usually the longest, or I longer or subequal than II, or I and II longer than IV. Thorax. Pronotum. Wider than base of scutellum; frontal angles obtuse, not projected; humeral angles obtuse or barely projected; anterolateral margins obliquely straight, smooth, or dentate, or tuberculate, and not emarginate; triangular process absent; calli smooth and polished or tuberculate. Mesosternum raised or not, with anterior margin in front of area between fore legs produced into narrowed subacute tubercle, posterior third between middle legs prominent, and provided with one tubercle at each side; lateral margin of mesopleura raised on a elongate tubercle, almost overlapping the propleuron; metasternum slender, rectangular, anterior margin raised on two large lobes, separated along midline by a wide or narrow furrow; each lobe overlapping with the two lobes of posterior border of mesosternum; posterior margin of metathorax straight, lateral angles projected into broad rect-

angular plate, lying against metacoxae, and at middle third bilobed or entirely flat, broad, and weakly declivent; metathorax laterally expanded, in dorsal view with metapleura and acetabulae prominently visible; metathoracic peritreme located near lower margin of metapleuron, with upper third closed; canal short, semicircular, with raised sides; anterior lobe variable throughout genera, posterior lobe short, obtuse, slightly exposed. Legs. Hind coxae strongly separated, visible beyond costal margins and sides of body in dorsal view, with outer apical angle tuberculate; hind trochanter conspicuously tuberculate and exposed, or weakly convex; fore and middle femora relatively slender, unarmed or armed with one to three subdistal tubercles; hind femur markedly incrassate, reaching at must the middle third of abdominal sternite VII, with dorsal surface smooth or tuberculate and ventral surface strongly armed with spines and tubercles; fore and middle tibiae unarmed, sulcate, and slightly expanded at posterior third; hind tibia curved, compressed, shorter than femur, with outer margin not expanded and remarkably sulcate, inner margin usually markedly expanded, and apically armed with a broad long spine. Scutellum. Longer than wide, and always longer than clavus; straight or coarctate near base; disc with Y-shaped elevation; apex rounded. Hemelytra. Macropterous; claval suture present but covered by apex of scutellum; clavus partially covered by scutellum; costal margin shallowly concave. Abdomen. Gradually narrowing beyond middle, and slightly expanded posteriorly; abdominal segment VII of male usually laterally exposed; abdominal sternite II visible, slender, with or without conical tubercle located close to posterior border of metathorax; abdominal sternite II near lateral angles with small or well developed conical tubercles laying against the metacoxae; abdominal sternite III weakly or clearly expanded, and in dorsal view with spiracle visible. Male genitalia. Genital capsule. Simple, semiglobose; posteroventral edge with broad tongue-like middle plate; lateral angles rounded, and weakly exposed. Paramere. Simple and straight; anterior lobe convex, continuous with the body; posterior lobe variable. Female genitalia. Abdominal sternite VII with plica and fissura; plica triangular; fissura with inner margin overlapping; gonocoxae I subtriangular, in caudal view closed, in lateral view almost straight, with upper border rounded; paratergite VIII triangular, with spiracle visible; paratergite IX squarish, longer than paratergite VIII. Spermatheca. Bulb elongated; spermethecal duct conspicuously coiled proximally, with two to four distal coils; flank distinct; chamber more or less globose.

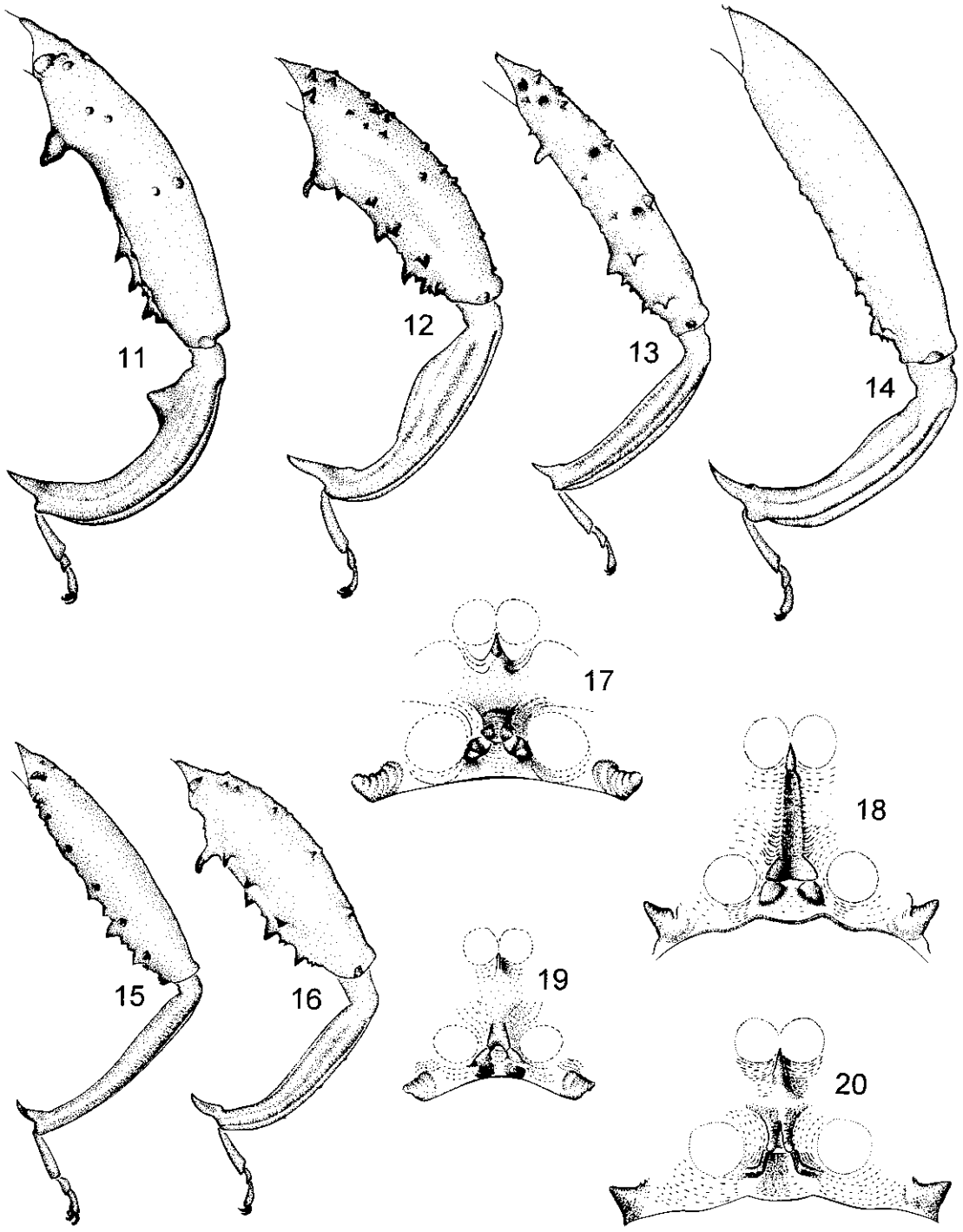
Integument. Head, collar, calli, clavus, corium, prosternum, mesosternum, metasternum, connexival segments, and pleural abdominal sterna impunctate; pronotal disc strongly punctate, and abruptly striate; scutellum punctate, except the Y-shaped elevation which is finely striate; propleura, posterior margin of metapleura, acetabulae, and abdominal sterna punctate; metapleura tuberculate; antennal segments and legs covered with short decumbent to suberect setae.

KEY TO GENERA OF MEROPACHYDINI

1. Posterior border of pronotum without a triangular projection 2
1'. Posterior border of pronotum with a triangular projection above each basal angle of scutellum 10
2. Head ventrally and posterior to buccula with a strong conical tubercle (Fig. 1) 3
2'. Head ventrally and posterior to buccula smooth, without a tubercle at most with an irregular callosity (Fig. 2) 7
3. Posterior margin of metasternum lateral to middle third bilobed (Fig. 19); calli densely tuberculate . . . . . *Serranoniella* new genus
3'. Posterior margin of metasternum at middle third flat (Figs. 17 and 20); calli smooth or with few tubercles 4
4. Posterior margin of metapleura with a creamy yellow hardened protuberance; mesosternum conspicuously raised, deeply sulcate at midline; male abdominal sternite III laterally with a creamy yellow hardened protuberance; male hind femur proximally without a strong conical spine-like projection (Fig. 14) . . . . . *Romoniella* new genus
4'. Posterior margin of metapleura without creamy yellow hardened protuberance; mesosternum weakly convex, not longitudinally sulcate; male abdominal sternite III laterally flat, without creamy yellow hardened protuberance; male hind femur proximally with strong conical spine-like projection (Fig. 11) 5
5. Calli smooth; body surface densely pubescent; male hind tibia proximally with strong conical spine-like projection (Fig. 11). . . . . *Badilloniella* new genus
57'. Calli tuberculate; body surface almost glabrous; male hind tibia basally without conical spine-like projection (Figs. 12-14) 6



Figs. 1 and 2. Head in lateral view. 1, *Badilloniella tristriatus* (Kormilev). 2, *Marichisme limbatus* (Stål). Fig. 3. Caudal view of male genital capsule of *Badilloniella tristriatus* (Kormilev). Figs. 4 and 5. Abdomen. 4, *Romoniella perfecta* Brailovsky and Barrera, New Species. 5, *Badilloniella tristriatus* (Kormilev). Figs. 6-10. Metathoracic peritreme. 6, *Peranthus longicornis* Dallas. 7, *Romoniella perfecta* Brailovsky and Barrera, New Species. 8, *Marichisme limbatus* (Stål). 9, *Badilloniella tristriatus* (Kormilev). 10, *Esparzaniella reclusa* Brailovsky and Barrera, New Species.



Figs. 11-16. Hind leg. 11, *Badilloniella tristriatus* (Kormilev). 12, *Esparzaniella reclusa* Brailovsky and Barrera, New Species. 13, *Marichisme limbatus* (Stål). 14, *Romoniella perfecta* Brailovsky and Barrera, New Species. 15, *Serranoniella amblysa* Brailovsky and Barrera, New Species. 16, *Peranthus longicornis* Dallas. Figs. 17-20. Thorax in ventral view showing mesosternum and metasternum. 17, *Esparzaniella reclusa* Brailovsky and Barrera, New Species. 18, *Romoniella perfecta* Brailovsky and Barrera, New Species. 19, *Serranoniella amblysa* Brailovsky and Barrera, New Species. 20. *Badilloniella tristriatus* (Kormilev).

6. Dorsal surface of hind femur conspicuously tuberculate (Fig. 12); posterior angles of male connexival segments III to V each armed with a large and blunt spine (female unarmed) . . . . . (Fig. 23) . . . . . *Esparzaniella* new genus

6'. Dorsal surface of hind femur smooth, or scarcely tuberculate (Figs. 14, 16); posterior angles of male connexival segments III to V unarmed . . . . . *Peranthus* Stål

7. Scutellar disc without a distinct Y-shaped elevation; posterior margin of mesosternum at each side with one short lobe touching anterior lobe of metasternum; posterior margin of metasternum flat; dorsal surfaces of hind femora smooth 8

7'. Scutellar disc with a clearly Y-shaped elevation; posterior margin of mesosternum at each side with one large lobe freely projecting backwards and bending up, not touching anterior lobe of metasternum; posterior margin of metasternum at middle third with a deep depression of capsule-like appearance; dorsal surfaces of hind femora weakly to strongly tuberculate from base to apex. 9

8. Scutellum remarkably slender abruptly narrowed on distal half, apex bifid; antennal segment I slender, less than 2.05 mm; metapleura not laterally expanded; hind femora scarcely incrassate; inner face of hind tibia weakly expanded; abdominal sternite III of male with small lateral prominences . . . . . *Larraldiella* Brailovsky

8'. Scutellum not remarkably slender, narrowing very gradually to distal end, apex rounded; antennal segment I robust, longer than 2.10 mm; metapleura laterally expanded; hind femur conspicuously incrassate; inner face of hind tibia expanded; abdominal sternite III of male smooth, without lateral prominences . . . . . *Gracchus* Stål

9. Dorsal surface of hind femora strongly tuberculate from proximal to distal end (Fig. 13); hind trochanter convex, not tuberculate; scutellum 1.7 to 2.2 times longer than wide, apically rounded; anterior margins of thoracic mesopleura each with a black elongate spot . . . . . *Marichisme* Kirkaldy

9'. Dorsal surface of hind femora weakly tuberculate from proximal to middle third; hind trochanter tuberculate; scutellum 3.3 to 3.8 times longer than wide, and apically acute; anterior margins of thoracic mesopleura without a black spot. . . . . *Soteloniella* Brailovsky

10. Head ventrally posterior to buccula with a strong conical tubercle (Fig. 1). 11

10'. Head ventrally posterior to buccula smooth, without a tubercle (Fig. 2) 13

11. Hind femur conspicuously clavate, slender towards base, and abruptly thickened beyond middle . . . . . *Possaniella* Brailovsky

11'. Hind femur never clavate, uniformly incrassate 12

12. Middle third of posterior margin of metasternum flat, without lateral lobes; anterior lobe of metathoracic peritreme with a black lunular spot; body surface densely pubescent; scutellum clearly contracted near base; dorsal surfaces of hind femur strongly tuberculate . . . . . *Flavius* Stål

12'. Middle third of posterior margin of metasternum with two lateral lobes; anterior lobe of metathoracic peritreme tooth-shaped without a black lunular spot; body surface not densely pubescent; scutellum not contracted near base; dorsal surfaces of hind femur smooth . . . . . *Alcocerniella* Brailovsky

13. Posterior margin of mesosternum trilobed, with mesial lobe expanded and broad, and lateral lobes short; scutellum strongly constricted near base; scutellar disc with a broad Y-shaped elevation. . . . . *Meropachys* Burmeister

13'. Posterior margin of mesosternum bilobed, or without lobes; scutellum not or weakly constricted near base; scutellar disc without a distinct Y-shaped elevation 14

14. Posterior margin of metasternum bilobed . . . . . *Hirilcus* Stål

14'. Posterior margin of metasternum not bilobed 15

15. Posterior margin of metasternum projected in a medial quadrangular plate directed straight downward; pronotal humeral angles obtuse . . . . . *Juaristiella* Brailovsky

15'. Posterior margin of metasternum flat, straight; pronotal humeral angles subacute, laterally expanded . . . . . *Salamancaniella* Brailovsky and Luna

Badilloniella Brailovsky and Barrera,
NEW GENUS

Type species: *Flavius tristriatus* Kormilev, 1951. Monobasic.

Description. Head. Distance between ocelli 3.3 to 3.6 times diameter of one ocellus; distance between ocelli and eye 1.0 to 1.1 times diameter of one ocellus; head ventrally and behind buccula strongly tuberculate (Fig. 1); rostral segment III shortest, IV longest, I subequal to II. Thorax. Pronotum. Anterolateral borders obliquely straight, smooth; posterior border barely convex; triangular process absent; calli raised, smooth, separated along midline. Mesosternum weakly convex, with posterior margin between middle legs prominent, bilobed, each lobe well separated from mesial line, overlapping the lobes of anterior margin of metasternum; metasternum slender, rectangular, anterior margin raised on two lobes, separated along midline by a wide furrow; each lobe touching the two lobes of posterior margin of mesosternum; posterior margin of metasternum almost straight, each lateral angle projected as a broad rectangular plate, laying against metacoxae, and at middle third flat, without lobes, and projected on a broad plate (Fig. 18). Anterior lobe of metathoracic peritreme raised, elongate, curved, with rounded angles (Fig. 9). Legs. Distance between hind coxae nearly 3.2 to 3.7 times the diameter of one coxa; fore and middle femora relatively slender, unarmed; hind femur markedly incrassate, attaining the middle third of abdominal sternite VII, with dorsal surface weakly tuberculate, and ventrally strongly armed with spines and tubercles in two irregular rows, as well as a strong conical tooth close to base in males and medium sized tubercle in females; inner margin of male hind tibia expanded, curved, and armed basally and distally with a broad spine (Fig. 11); inner margin of female hind tibia expanded, curved, and armed only distally with a broad spine. Scutellum. 1.9 to 2.2 times longer than wide, longer than clavus, coarctate near base; disc with Y-shaped elevation. Abdomen. Posterior angle of male connexival segments III to VI armed with a medium sized and blunt spine (Fig. 5) (female unarmed); abdominal sternite III laterally flat, without conical lobes.

Integument. Body surface densely covered with mixed short and large decumbent to suberect setae.

Badilloniella tristriatus was originally placed in the Merocorinae genus *Flavius* Stål due to the head ventrally with a conical tubercle behind the bucculae, fore and middle femora unarmed, and pronotal disc and scutellum densely covered with long to short decumbent to suberect setae. However *Badilloniella* differs from *Flavius* by lacking a triangular projection at the posterior border of the pronotum, by having on the hind femora and hind tibiae of the male a strong conical projection spine-like near the base, the anterior lobe of metathoracic peritreme without a black lunular spot, the mesosternal disc weakly convex, total length of scutellum 1.9 to 2.3 longer than wide, and hind femur in dorsal view smooth. In *Flavius* the posterior border of the pronotum has a triangular projection, the hind femora and hind tibiae of the male lacks a strong conical projection spine-like near the base, the anterior lobe of the metathoracic peritreme has a black lunular spot, mesosternal disc conspicuously raised, total length of scutellum 3.0 to 3.2 longer than wide, and hind femur in dorsal view strongly tuberculate.

Badilloniella and *Peranthus* Stål share the following characters: head ventrally and behind buccula with a strong conical tubercle (Fig. 1), posterior border of pronotum lacking a triangular projection, mesosternal disc weakly convex, hind femur of male basally with a strong conical spine-like projection, hind femora of both sexes dorsally smooth, and fore and middle femora unarmed (Figs. 11 and 16). In *Badilloniella* the posterior angle of male connexival segments III to VI are each projected as a large and blunt spine (Fig. 5), the hind tibiae of male basally with a strong conical projection like-spine (Fig. 11), calli smooth, and Pronotal disc and scutellum densely covered with long to short decumbent to suberect setae. In *Peranthus* the posterior angles of male connexival segments are unarmed, the male hind tibiae basally lack a conical projection like-spine (Fig. 16), calli tuberculate, and pronotal disc and scutellum almost glabrous.

Etymology. Named for Humberto Badillo Gomez, distinguished Mexican gastroenterologist and specialist in Internal Medicine.

Badilloniella tristriatus (Kormilev),
NEW COMBINATION
Flavius tristriatus Kormilev 1951: 42-44
Figs. 1, 3, 5, 9, 11, 20-21

Redescription. Male. Dorsal coloration. Head including antennal segments I to IV bright orange; pronotum bright orange with three broad and diffuse longitudinal stripes black to dark brown; scutellum bright orange with three bright red to reddish brown longitudinal stripes, one at middle third and two lateral to middle line; clavus black to dark brown with vein and outer face yellow; corium pale brown to black with veins, and costal and apical margin yellow; hemelytral membrane dark ambarine with veins and basal angle darker; connexival segments III to VI yellow and VII reddish brown with anterior angle yellow; dorsal abdominal segments black with senescent scars IV-V and V-VI yellow. Ventral coloration. Bright orange; apex of rostral segment IV, ventral spines of hind femur, and anterior lobes of mesosternum black; pleural abdominal sterna, tubercles of metapleura,

and several discoidal spots scattered on mesopleura and hind femur yellow to yellow orange; hind tibiae reddish with outer and inner margin black. Genital capsule. Posteroventral edge entire, straight, with small medial plate, and laterally with the angles rounded (Fig. 3): Paramere. Posterior lobe short, broad, apically curved.

Measurements. ♂. Head length 1.70; width across eyes 2.25; interocular space 1.17; interocellar space 0.53; distance ocellus to eye 0.16; diameter of ocellus 0.15; preocular distance 1.15. Length antennal segments: I, 3.17; II, 2.55; III, 2.45; IV, 4.10. Length rostral segments: I, 0.62; II, 0.62; III, 0.52; IV, 0.70. Pronotum: Total length 4.45; width across frontal angles 2.60; width across humeral angles 5.40. Scutellar length 4.80; maximum width of anterior lobe 2.10; maximum width of posterior lobe 1.40. Hind leg: femoral length 8.60; tibial length 5.80. Total body length 18.50.

Female. Coloration. Similar to male. Connexival segments VIII IX chestnut orange; dorsal abdominal segments VIII and IX black; genital plates bright orange and scattered with dark brown diffuse spots. Spermatheca. Spermathecal duct with three to four distal coils.

Measurements. ♀. Head length 1.77; width across eyes 2.10; interocular space 1.12; interocellar space 0.48; distance ocellus to eye 0.17; diameter of ocellus 0.15; preocular distance 1.20. Length antennal segments: I, 2.90; II, 2.32; III, 2.30; IV, 3.30. Length rostral segments: I, 0.58; II, 0.58; III, 0.42; IV, 0.62. Pronotum: Total length 4.50; width across frontal angles 2.50; width across humeral angles 5.20. Scutellar length 3.90; maximum width of anterior lobe 2.00; maximum width of posterior lobe 1.15. Hind leg: femoral length 7.10; tibial length 5.45. Total body length 16.90.

Distribution. Previously known from the type series collected in Yungas, and Chapare, Bolivia (Kormilev 1951).

Material examined. PERU: 2 ♀♀, Ucayali (Middle Rio), 19-VII-1928, H. Bassler (AMNH); 1 ♀, Madre de Dios, Rio Tambopata Res., 30 km (air), SW Puerto Maldonado, 290m, 20-31-X-1982, R. Wilkerson (FSCA). BOLIVIA: 1 ♂, Cuatro Ojos, XI-1913, Steinbach (CMN); 1 ♀, Departamento Santa Cruz, Provincia Ichilo, Parque Amhoro, Rio Saguayo, 500m, 30-XII-1988, P. Bettella (UNAM); 3 ♀♀, Las Juntas, XII-1913, Steinbach (CMN).

Esparzaniella Brailovsky and Barrera,
NEW GENUS

Type species: *Esparzaniella reclusa* Brailovsky & Barrera, Monobasic.

Description. Head. Distance between ocelli 3.4 to 3.6 times the diameter of one ocellus; distance between ocellus and eye 0.8 to 1.1 times the diameter of one ocellus; head ventrally and behind buccula tuberculate (Fig. 1); rostral segment III shortest, IV longest, I longer or subequal to II. Thorax. Pronotum. Anterolateral borders obliquely straight, anterior third dentate to tuberculate, and posterior third smooth; posterior border weakly convex; triangular projection absent; calli entire, uniformly elevated, tetralobulate on males, hexalobulate in females, and not separated at midline. Mesosternum waekly convex, with posterior margin between middle legs bilobed; metasternum slender, rectangular, anterior margin raised on two large quadrangular plates, separated along midline by a wide furrow; each plate touching the two lobes of posterior margin of mesosternum; posterior margin of metasternum straight, each lateral angle projected as a broad rectangular plate, laying against metacoxae and at middle third flat, entire, without lobes (Fig. 17). Anterior lobe of metathoracic peritreme strongly raised, elongate, with rounded angles (Fig. 10). Legs. Distance between hind coxae 2.9 to 3.2 times the diameter of one coxa; fore and middle femora slender, ventrally armed with two subdistal spines, and one row of broad tubercles; hind femur of males markedly incrassate, attaining the middle third of abdominal sternite VII; dorsal surface biseriately tuberculate from base to apex, and ventrally strongly armed with spines and tubercles on two irregular rows, as well as one broad and large conical projection near the base; hind femur of females similar but without long and broad conical tubercle or spine near base; inner margin of hind tibia armed distally with a broad spine (Fig. 12). Scutellum. 1.7 to 1.9 times longer than wide, elongate, longer than clavus, and slightly coarctate near base; disc with Y-shaped elevation; anterior third medially without circular depression. Abdomen. Posterior angle of male connexival segments III to V armed with a large blunt spine and segments II, VI and VII entire (Fig. 23); posterior angle of female connexival segments II to VII entire, slightly broadened but never projected on a spiny-like projection; abdominal sternite III laterally flat, without conical lobes.

Integument. Body surface rather dull, almost glabrous; propleura close to acetabulae densely and irregularly tuberculate; middle third of pronotal disc with two broad and large conical tubercles.

Etymology. Named for Elvia Esparza, distinguished Mexican artist.

Discussion. *Esparzaniella* and *Peranthus* Stål share the following characters: head ventrally and behind buccula with a conical tubercle (Fig. 1), posterior border of pronotum lacking a triangular projection, hind femur basally with large broad spine (Figs. 12, 16), calli uniformly elevated with 4 to 6 conical tubercles and middle third of posterior margin of metasternum smooth, flat. In *Esparzaniella* the male posterior angle of connexival segments III to V are armed with large spiny-like projection (Fig. 23); the hind femur of both

sexes dorsally armed with two rows of black tubercles, and the anterior lobe of metathoracic peritreme clearly differs in both genera (Figs. 6, 10). In *Peranthus* the male posterior angle of connexival segments III to V are unarmed (Fig. 4), and the hind femur of both sexes dorsally smooth.

Marichisme Kirkaldy like *Esparzaniella* has the dorsal surface of hind femur strongly tuberculate from proximal to distal ends (Figs. 12 and 13), and posterior border of pronotum lacking a triangular projection. *Marichisme* differs by the following characters: Head ventrally and behind buccula smooth, without tubercle (Fig. 2), posterior angle of male connexival segments III to V entire, without spine-like projections (Fig. 4), middle third of posterior margin of metasternum with deep capsule-like depression, shape of metathoracic peritreme (Fig. 8), and hind femur of both sexes more elongate, and not markedly incrassate like *Esparzaniella*, whose metasternal posterior margin is flat (Fig. 17).

Esparzaniella reclusa Brailovsky & Barrera,
NEW SPECIES
Figs. 10, 12, 17, 23

Description. Holotype male.Dorsal coloration.Head, antennal segments, pronotum and scutellum bright chestnut orange; latter with medial and lateral longitudinal stripes reddish brown; clavus black with vein and lateral margin yellow; corium dark brown with veins, and costal and apical margin yellow; hemelytral membrane dark ambarine with basal angle and veins dark brown; connexival segments III to VI yellow and VII reddish brown; dorsal abdominal segments reddish brown with odoriferous scars IV-V and V-VI yellow, and segment VII almost black. Ventral coloration. Bright chestnut orange, with pleural margins of abdominal sterna yellow; hind femur bright chestnut orange with spines and tubercles black; hind tibiae reddish orange with lateral margin and spines black; hind tarsi with basal segment reddish brown and chestnut orange reflections, and medial and distal segments bright chestnut orange; apex of rostral segment IV black; external tubercles of metacoxae reddish brown; tubercles of propleura, mesopleura and metapleura bright orange yellow; evaporating area of metathoracic peritreme dull orange. Genital capsule. Posteroventral edge with broad tongue-like middle plate; lateral angles convex, weakly exposed. Paramere. Posterior lobe elongate, apically ending in a sharp tooth.

Measurements. ♂. Head length 1.60; width across eyes 2.15; interocular space 1.15; interocellar space 0.55; distance ocellus to eye 0.17; diameter of ocellus 0.15; preocular distance 1.10. Length antennal segments: I, 3.80; II, 2.80; III, 2.77; IV, 4.40. Length rostral segments: I, 0.68; II, 0.62; III, 0.40; IV, 0.78. Pronotum: Total length 4.20; width across frontal angles 2.65; width across humeral angles 4.90. Scutellar length 3.95; maximum width of anterior lobe 2.00; maximum width of posterior lobe 1.10. Hind leg: femoral length 7.60; tibial length 6.10. Total body length 17.38.

Female. Coloration. Similar to male. Connexival segments VII to IX bright chestnut orange; dorsal abdominal segment VII bright orange with posterior margin dark brown; genital plates bright chestnut orange with dark brown reflections.

Measurements. ♀. Head length 1.50; width across eyes 2.15; interocular space 1.12; interocellar space 0.52; distance ocellus to eye 0.12; diameter of ocellus 0.15; preocular distance 1.10. Length antennal segments: I, 3.30; II, 2.60; III, 2.60; IV, 3.90. Length rostral segments: I, 0.68; II, 0.58; III, 0.38; IV, 0.74. Pronotum: Total length 4.05; width across frontal angles 2.35; width across humeral angles 4.95. Scutellar length 3.40; maximum width of anterior lobe 2.00; maximum width of posterior lobe 1.00. Hind leg: femoral length 6.70; tibial length 5.50. Total body length 16.78.

Holotype: ♂ BOLIVIA, Beni, Guayaramerin, XII-1956, coll. V. Fritz (AMNH).

Paratypes: 1 ♂, 2 ♀♀. Same data as holotype (AMNH, UNAM).

Etymology. The specific name refers to the elusive nature of this species.

Distribution. Only known from the type series collected in Bolivia.

Romoniella Brailovsky and Barrera,
NEW GENUS

Type species: *Romoniella perfecta* Brailovsky & Barrera, Monobasic.

Description. Head.Distance between ocelli 2.8 to 3.3 times the diameter of one ocellus; distance between ocellus and eye 1.3 to 1.4 times the diameter of one ocellus; head ventrally and behind buccula tuberculate (Fig. 1); rostral segment III the shortest, IV the longest, and I longer or subequal than II. Thorax. Pronotum. Anterolateral borders obliquely straight, smooth; posterior border straight; triangular projection absent; calli smooth, slightly raised, separated at midline by a short longitudinal furrow. Mesosternum conspicuously raised, deeply sulcated, with posterior margin between middle legs bilobed; metasternum slender, rectangular, anterior margin remarkably raised on two large tubercles, separated along midline by a short furrow; each tubercle overlapping the two lobes of posterior margin of mesosternum; posterior margin of metasternum not bilobed, expanded in a broad, declivent plate, with lateral angles projected in a wide conical tubercle, laying against the metacoxae; posterior margin of metapleura slightly curved, and raised on a creamy hardened protuberance (Fig. 18). Metathoracic peritreme bilobulate, with each lobe rounded; evaporating area

deeply concave, with raised sides (Fig. 7). Legs. Distance between hind coxae 3.2 to 3.5 times the diameter of one coxa; fore and middle femora slender, ventrally armed with two subdistal spines, and one row of broad tubercles; hind femur not markedly incrassate, attaining the middle third of abdominal sternite VI; dorsal surface smooth, ventrally armed with two subdistal spines and one row of broad spines and tubercles, running from base to apex; hind tibia armed distally with a broad spine (Fig. 14). Scutellum. 1. 7 to 1.9 times longer than wide, elongate, longer than clavus, and slightly coarctate near base; disc with Y-shaped elevation; anterior third medially without circular depression. Abdomen. Posterior angle of connexival segments III to VII unarmed; male abdominal sternite III clearly expanded, laterally with medium sized creamy yellow hardened protuberance, absent in females.

Integument. Body surface rather dull, and glabrous.

Etymology. Named for Ranulfo Romo, distinguished Mexican neurologist.

Discussion. *Badilloniella* Brailovsky and Barrera, *Esparzaniella* Brailovsky and Barrera, *Gracchus* Stål, *Larraldiella* Brailovsky, *Marichisme* Kirkaldy, *Peranthus* Stål, *Romoniella* here described, and *Soteloniella* Brailovsky are the only known genera in the tribe Meropachydini without a triangular projection on the posterior border of the pronotum (Figs. 21 and 22). In *Badilloniella*, *Esparzaniella*, *Peranthus* and *Romoniella* the head ventrally and behind buccula has an strong tubercle (Fig. 1), lacking in the other genera (Fig. 2). *Romoniella* is clearly segregated because the posterior margin of the metapleura is projected in a creamy yellow hardened prominence, the male abdominal sternite III laterally has a creamy yellow hardened protuberance lacks in the other genera, the hind femur is not markedly incrassate, and the mesosternum conspicuously raised and mesally sulcate (Fig. 18).

Romoniella perfecta Brailovsky & Barrera,
NEW SPECIES
Figs. 4, 7, 14, 18, 22

Description. Holotype male.Dorsal coloration. Head, and antennal segments I to III yellow; antennal segment IV pale chestnut orange; pronotum yellow with medial and lateral longitudinal stripes pale chestnut red located at anterior lobe; scutellum yellow except basal third with broad and short longitudinal stripe pale chestnut red; clavus and corium pale orange brown; hemelytral membrane dark ambarine with veins brown; connexival segments II to VI yellow and VII dark reddish brown with upper anterior margin yellow; dorsal abdominal segments pale orange, and VII reddish orange with posterior margin reddish brown. Ventral coloration. Head, rostral segments (apex of IV dark brown), legs, and acetabulae yellow; tarsi, abdominal sterna III to VI and pleural abdominal sterna III to VI yellow with olive green reflections; abdominal spiracle creamy yellow; abdominal sternite VII and pleural abdominal sternite VII yellow with posterior margin chestnut orange; genital capsule chestnut orange; prothorax yellow, with broad anterior stripe close to propleura; mesothorax and metathorax chestnut orange, with posterior margin of mesopleura yellow; posterior margin of metapleura with hardened prominence creamy yellow; hind tibia yellow with basal third dark chestnut red; anterior and posterior lobe of metathoracic peritreme and evaporating area dark chestnut orange. Genital capsule. Posteroventral edge with broad tongue-like middle plate; lateral angles rounded. Paramere. Posterior lobe broad and apically curved.

Measurements. ♂. Head length 1.95; width across eyes 2.30; interocular space 1.25; interocellar space 0.50; distance ocellus to eye 0.20; diameter of ocellus 0.15; preocular distance 1.15. Length antennal segments: I, 4.05; II, 3.10; III 2.90; IV, 4.65. Length rostral segments: I, 0.70; II, 0.70; III, 0.46; IV, 0.78. Pronotum: Total length 4.50; width across frontal angles 2.30; width across humeral angles 5.50. Scutellar length 4.47; maximum width of anterior lobe 2.30; maximum width of posterior lobe 1.20. Hind leg: femoral length 9.30; tibial length 6.12. Total body length 21.70.

Female. Coloration. Similar to male. Connexival segments III to V yellow, VI dark reddish brown with anterior and posterior border and upper margin yellow, and VII to IX dark reddish brown; dorsal abdominal segments III, VI and VIII yellow, IV-V yellow with lateral margins black, VII pale reddish orange, and IX yellow with posterior margin chestnut orange. Ventrally with head, rostral segments (apex of IV dark brown), propleura, mesopleura and metapleura, abdominal sterna, and genital plates orange yellow; posterior margin of metapleura with hardened prominence creamy yellow; pleural abdominal sterna pale yellow; fore and middle coxae chestnut brown; fore and middle trochanter, femora, tibiae, and tarsi orange yellow; hind leg chestnut orange with spines and tubercles chestnut brown; mesosternum, and metasternum dark brown to black; anterior lobe of metathoracic peritreme dirty orange yellow, posterior lobe and evaporating area black. Spermatheca. Spermathecal duct with two distal coils.

Measurements. ♀. Head length 1.60; width across eyes 2.15; interocular space 1.15; interocellar space 0.43; distance ocellus to eye 0.21; diameter of ocellus 0.15; preocular distance 1.12. Length antennal segments: I, 3.25; II, 2.55; III 2.50; IV, 4.10. Length rostral segments: I, 0.68; II, 0.64; III, 0.42; IV, 0.78. Pronotum: Total length 3.65; width across frontal angles 2.25; width across humeral angles 4.70. Scutellar length 3.25; maximum

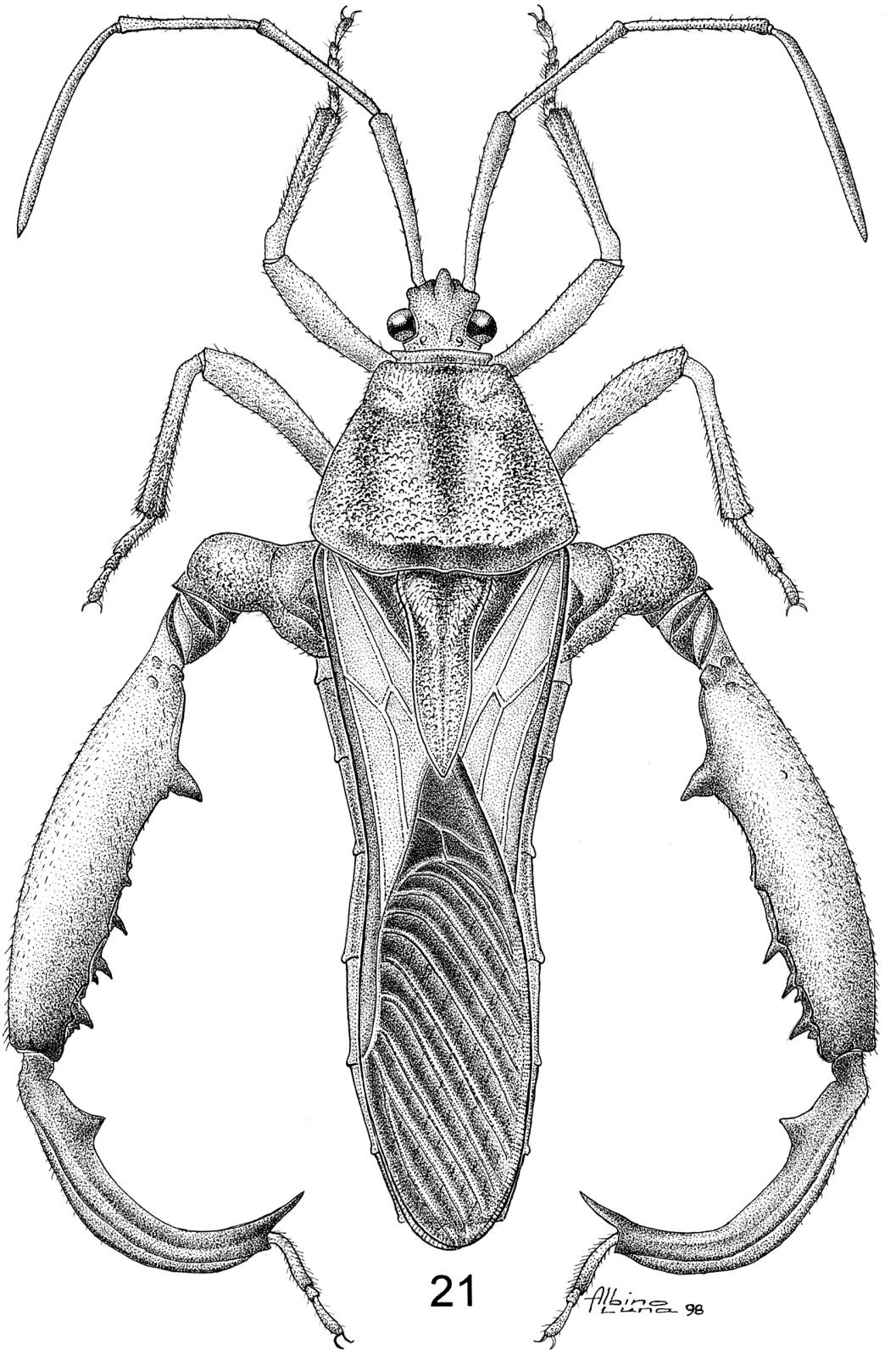


Fig. 21. *Badilloniella tristriatus* (Kormilev), dorsal view.

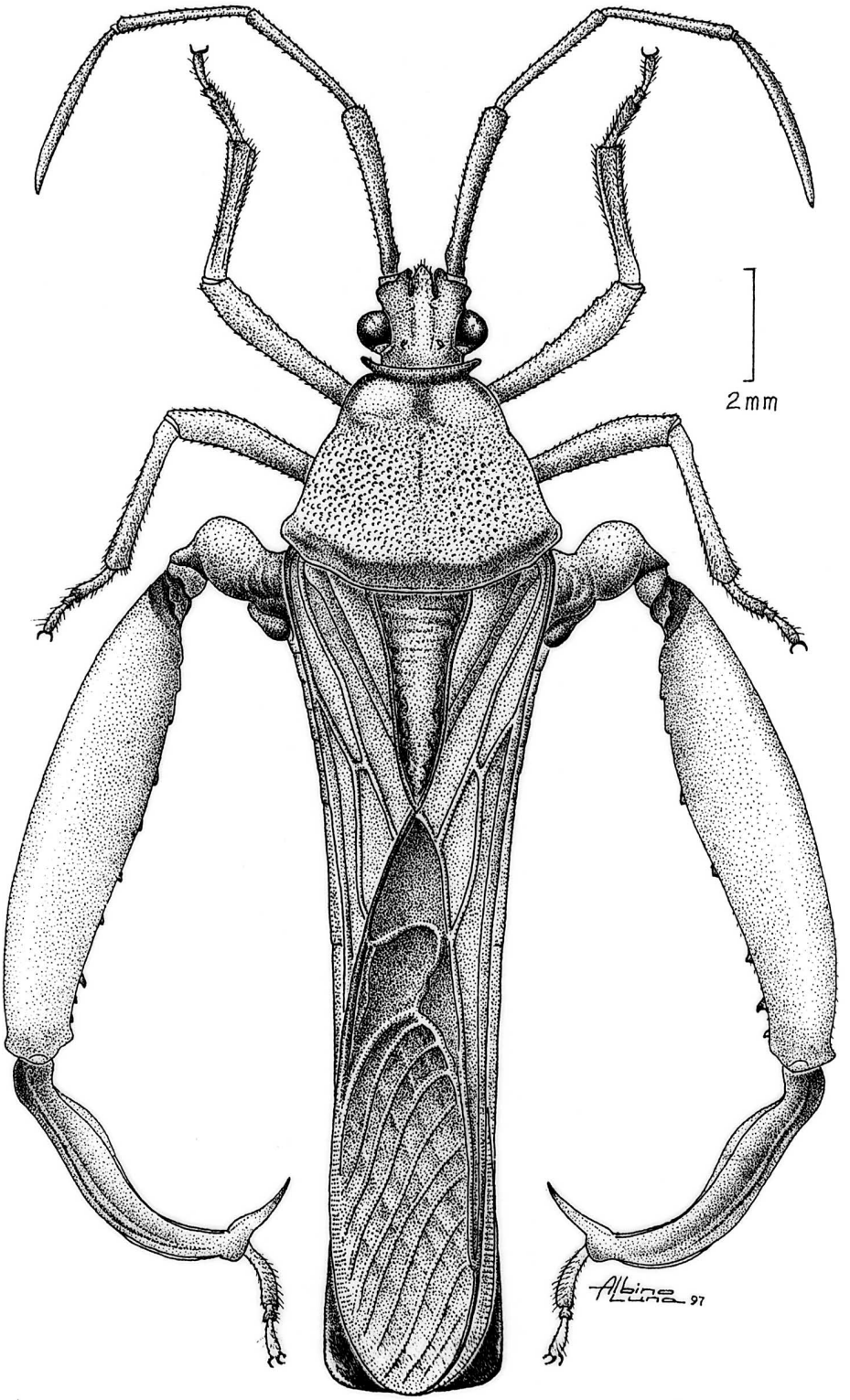


Fig. 22. *Romoniella perfecta* Brailovsky and Barrera, New Species, dorsal view.

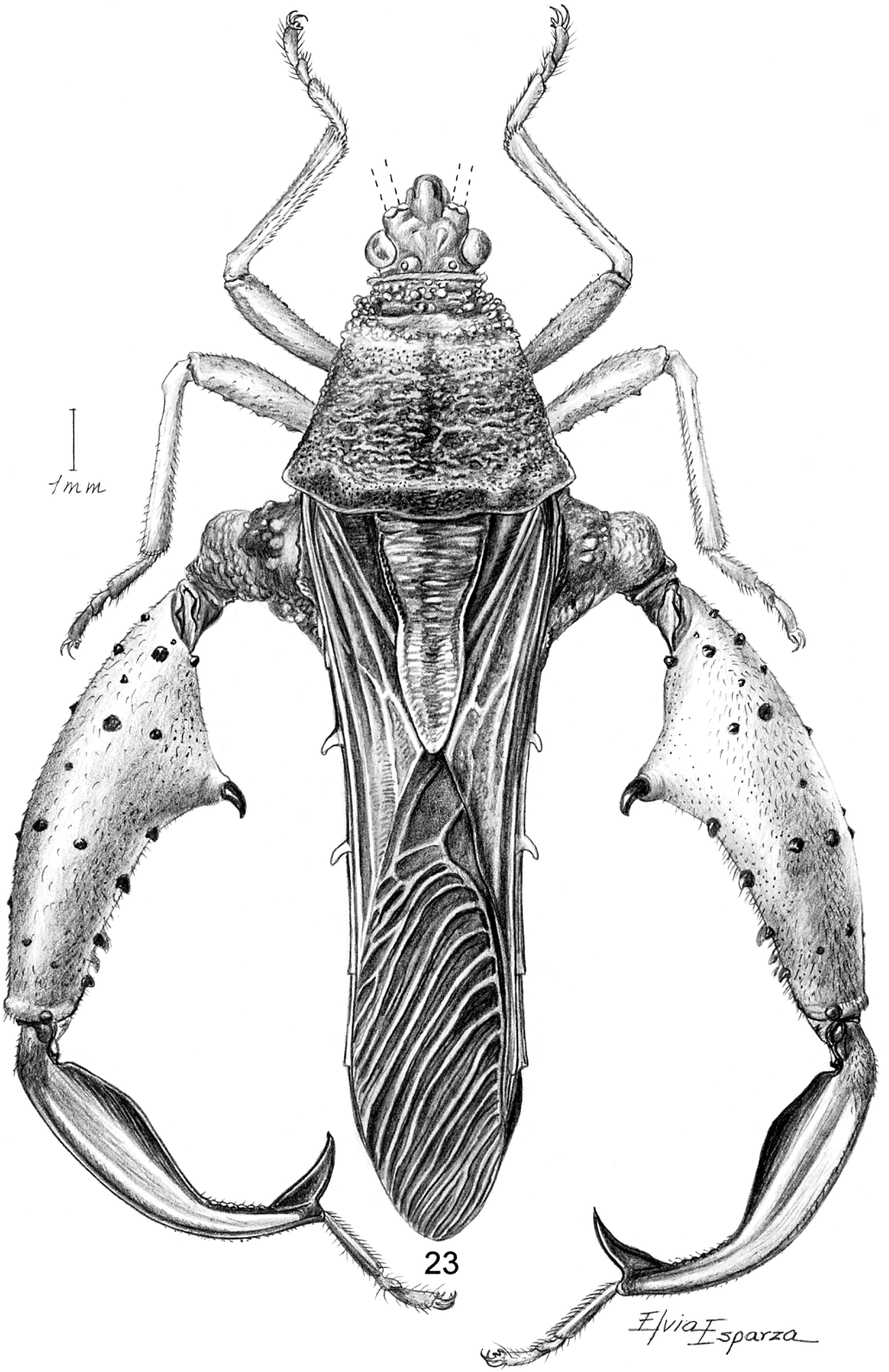


Fig. 23. *Esparzaniella reclusa* Brailovsky and Barrera, New Species, dorsal view.

width of anterior lobe 1.85; maximum width of posterior lobe 0.80. Hind leg: femoral length 6.70; tibial length 5.10. Total body length 17.26.

Variation. 1, Head, antennal segments I to III, pronotum, scutellum, connexival segments, legs, abdominal sterna, and pleural abdominal sterna yellow with olive green reflections. 2, Mesosternum, and metasternum yellow to dark brown. 3, Anterior and posterior lobe of metathoracic peritreme and evaporating area yellow to dark brown.

Holotype: ♂ MEXICO, Chiapas, Ruinas de Bonampak, 21-V-1980, coll.H. Brailovsky (UNAM).

Paratypes. MEXICO: 1 ♂ Chiapas, Tuxtla Gutierrez, El Chorreadero, 26-IX-1961, coll. F. Pacheco (UNAM). 1 ♂ Chiapas, Cascada El Aguacero, about 20 km W of Ocozocoautla, 24-VIII-1974, coll. D. E. and J. A. Breedlove (CAS). 1 ♀ Chiapas, 2.4 km W of Soyalo on road to Chicoasen, 1219 m, 7-IX-1974, coll. D. E. and J. A. Breedlove (CAS). BELIZE: 1 ♀ Belize S. C. Mile 20 Southern Hwy., 19-VIII-1977, coll. C. W. and L. OBrien and Marshall (UMRM). HONDURAS: 1 ♀ Olaucho, El Boqueron, 20-XII-1983, coll. R. W. Jones (TAMU). EL SALVADOR. 1 ♀ San Salvador, IX-1960, coll. Virkki (CNCI). COSTA RICA 1 ♂ Provincia Guanacaste, Estacion Santa Rosa, 300 m, I-1989, coll. GNP Biodiversity Survey (INBIO).

Etymology. The name *perfecta*, refers to the fine proportions and appearance of this species.

Distribution. Widely distributed throughout Southern Mexico and Central America.

Serranoniella Brailovsky and Barrera,
NEW GENUS

Type species: *Serranoniella amblysa* Brailovsky & Barrera, Monobasic.

Description. Head. Distance between ocelli 3.8 to 4.5 times the diameter of one ocellus; distance between ocellus and eye 1.5 to 1.6 times the diameter of one ocellus; head ventrally and behind buccula tuberculate (Fig. 1); rostral segment III shortest, I longest, II longer than IV. Thorax. Pronotum. Anterolateral borders obliquely straight, anterior third weakly tuberculate, posterior third smooth; posterior border barely convex; triangular projection absent; calli weakly raised, and densely tuberculate. Mesosternum weakly convex with posterior margin between middle legs prominent, bilobed, with each lobe well separated from mesial line and overlapping the lobes of anterior margin of metasternum; metasternum slender, rectangular, anterior margin raised on two large lobes, separated along midline by a wide furrow; each lobe touching the two lobes of posterior margin of mesosternum; posterior margin of metasternum almost straight, lateral angles projected as a broad rectangular plate, laying against metacoxae, and at middle third bilobed (Fig. 19). Anterior lobe of metathoracic peritreme raised, elongate, curved to hemispheric, with rounded angles. Legs. Distance between hind coxae nearly 2.6 to 3.2 times the diameter of one coxa; fore and middle femora relatively slender, unarmed; hind femur markedly incrassate, attaining the middle third of abdominal sternite VII, dorsal surface practically smooth with few tubercles hard to see, ventral surface strongly armed with spines and tubercles in two irregular rows, and male and female without strong conical tooth close to the base; inner margin of hind tibia armed distally with a broad spine (Fig. 15). Scutellum. 1.7 to 1.9 times longer than wide, longer than clavus, straight, not coarctate near base; disc with Y-shaped elevation. Abdomen. Posterior angle of connexival segments unarmed; abdominal sternite III laterally flat, without conical lobes.

Integument. Body surface almost glabrous, scattered with short decumbent to suberect setae.

Etymology. Named after Araceli Silvia Reyes Serrano wife of the junior author.

Discussion. *Serranoniella* like *Hirilcus* Stål with posterior margin of metasternum bilobed, and hind femur basally without strong conical expansion like spine (Fig. 15). In *Hirilcus* the posterior border of the pronotum has a triangular projection above each basal angle of scutellum, the head ventrally and behind buccula smooth or at most with an irregular callosity, and the scutellum is clearly coarctate and not simple and straight like in *Serranoniella* which pronotum lack a triangular projection and the head ventrally and behind buccula has a strong conical tubercle.

Serranoniella amblysa Brailovsky & Barrera,
NEW SPECIES
Figs. 15, 19, 24

Description. Holotype male. Dorsal coloration. Head, antennal segments and pronotum bright chestnut orange; scutellum chestnut orange with medial, and lateral longitudinal stripes bright orange red; clavus and corium chestnut orange with claval and corial veins, and costal and apical margin dull yellow; hemelytral membrane dark ambarine with basal angle and veins brown; connexival segments III to VI yellow, and VII dark brown with posterior third yellow; dorsal abdominal segments dark brown, with odoriferous scars IV-V and V-VI yellow. Ventral coloration. Chestnut orange; apex of rostral segment IV, and spines and tubercles of hind femur dark brown; pleural abdominal sterna III to VI yellow, and VII bright chestnut orange; hind tibia bright chestnut orange with pale reddish reflections. Genital capsule. Posteroventral edge entire, straight, with small medial plate, and laterally with the angles rounded. Paramere. Posterior lobe remarkably elongate, apically curved.

Measurements. ♂. Head length 1.50; width across eyes 2.05; interocular space 1.15; interocel-

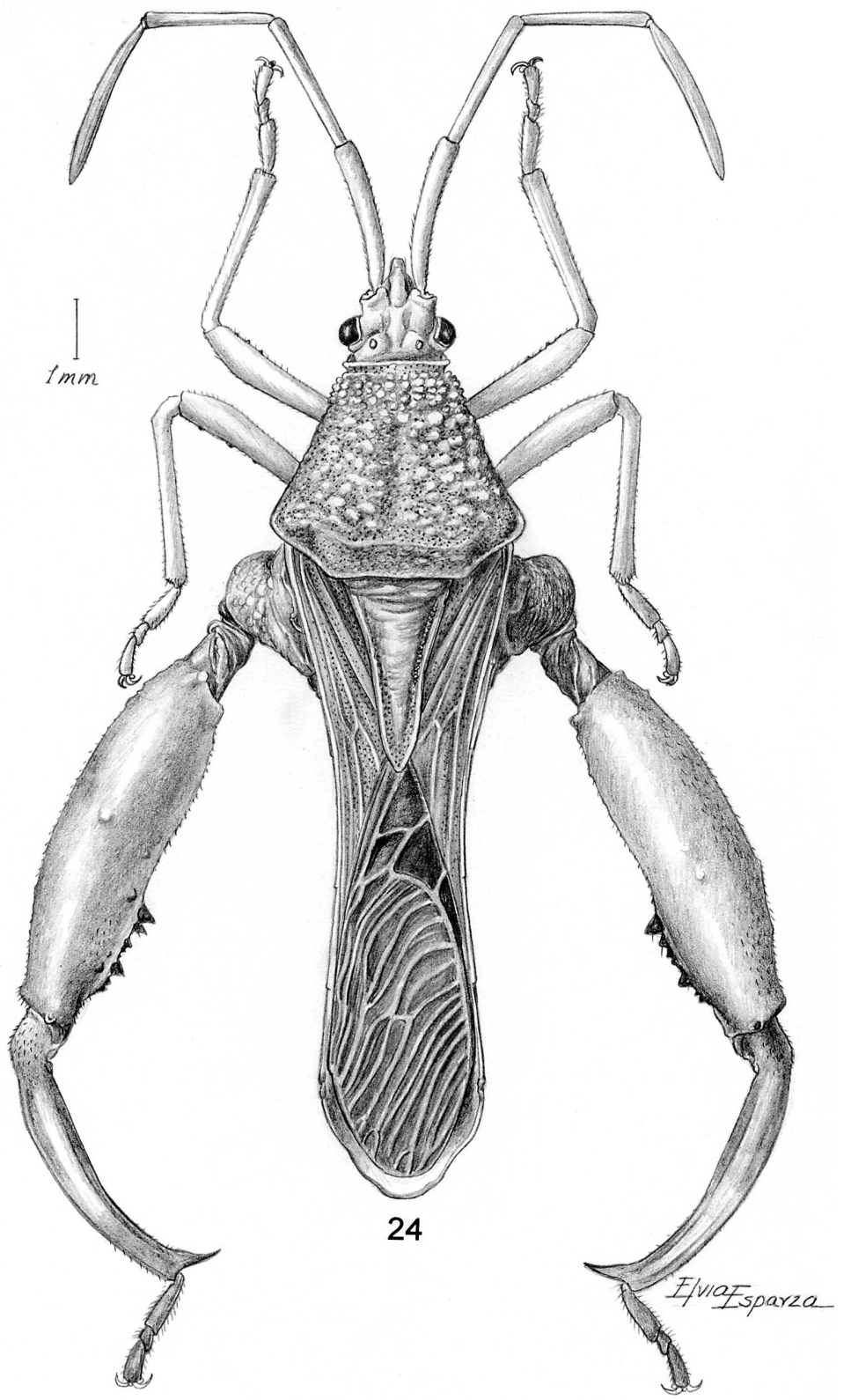


Fig. 24. *Serranoniella amblysa* Brailovsky and Barrera, New Species, dorsal view.

lar space 0.55; distance ocellus to eye 0.20; diameter of ocellus 0.12; preocular distance 1.05. Length antennal segments: I, 3.00; II, 2.32; III, 2.17; IV, 3.20. Length rostral segments: I, 0.76; II, 0.72; III, 0.56; IV, 0.66. Pronotum: Total length 3.75; width across frontal angles 2.35; width across humeral angles 4.45. Scutellar length 3.40; maximum width of anterior lobe 1.80; maximum width of posterior lobe 0.85. Hind leg: femoral length 6.85; tibial length 5.30. Total body length 16.47.

Female. Coloration. Similar to male. Dorsal surface of hind tibia chestnut orange with pale reddish reflections and ventral surface with anterior third dark chestnut red, and posterior third pale chestnut orange; connexival segments VIII-IX dark chestnut orange; dorsal abdominal segments VIII-IX dark brown; genital plates bright chestnut orange. Spermatheca. Spermathecal duct with two distal coils.

Measurements. ♀. Head length 1.40; width across eyes 1.85; interocular space 0.95; interocellar space 0.42; distance ocellus to eye 0.17; diameter of ocellus 0.11; preocular distance 1.15. Length antennal segments: I, 2.55; II, 2.10; III, 2.05; IV, 3.30. Length rostral segments: I, 0.74; II, 0.70; III, 0.50; IV, 0.66. Pronotum: Total length 2.95; width across frontal angles 1.80; width across humeral angles 3.65. Scutellar length 2.60; maximum width of anterior lobe 1.50; maximum width of posterior lobe 0.70. Hind leg: femoral length 5.30; tibial length 4.40. Total body length 13.30.

Holotype: ♂ BRAZIL, Santarem (acc. 6324), IV-1919, coll. S. M. Klages (CMNH).

Paratypes. BRAZIL: 3 ♀♀. Sama data as for holotype (CMNH, UNAM). 1 ♂ Santarem (acc. 2966), coll. S. M. Klages (UNAM). Santarem (acc. 6324), VI-1919, coll. S. M. Klages (CMNH). 1 ♀ Para, Santarem, 6-IV-1956, coll. Elias & Roppa (UNAM). 1 ♂, 1 ♀ Para, Unt Amazonas, J. A. P. ded Eing. nr. 145, 1933 (ZMUH).

Etymology. From the Greek word *amblys* meaning blunt, obtuse, for the blunt body shape.

Distribution. Only known from Brazil.

Acknowledgments

We thank the following colleagues and institutions for the loan of specimens and other assistance relevant to this study: Randall T. Schuh (AMNH); Mick Webb (BMNH); Norman D. Penny (CAS); John Rawlins and Robert Davidson (CMNH); Michael Schwartz (CNCI); Frank W. Mead (formerly at FSCA); Jesus Ugalde (INBIO); Joseph Schaffner (TAMU); Robert W. Sites (UMRM); Hans Strumpel (ZMUH). Special thanks are extended to Albino Luna (UNAM), Elvia Esparza (UNAM) and Jesus Contreras (UNAM) for the preparation of dorsal view illustrations. The Senior author gives thanks to the Dirección General de Asuntos del Personal Academico de la Universidad Nacional Autónoma de México (DGAPA-UNAM) for economic support of the project IN201497.

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EFFECTS OF THE INSECT GROWTH REGULATOR FENOXYCARB ON IMMATURE *CHRYSOPERLA RUFILABRIS* (NEUROPTERA: CHRYSOPIDAE)

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ABSTRACT

Fenoxycarb (Comply®), a juvenile hormone analog, was tested in the laboratory at three concentrations (0.1, 1.0 and 10.0 mg [AI]/l) for toxicity to eggs, three larval instars and pupae of *Chrysoperla rufilabris* (Burmeister). Significant effects of fenoxycarb on all immature stages of *C. rufilabris* were found and the degree of effects depends on the stages treated and the concentrations used. Fenoxycarb showed significant ovicidal effect on *C. rufilabris* eggs, with 66.7, 76.6 and 86.7% survival rates at 0.1, 1.0 and 10.0 mg (AI)/l, respectively. Lethal effects on larvae varied greatly with high survival rates when the larvae were treated in the first and second instars (76.7-86.7% and 90.0-93.3%, respectively), and low survival rates (6.7-16.7%) when third instars were treated. Mortality at the pupal stage ranged from 90.0 to 93.3%. Fenoxycarb significantly delayed the developmental times from the stage treated to adult emergence for all immatures of *C. rufilabris* that successfully developed to adults by 3.2-4.6, 2.3-3.0, 2.1-2.8, and 4.6-7.5 days when egg, first, second and third instars were treated, respectively, compared with water treated control. When treated as pupae, fenoxycarb had no significant effects on pupal development. Among the three larval stages, the third instar is the most susceptible and vulnerable stage. The compatibility of fenoxycarb in integrated pest management programs is discussed.

Key Words: Lacewing, predators, aphids, whiteflies, insect growth regulators, juvenile hormone

RESUMEN

El fenoxycarb (Comply®), una hormona juvenil análoga fue probada en el laboratorio en tres concentraciones (0.1, 1.0 y 10.0 mg [AI]/l) para determinar la toxicidad a huevos, tres instares de larvas y pupas de *Chrysoperla rufilabris* (Burmeister). Se encontraron efectos significativos del fenoxycarb en todas las etapas inmaduras de *C. rufilabris* y el grado de los efectos depende de las etapas tratadas y las concentraciones usadas. Fenoxycarb mostró un efecto ovicida significativo sobre los huevos de *C. rufilabris*, con tasas de supervivencia de 66.7, 76.6 y 86.7% a las concentraciones 0.1, 1.0 y 10.0 mg [AI]/l, respectivamente. Los efectos letales sobre las larvas variaron mucho con tasas altas de supervivencia cuando las larvas fueron tratadas en el primer y segundo instar (76.7-86.7% y 90.0-93.3%, respectivamente), y tasas bajas de supervivencia (7.6%-16.7%) cuando el tercer instar fue tratado. La mortalidad en la etapa pupal varió entre 90.0 a 93.3%. El fenoxycarb retardó significativamente el periodo de desarrollo de la etapa tratada para la emergencia de los adultos en todos los inmaduros de *C. rufilabris* que se desarrollaron bien hasta adultos por 3.2-4.6, 2.3-3.0, 2.1-2.8 y 4.6-7.5 días cuando respectivamente fueron tratados huevo, primer, segundo y tercer instares, en comparación con los del grupo control que fue tratado con agua. Fenoxycarb no tuvo efectos significativos en el desarrollo pupal cuando las pupas fueron tratadas. Entre las tres etapas larvales, el tercer instar es la etapa más susceptible y vulnerable. Se discute la compatibilidad de fenoxycarb en los programas de manejo integrado de plagas.

Fenoxycarb, a non neurotoxic carbamate, exhibits juvenile hormone analog (JHA) activities on many insects despite being structurally dissimilar to insect juvenile hormone (JH) (Dorn et al. 1981; Grenier & Grenier 1993). It has shown JHA activities against insects in several orders including Lepidoptera, Coleoptera, Homoptera, Dictyoptera, Diptera, and Orthoptera (Masner et al. 1980; Grenier & Grenier 1993), but also exhibits some non JHA-specific effects on many insects (Retnakaran et al. 1985).

Integrated pest management (IPM) requires the use of selective pesticides that preserve the natural enemies of the pests. Therefore, knowledge about the effects of pesticides on beneficials is indispensable. However, few studies have been conducted to determine the effects of fenoxycarb on nontarget beneficials. In a laboratory test, Bigler & Waldburger (1994) found that fenoxycarb at 150 mg [AI]/l was extremely toxic to the larvae of the common green lacewing *Chrysoperla carnea* (Stephens). Celli et al. (1997) investigated the activity of fenoxycarb on immatures of *C. carnea* and observed extremely high embryonic and larval mortality and numerous, often lethal, effects on larval development. Fenoxycarb was also found to be harmful (>50% mortality) to brown lacewing, *Micromus tasmaniae* (Walker), in the laboratory,

and slightly harmful (25-50% mortality) in the field (Rumpf & Penman, 1993; Rumpf et al. 1997, 1998). Hassan et al. (1991) reported that fenoxycarb (150 mg [AI]/l) was harmless or slightly harmful to 19 species of beneficial organisms, except for *C. carnea* and *Anthocoris nemoralis* (F.), and while it was harmful to these two predators in the laboratory, it was only slightly harmful to *C. carnea* in a semi-field test. Vogt (1994) found that fenoxycarb (100 mg [AI]/l) was moderately harmful to *C. carnea* larvae in the field.

The green lacewing, *C. rufilabris* (Burmeister), is a polyphagous predator in North America. *C. rufilabris* has potential as a biological control agent against several species of major insect pests, including silverleaf whitefly, *Bemisia argentifolii* Bellow & Perring (formerly known as *B. tabaci* [Gennadius]) (Breene et al. 1992; Legaspi et al. 1994; Nordlund & Morrison 1990); cotton aphid, *Aphis gossypii* Glover (Nordlund & Morrison 1990); Colorado potato beetle, *Leptinotarsa decemlineata* (Say) (Nordlund et al. 1991); tobacco budworm, *Heliothis virescens* (F.) (Nordlund & Morrison 1990); and corn earworm, *Helicoverpa zea* (Boddie) (Lingren et al. 1968). However, few studies on fenoxycarb have dealt with beneficial insects (Grenier & Grenier 1993), and no information is available in the literature on the effects on the green lacewing *C. rufilabris.*

The objective of this study was to determine the effects of fenoxycarb on all immature stages of *C. rufilabris*, the most common lacewing species preying on aphids, whiteflies and many other insects in south Texas and other southern states.

Materials and Methods

Chrysoperla rufilabris

Chrysoperla rufilabris were obtained from a commercial supplier (Biofac Crop Care, Inc., Mathis, TX). Eggs (24-h old) were maintained in a growth chamber at 20 ± 2°C, 50 ± 5% relative humidity and a photoperiod of 16:8 (L:D) h. For egg bioassays, the eggs were used as soon as they were obtained. To obtain desired stages of larvae and pupae, the eggs were allowed to hatch in the growth chamber. After the eggs hatched, the first instars were reared individually in clear plastic petri dishes (5.5 cm diam. × 1.0 cm deep) and were fed with *A. gossypii* feeding on cotton leaves. The larvae were reared until they developed to the desired instars. They were used ≈24 h after the previous molting. To obtain pupae, 2-day old cocoons (pupae) were used because it took about 1 to 2 days to further develop from prepupa to pupa (Legaspi et al. 1994).

Treatments

Fenoxycarb (Comply® 40WP; Novartis, Greensboro, NC) was used at three concentrations: 0.1, 1 and 10 mg (AI)/l, and purified water (reverse osmosis, 7 ppm solids) was used as control. *Chrysoperla rufilabris* eggs, larvae or pupae were dipped in the dilutions or water for 3 s. The treated eggs, larvae or pupae were placed on paper tissues for ≈2 h to absorb extra dilution and air-dry. The insects were then individually placed in petri dishes. Each treatment had 10 replications, and each replication had 10-20 individuals. The larvae treated directly or hatched from treated eggs were fed with *A. gossypii* ad lib. Survival and development were recorded daily. We considered larvae dead if they no longer moved or twitched when being touched 2-3 times with a brush. Pupae were regarded as dead if they turned black, or showed signs of desiccation.

Data Analysis

Percentage survival rates and developmental times (days) for all stages were analyzed using the general linear model (PROC GLM). Means were distinguished using the least significant difference test (LSD) after a significant F-test at P = 0.05 (SAS Institute 1996).

Results

Effects of Fenoxycarb on Survival of *C. rufilabris*

The survivorship of the different developmental stages of *C. rufilabris* treated at different stages is shown in Fig. 1. When eggs were treated, survival rates varied among the three fenoxycarb concentrations (F = 9.33-34.67; df = 3, 8; P = 0.0008-0.0054) (Fig. 1A). The egg hatching rate was 66.7% at the highest concentration (10 mg [AI]/l), and 86.7% at the lowest rate (0.1 mg [AI]/l), compared with 100% in the water control. When first instars were treated, the survival rate decreased significantly at the two higher concentrations with 86.7% at 10 mg [AI]/l and 90.0% at 1 mg [AI]/l compared with 100% in the water control (F = 6.67; df = 3, 8; P = 0.0144) (Fig. 1B). However, the survival rates were not significantly decreased in subsequent developmental stages. When second instars were treated, 93.3-96.7% developed to adults, with no significant difference among the 4 treatments (F = 0.44-0.67; df = 3, 8; P = 0.5957-0.7278) (Fig. 1C). The most significant effects were found when third instars were treated (Fig. 1D). The survival rate of third instars (cocooning or pupation rate) was reduced significantly, and only 40.0-53.3% pupated compared with 100% in the water control (F = 5.67; df = 3, 8; P = 0.0222). Subsequently, only 6.7-16.67% successfully developed to adults compared with100% in the water control (F = 76.0; df = 3, 8; P = 0.0001). Fenoxycarb had no significant lethal effects on pupae when they were treated at pupal stage (F = 0.89; df = 3, 8; P = 0.4872) (Fig. 1E).

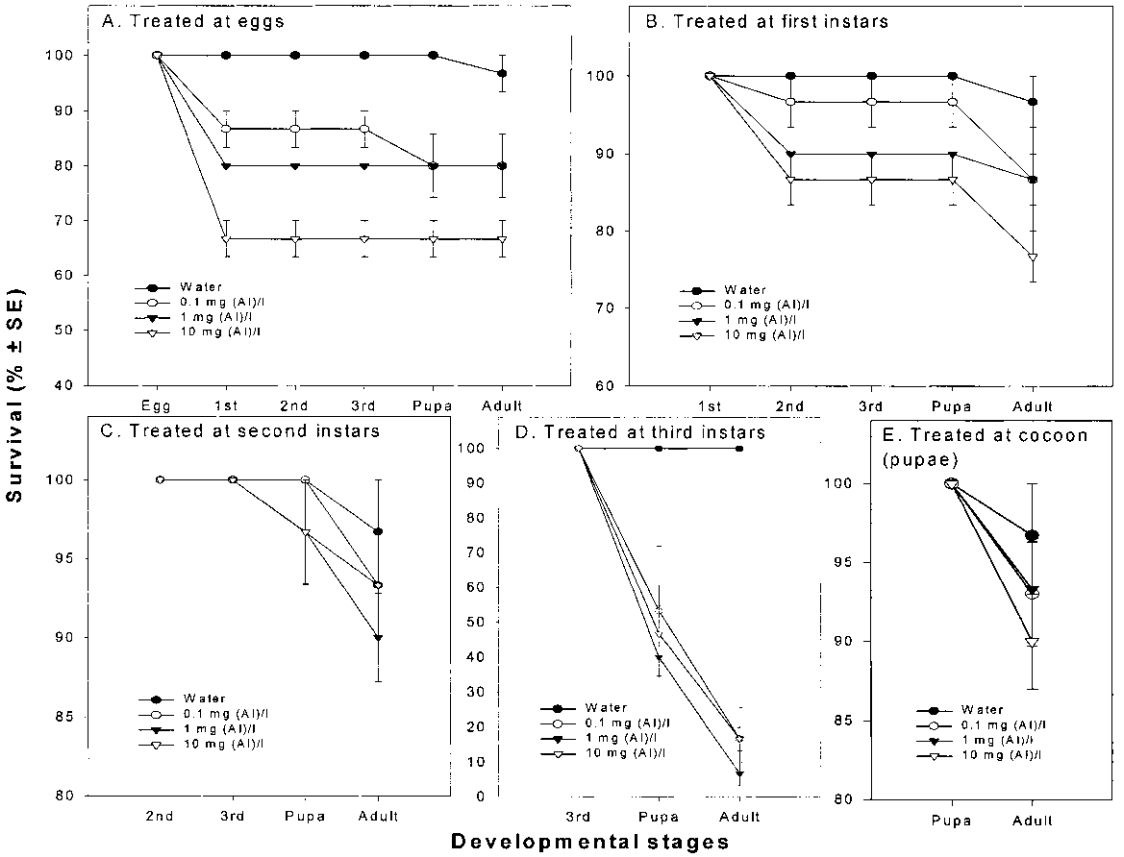

Fig. 1. Percentage of survival of eggs, larvae, and pupae of *Chrysoperla rufilabris* after treatment with three concentrations of fenoxycarb at different developmental stages.

Effects of Fenoxycarb on Development of Immature *C. rufilabris*

Developmental times of all stages of *C. rufilabris* after being treated with fenoxycarb are shown in Fig. 2 and Table 1. When eggs were treated, there were no significant effects on the developmental times of eggs at the two lower concentrations, but the developmental time of eggs was delayed 0.5 days at the highest concentration compared with that in the water control (F = 71.28; df = 3, 88; P = 0.0001) (Fig. 2A). Significant development delays were also found in the third instar and pupal stage at all three of the concentrations. The developmental time of third instars was 2.3-2.8 days longer than that in the water control (F = 43.80; df = 3, 86; P = 0.0001), and that of the pupae was 0.4-0.8 days longer than that in the water control (F = 5.01; df = 3, 84; P = 0.003). The overall developmental time from egg to adult emergence was 26.5-27.9 days, 3.2-4.6 days longer than 23.3 days in the water control (F = 104.53; df = 3, 84; P = 0.0001) (Table 1). When first instars were treated, there were no significant effects on the subsequent development of the first instar (F = 1.63; df = 3,100; P = 0.1868) and the second instar (F = 0.78; df = 3, 100; P = 0.51) (Fig. 2B). However, the developmental times of treated first instars were delayed at the third instar and pupal stages at all of the three concentrations. The developmental time of the third instar was 1.6-2.1 days longer than that in the water control (F = 32.02; df = 3,100; P = 0.0001), and that of the pupae was 2.6-3.0 days longer than that in the water control (F = 3.13; df = 3, 92; P = 0.0295). The overall developmental time from first instar to adult emergence was 21.7-22.3 days compared with 19.3 days in the water control (F = 24.80; df = 3, 92; P = 0.0001) (Table 1). When second instar was treated, the developmental time of the second instar was prolonged 0.3-0.5 days (F = 2.86; df = 3, 108; P = 0.0404), and that of the third instar was prolonged 1.4-2.0 days (F = 27.48; df = 3, 106; P = 0.0001) compared to that in the water control (Fig. 2C). The developmental time of pupae was not significantly prolonged among the four treatments (F =1.87; df = 3, 100; P = 0.1393). The overall developmental time from second instar to adult emergence was 19.8-20.5 days compared with 17.7 days in the water control (F = 28.43; df = 3,

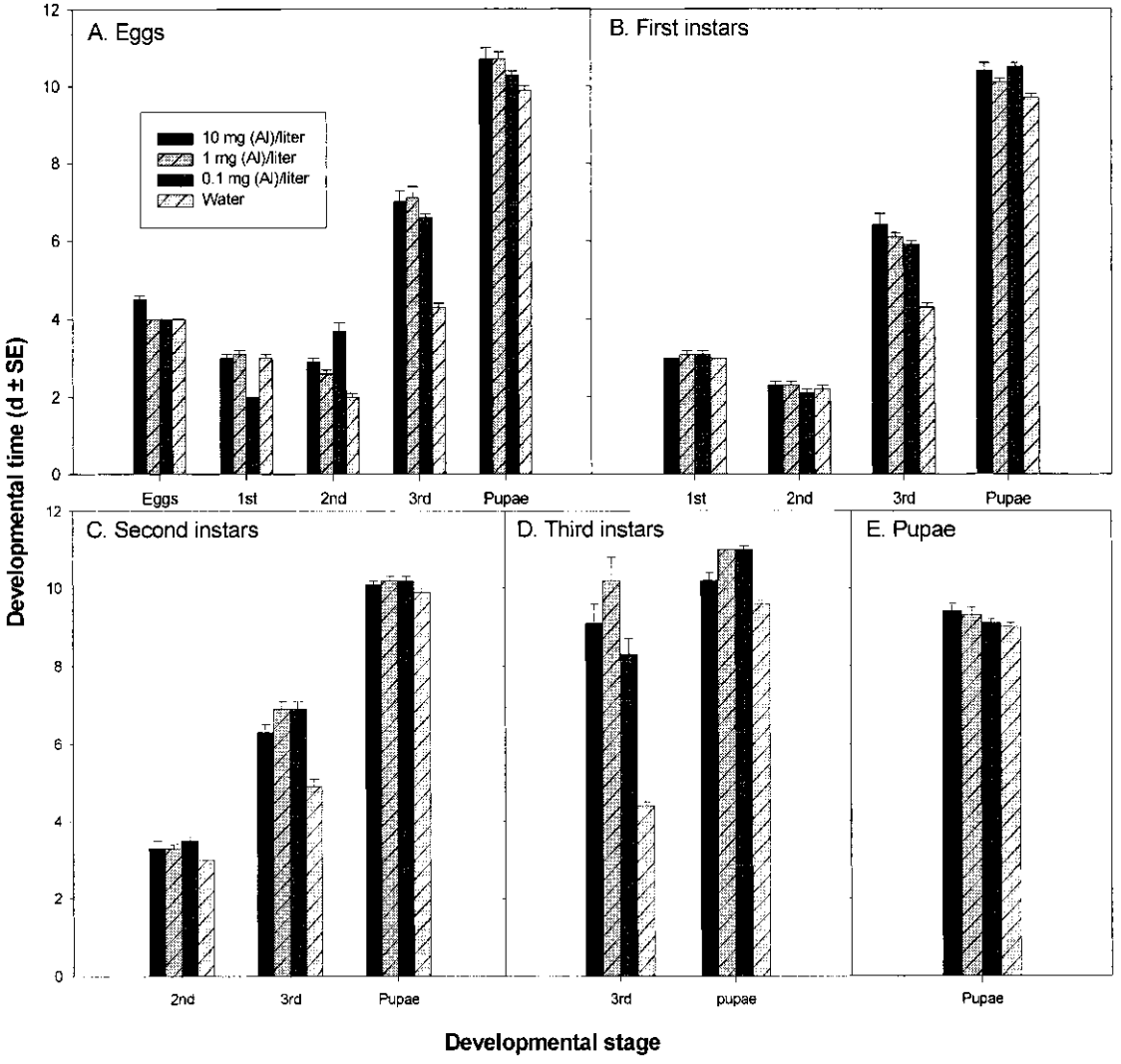

Fig. 2. Developmental time of eggs, larvae and pupae of *Chrysoperla rufilabris* after treatment with three concentrations of fenoxycarb at different developmental stages.

100; P = 0.0001) (Table 1). When third instars were treated, developmental time was delayed at the third instar and pupal stage (Fig. 2D). The developmental time of the third instar was 3.9-4.7 days longer than that in the water control (F = 67.20; df = 3, 60; P = 0.0001), and that of the pupae was 0.6-1.4 days longer than that in the water control (F = 8.28; df = 3, 32; P = 0.0001). The overall developmental time from third instar to adult emergence was 18.6-20.0 days compared with 14.0 days in the water control (F = 96.37; df = 3, 32; P = 0.0001) (Table 1). When pupae were treated, the developmental times of pupae did not differ significantly among the four treatments (F = 1.83; df = 3, 100; P = 0.1469) (Fig. 2E, Table 1).

Discussion

Our results indicated that application of fenoxycarb to eggs and larvae of *C. rufilabris* resulted in decreased survival rates and prolonged development times when treated at different immature stages and at different concentrations. Fenoxycarb showed significant ovicidal effect on *C. rufilabris* eggs, with 66.7-80.0% survival rates, depending on the larval stages treated and the concentrations used. Generally, the higher concentrations exhibited greater effects on the larval stages treated and the subsequent stages of the larvae. Similar effect has been reported on *C. carnea* by Bigler and Waldburger (1994) and Celli

TABLE 1. EFFECT OF FENOXYCARB ON THE DEVELOPMENT OF CHRYSOPERLA RUFILABRIS WHEN TREATED AT DIFFERENT DEVELOPMENTAL STAGES.

Concentration, Mg (AI)/liter	*Stage treated and developmental time (d ± SE)*[a]				
	Eggs	1st instars	2nd instars	3rd instars	Pupae
10	27.9 ± 0.3a	22.3 ± 0.3a	19.8 ± 0.4b	20.0 ± 0.8b	9.4 ± 0.2
1	27.2 ± 0.3b	21.7 ± 0.5a	20.5 ± 0.2a	21.5 ± 2.5a	9.3 ± 0.2
0.1	26.5 ± 0.2c	21.6 ± 0.2a	20.5 ± 0.2c	18.6 ± 0.6c	9.1 ± 0.1
Water	23.3 ± 0.2d	19.3 ± 0.1b	17.7 ± 2.d	14.0 ± 0.1d	9.0 ± 0.1
F	104.53	24.81	28.43	96.37	1.83
P	0.0001	0.0001	0.0001	0.0001	0.1469
df	3, 84	3, 92	3,100	3, 32	3, 100

[a]Means in the same column followed by the same letters do not differ significantly at $P = 0.05$ (LSD, SAS Institute 1996).

et al. (1997). We do not know why fenoxycarb shows ovicidal effects on some insects (including *Chrysoperla*), but not on others. Charmillot et al. (1985) observed that fenoxycarb showed more severe effects on the eggs laid singly than those laid in egg masses. They suggested that the difference may be due to a lack of contact or a reduction of contact between the eggs in masses and the treated leaf surfaces. This explanation is consistent with the poor ovicidal performance of fenoxycarb on some insects with egg masses, but exhibiting severe ovicidal effect on *Chrysoperla* spp. that lay their eggs singly.

We observed that among the immature stages, the third instar was the most susceptible and vulnerable stage with the highest mortality and longest developmental delay regardless whether the egg, first, second, or third instar was treated. We do not know why the third instar is the most susceptible stage. Generally, the juvenile hormone (JH) titers gradually decrease as the larvae approach pupation, in this case, the third instar larvae of *C. rufilabris*. One possible explanation might be that application of fenoxycarb to third instar larvae overdosed the JH level in the larvae, and the JHA fenoxycarb could not be metabolized before the metamorphosis. As a result, metamorphosis (pupation) is disturbed or blocked. We observed that some third instars that survived had difficulty spinning cocoons. Some did not have silk to make the cocoon, whereas others produced isolated silk threads, but could not make a complete cocoon. Some larvae managed to pupate even in an incomplete cocoon. All those that did not make cocoons or did not have a complete cocoon died at the pupal stage or as pharate adults. Compared with the third instars, the first and the second instars have relatively high levels of JH, and have sufficient time and ability to metabolize the added juvenile analog.

Fenoxycarb not only causes high mortalities and prolonged developmental times on *Chrysoperla* spp., but also inhibits egg production of the adult *C. carnea* when second or third instars were treated (Celli et al. 1997). As reported in the literature (i.e., Grenier & Plantevin 1990; Grenier & Grenier 1993), fenoxycarb is toxic to other predators and parasitoids, such as *Anthocoris*, *Chilocorus*, and some species in Tachinidae, Braconidae and Aphelinidae, as well as many other beneficial insects, such as silkworms and bees. Our results indicate that fenoxycarb is nonselective to *Chrysoperla* spp. and cannot be used where these predators are dominant. Although data obtained from laboratory toxicity studies have been sufficient to decide upon the use of insecticides in IPM (in cases where mortality was low in laboratory experiments) (Barrett el al. 1994), semi-field and field studies are still needed. More research on the effects of fenoxycarb on lacewings, and other predators and parasitoids under different agroecosystems is also needed to elucidate how to use IGRs in IPM programs.

ACKNOWLEDGMENTS

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FEEDING ON METHYL EUGENOL AND *FAGRAEA BERTERIANA* FLOWERS INCREASES LONG-RANGE FEMALE ATTRACTION BY MALES OF THE ORIENTAL FRUIT FLY (DIPTERA: TEPHRITIDAE)

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ABSTRACT

Males of the oriental fruit fly, *Bactrocera dorsalis* (Hendel), are strongly attracted to methyl eugenol. Recent evidence indicates that treated males fed methyl eugenol have higher mating success and signaling (wing-fanning) activity than control (unfed) males. Chemical analyses have further shown that metabolites of methyl eugenol are incorporated into the male sex pheromone, and laboratory tests revealed that, at least over short distances (<2 m), the pheromonal signals of methyl eugenol-fed males are more attractive to females than those of unfed males. The main goal of the present study was to determine whether feeding on methyl eugenol or flowers of *Fagraea berteriana* A. Gray that contain a methyl eugenol-like compound increases the long-distance attractiveness of male *B. dorsalis* under field conditions. Male aggregations, composed of either treated or control males, were established on orange trees, females were released from a central point (12 m from the male groups), and male wing-fanning and female visitation were recorded. For both methyl eugenol and *F. berteriana* flowers, aggregations of treated males had higher wing-fanning levels and attracted more females on both an absolute (total female sightings per male group) and relative (female sightings per wing-fanning male per group) basis than aggregations of control males. In an additional laboratory experiment, males that fed upon *F. berteriana* flowers were found to be more attractive to females over short distances (<2 m) than control males, consistent with results from other methyl eugenol-containing plant species.

Key Words: *Bactrocera dorsalis*, methyl eugenol, pheromone, lek

RESUMEN

Los machos de la mosca oriental de la fruta, *Bactrocera dorsalis* (Hendel), son atraídos fuertemente por el metil eugenol. Evidencias recientes indican que los machos tratados (alimentados) con metil eugenol tienen un alto éxito de apareamiento y actividad de comunicación (abanicado de alas) comparados con los machos control (no alimentados). Análisis químicos también han demostrado que los metabolitos del metil eugenol son incorporados en la feromona sexual del macho, y pruebas de laboratorio han revelado que, al menos en distancias cortas (<2 m), las señales feromonales de los machos alimentados con metil eugenol son más atractivas a las hembras que aquellas de machos no alimentados. La meta principal de este estudio fue determinar si la alimentación con metil eugenol ó flores de *Fagraea berteriana* A. Gray, que contienen un compuesto similar al metil eugenol, incrementa la atracción a larga distancia de machos de *B. dorsalis* bajo condiciones de campo. Agregaciones de machos, tanto tratados como no tratados, fueron establecidas en árboles de naranja, las hembras fueron liberadas desde un punto central (a 12 m del grupo de machos), y se tomo nota del abanicado de alas por los machos y de la visita por las hembras. Tanto para metil eugenol como para las flores de *F. berteriana*, las agregaciones de machos tratados mostraron niveles más altos de abanicado de alas y atrajeron a más hembras, en base absoluta (observación del total de hembras por grupo de machos) y relativa (observación de hembras por macho abanicando sus alas por grupo), comparado con las agregaciones de machos-control. En un experimento de laboratorio adicional, se encontró que machos alimentados con flores de *F. berteriana* fueron mas atractivos a las hembras en cortas distancias (<2 m) en comparación con los machos-control, siendo esto consistente con resultados de otras especies que contienen metil eugenol.

Males of many *Bactrocera* species are strongly attracted to methyl eugenol, a naturally occurring compound found in at least 10 plant families (Metcalf 1990). This attraction is so powerful that methyl eugenol in combination with insecticides has been used successfully in programs of "male annihilation" against the oriental fruit fly, *Bactrocera dorsalis* (Hendel) (Steiner et al. 1965, 1970). Until recently, however, little attention was given to the underlying biological basis of male attraction. Research completed in Asia (Tan & Nishida 1996; Hee & Tan 1998) and Hawaii (Shelly & Dewire 1994; Shelly et al. 1996; Shelly 2000a, 2001a) provides strong evidence that ingestion of methyl eugenol enhances male mating success in several *Bactrocera* species, including *B. dorsalis*. Although most of the cited studies used pure, synthetic methyl eugenol, additional experiments us-

ing natural sources of methyl eugenol or methyl eugenol-like compounds have also documented a large positive effect on the mating success of male *B. dorsalis* (Nishida et al. 1997; Shelly 2000a, 2001a).

The factor(s) underlying this increase in male mating competitiveness is not known. For *B. dorsalis*, chemical analysis of the rectal gland contents (the presumed storage reservoir of male pheromone) of males fed methyl eugenol revealed the presence of metabolites of methyl eugenol, suggesting they function in pheromonal synthesis (Nishida et al. 1988). Behavioral assays conducted in laboratory cages furnished supporting data: *B. dorsalis* males that fed on methyl eugenol (Shelly & Dewire 1994) or methyl eugenol-containing flowers (Shelly 2000a) were found to signal more frequently and to attract more females than did control males. Similar results were reported by Hee & Tan (1998). Although supportive, these behavioral studies were conducted in artificial environments and monitored female attraction over short distances (<2 m).

The main objective of the present study was to determine whether exposure of *B. dorsalis* males to pure methyl eugenol or flowers of the puakenikeni tree, *Fagraea berteriana* A. Gray, which contain a methyl eugenol-like compound (Nishida et al. 1997), enhances female attraction over long distances (>10 m) in the field. To supplement previous experiments with methyl eugenol and flowers of the golden shower tree, *Cassia fistula* L., a laboratory experiment was conducted using an indoor cage to test whether exposure to puakenikeni flowers affected short-range attractiveness of males.

B. dorsalis appears to display a lek mating system. Males aggregate on the foliage of host trees approximately 1 h before dusk and defend individual leaves as mating territories (Shelly & Kaneshiro 1991). While perching, males engage in vigorous wing-fanning, an activity that both produces an audible buzz and disperses a pheromone attractive to females (Fletcher 1987). Upon detecting a female in their territory, males immediately cease wing-fanning and jump on the female (Shelly & Kaneshiro 1991). The female then either decamps or copulation ensues. Mating couples remain paired through the night and separate at sunrise (Fletcher 1987).

Materials and Methods

Study Animals

Because wild flies were reluctant to wing-fan in small cages, the flies used in this study were from a colony maintained by the USDA-ARS Tropical Fruit, Vegetable, and Ornamental Crop Laboratory (USDA-ARS), Honolulu, for about 70 generations (Tanaka et al. 1969). Non-irradiated pupae were obtained 2 d before eclosion, and adults were separated by sex within 5 d of emergence (sexual maturity in this stock is attained at about 10 d of age; Shelly, unpublished data). Adults were held in plastic buckets (5-liter volume; 60-80 individuals per bucket) covered with screen mesh and supplied with ample food (a mixture of honey and protein hydrolysate) and water. Room temperature was maintained at 23-26°C and relative humidity at 65-85%. When used in the experiments, males were 14-20 d old, and females were 13-19 d old.

Field Experiments

Field work was conducted in a grove of approximately 30 orange trees, *Citrus sinensis* (L.) Osbeck, at the Agricultural Experiment Station of the University of Hawaii in Waimanalo, Oahu, during September-October, 1994. Several trees in the orchard had fruit, but none of these was included in the set of test trees (see below). Air temperatures during the trials ranged from 26-29°C.

The same protocol was followed to examine the influence of methyl eugenol and puakenikeni flowers on female attraction to calling males. Groups of 5 treated (methyl eugenol- or floral-exposed) or control (unexposed) males were placed in transparent cups (400 ml) that were covered on both ends with wire mesh. Cups were transported to the field and hung, two per tree within 30 cm of one another, in the canopy of the test trees. Cups were suspended horizontally (i.e. with the long axis of the cup parallel to the ground) with wire at a height of approximately 1.5 m, and strips of green masking tape on the upper surface of the cups provided shaded, leaf-like perching sites for the males. Cups were placed in 8 different orange trees, with 4 trees containing 10 treated males (2 cups) exclusively and 4 trees containing 10 control males (2 cups) exclusively. The test trees were located in a circle (12 m radius) around a central tree that served as the female release point. For a given replicate, treated and control males were alternated between adjacent trees, and, for a given tree, they were alternated between successive replicates.

Treated males exposed to methyl eugenol were given unrestricted access during a 1-h period to a cotton wick (5 cm long) to which 1.5 ml of methyl eugenol had been applied. The wick, held upright in a small plastic container, was placed in a cubical screen cage (30 cm on a side) during midday, and 50-60 males were introduced into the cage. At the end of the exposure period, the wick was removed, and males were provided with food and water and held 2 d before use in the experiment. Treated males exposed to puakenikeni flowers were given unrestricted access to 25-35 flowers during a 6-h period (0900-1500 hours). Fresh flowers were obtained from lei shops and placed

in a screen cage the same day as purchase along with 50-60 males. Flowers were held in a plastic tray, and at the end of the exposure period the tray was removed. As with methyl eugenol, males were used 2 d after floral exposure. Although systematic observations were not made, groups of males were frequently observed dabbing the methyl eugenol-containing wick and the puakenikeni flowers with their mouth parts. For both treatments, exposure was performed outdoors to minimize exposure of volatiles to control males.

Males were placed in the trees between 1800-1815 hours, and 10 min later 300 females were released from the central tree. Numbers of wing-fanning males and female sightings at each aggregation (both cups combined) were recorded at 5 min intervals for the next 60 min (i.e. 13 observations per tree per replicate). Females were scored if they were perching directly on or within 15 cm of the cups. Because females were unmarked, the number of female sightings at a lek was a composite score that included both arrival and retention at a given site. Six and 7 replicates were performed for methyl eugenol and puakenikeni floral exposure, respectively. Replicates were conducted ≥2 d apart to guarantee dispersal of released females from the study area.

Laboratory Experiment

A laboratory experiment was performed to investigate the influence of puakenikeni flowers on male attractiveness over shorter distances, likely characteristic of intersexual communication within a tree canopy. Tests were conducted on groups of 8 males (4 treated, 4 control) in a screen cage (1.2 m by 0.6 m by 0.6 m) that contained 3 potted plants *Ficus* sp. Treated males were exposed to puakenikeni flowers in the manner described above and were used 2 or 7 d after exposure. Approximately 3 h before sunset, males were placed singly in smaller cages (wire screen cylinders 6 cm long and 3 cm diameter suspended from branches with a wire hook), which were placed at specific locations on the caged plants. The mean nearest-neighbor distance between the small cages was 20 cm (range: 16-22 cm). Small cages were placed at the same locations over all trials, but male type (treated or control) at a given location was assigned randomly at the start of a trial. Immediately after the males were in place, 40 females were released into the large cage containing the *Ficus* plants. The room lights were extinguished, and the cage, which was adjacent to a west-facing window, received only natural light. Starting 1 h before sunset, males were checked at 1-min intervals for the presence/absence of wing-fanning and for the number of females resting on the individual small cages. Observations were made on 8 d and 5 d for the 2-d and 7-d post-exposure intervals, respectively.

Statistical Analyses

In both field experiments, male wing-fanning activity for individual leks was expressed as the mean over all observations in a replicate. In the laboratory study, signaling activity for individual males was the number of 1-min checks during which males were wing-fanning. In both the field and laboratory experiments, female sightings were compared between treated and control males on an absolute basis (total female sightings per aggregation or per individual male) and a relative basis (female sightings per wing-fanning male or per min wing-fanning). Comparisons between aggregations of treated versus control males (field experiments) and between individual treated versus control males (laboratory experiment) were made using the Mann-Whitney test (test statistic *T*).

RESULTS

Field Experiments

Males exposed to methyl eugenol displayed higher levels of wing-fanning than control males (Fig. 1a). Among the individual leks, an average of 2.9 treated males were wing-fanning per observation compared with 2.1 control males ($T = 727.0$; $P < 0.05$; $n_1 = n_2 = 24$ for this experiment). Similarly, the total number of female sightings was greater for groups of treated males ($x = 3.8$) than control males ($\bar{x} = 0.4$; $T = 806.0$; $P < 0.001$; Fig. 1b). When ratios of female sightings to wing-fanning males were calculated on a per observation basis, the leks consisting of treated males were characterized by significantly higher values ($\bar{x} = 0.05$) than leks composed of control males ($\bar{x} = .01$; $T = 808.5$; $P < 0.001$; Fig. 1c).

Similar results were obtained in the experiment testing puakenikeni flowers. Males exposed to flowers displayed higher levels of wing-fanning than control males (Fig. 2a). Among the individual leks, a mean of 2.6 treated males were wing-fanning per observation compared to 1.3 control males ($T = 1106.5$; $P < 0.001$; $n_1 = n_2 = 28$ for this experiment). Similarly, number of female sightings was greater for groups of treated males ($x = 6.0$) than control males ($\bar{x} = 1.9$; $T = 1039.0$; $P < 0.001$; Fig. 2b). When ratios of female sightings to wing-fanning males were calculated on a per observation basis, the leks consisting of treated males were characterized by significantly higher values ($\bar{x} = 0.08$) than leks composed of control males ($\bar{x} = .05$; $T = 927.5$; $P < 0.05$; Fig. 2c).

Laboratory Experiment

Floral exposure had a significant effect on male wing-fanning and female sightings in tests run 2 d after exposure. On average, treated males wing-

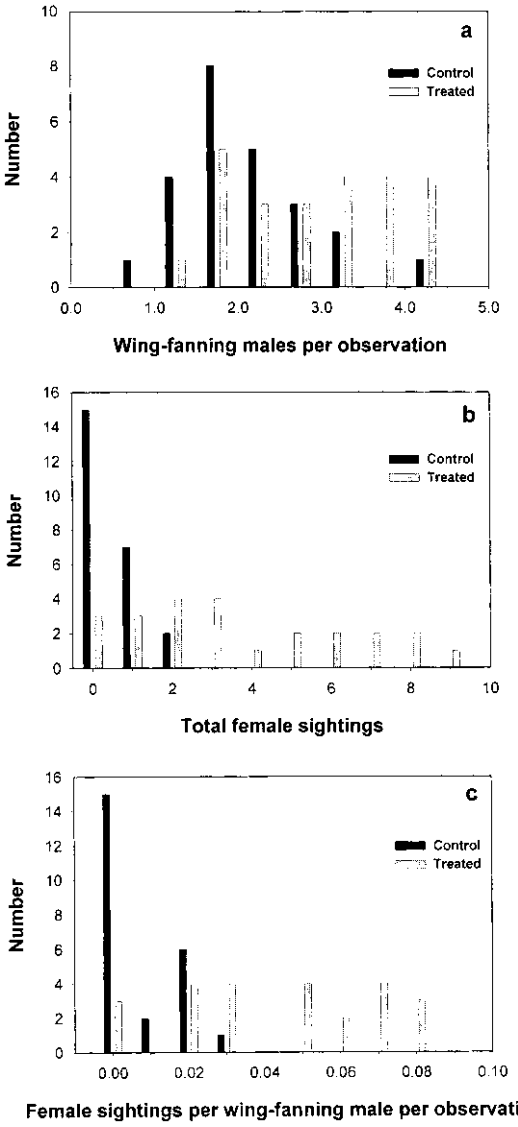

Fig. 1. Results of the field experiment comparing (treated) males exposed to methyl eugenol 2 d before use with (control) males not given access to the chemical. (a) Frequency distribution of male signaling levels among individual leks (n = 24 per treatment). The abscissa represents the mean number of males observed wing-fanning per lek per observation. (b) Frequency distribution of female sightings among individual leks. The abscissa represents the total number of female sightings recorded per lek per replicate. (c) Frequency distribution of female:signaling male ratios among individual leks. The abscissa represents the mean ratio of female sightings to wing-fanning males per lek per observation. In all plots, the ordinate represents the number of individual leks assigned to a particular interval along the abscissa.

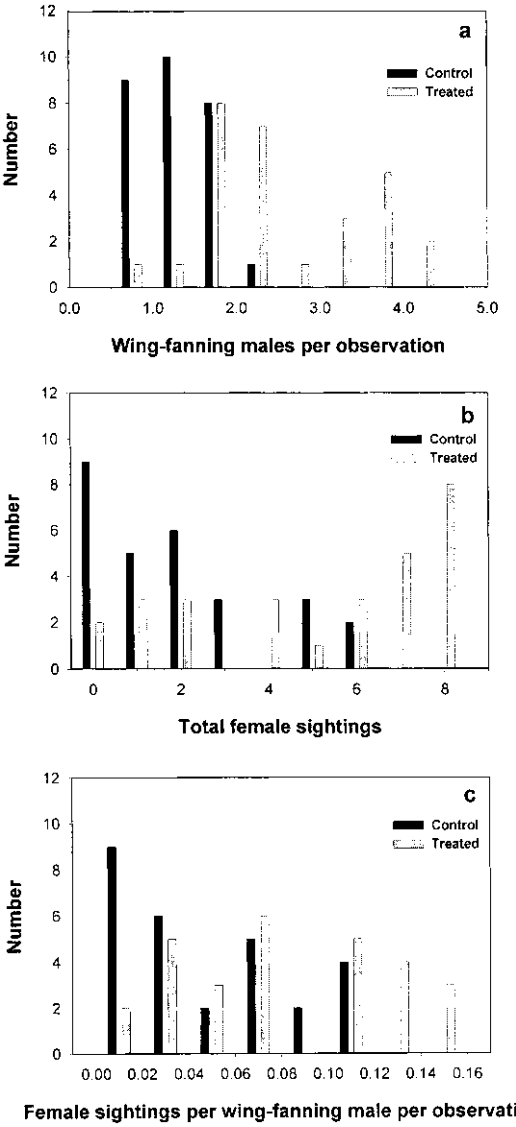

Fig. 2. Results of the field experiment comparing (treated) males exposed to puakenikeni flowers 2 d before use with (control) males not given access to the flowers. (a) Frequency distribution of male signaling levels among individual leks (n = 28 per treatment). (b) Frequency distribution of female sightings among individual leks. (c) Frequency distribution of female:signaling male ratios among individual leks. Axes are the same as Fig. 1.

fanned for 16.3 min compared to 10.5 min for control males ($T = 1202.5$; $P < 0.05$; $n_1 = n_2 = 32$; Fig. 3a). Female sightings were also greater for treated ($\bar{x}$ = 22.4 sightings) than control ($\bar{x}$ = 6.3 sightings) males ($T = 1336.0$; $P < 0.001$; $n_1 = n_2 = 32$; Fig. 3b). In addition to this difference in absolute numbers, female sightings per min of wing-fanning were also greater for treated ($\bar{x}$ = 1.6 females/min wing-fanning) than control ($\bar{x}$ = 0.6 females/min wing-fanning) males ($T = 460.0$; $P < 0.001$; $n_1 = 26$, $n_2 = 29$; Fig. 3c).

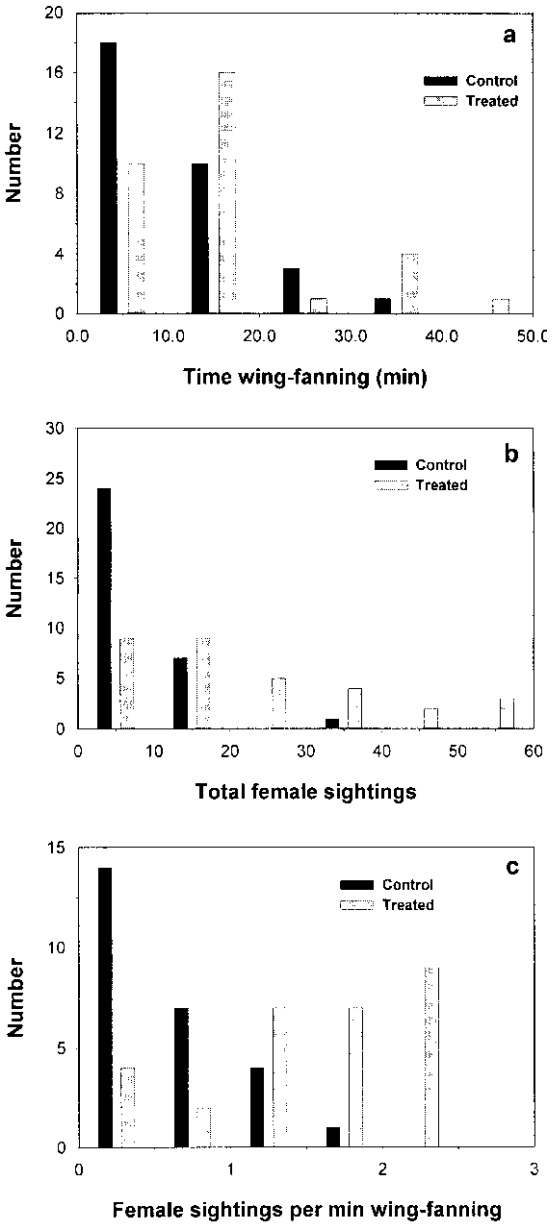

Fig. 3. Results of the laboratory test comparing (treated) males exposed to puakenikeni flowers 2 d before use with (control) males not given access to the flowers. (a) Frequency distribution of signaling activity among individual males (n = 32 per treatment). The abscissa represents the time spent wing-fanning by individual males during 1-h observation periods. (b) Frequency distribution of female sightings among individual males. The abscissa represents the total number of female sightings recorded per male per replicate. (c) Frequency distribution of female:signaling effort ratios among individual males. The abscissa represents the ratio of female sightings-to-time spent wing-fanning for individual males. In all plots, the ordinate represents the number of individual males assigned to a particular interval along the abscissa.

In tests conducted 7 d after exposure, floral exposure had no detectable effect on male wing-fanning level but had a significant effect on female sightings (Fig. 4). On average, treated males wing-fanned for 15.7 min compared to 12.4 min for control males (T = 443.0; NS; $n_1 = n_2 = 20$; Fig 4a). Despite this similarity, female sightings were significantly greater for treated (x = 16.5 female sightings) than control (x = 3.8 sightings) males (T = 503.0; $P < 0.05$; $n_1 = n_2 = 20$; Fig. 4b). Likewise, when calculated on the basis of time spent wing-fanning, female sightings were greater for treated ($\bar{x}$ = 1.1 females/min wing-fanning) than control ($\bar{x}$ = 0.3 females/min wing-fanning) males (T = 159.5; $P < 0.01$; $n_1 = 15$, $n_2 = 16$; Fig. 4c).

Discussion

Coupled with previous findings (Shelly & Dewire 1994; Nishida et al. 1997; Shelly 2000a, 2001a), the results described here indicate that *B. dorsalis* males that feed on methyl eugenol or flowers containing methyl eugenol or methyl eugenol-like compounds have an advantage over unfed males at different spatial scales in sexual competition. In the aforementioned studies, treated males obtained 61-89% of all matings in tests conducted in small cages (30 cm^3), where long-distance attraction had little or no role and close-range, courtship signals were presumably the prime determinant of male mating success. Likewise, prior studies along with the present findings showed that female sightings were approximately 2-5 times more frequent near treated males than control males in tests performed in large cages (1.2 by 0.6 by 0.6 m) that mimicked the environment in which "intra-tree" communication occurs between the sexes. Finally, the present field experiments demonstrated that treated males attracted more females than control males over a large distance (12 m), indicating an advantage in "inter-tree" signaling as well.

The increased female visitation observed for treated males appears to reflect both an increase in wing-fanning activity and the attractiveness of the pheromonal signal per se. This dual effect was noted following feeding on pure methyl eugenol (Shelly & Dewire 1994) or flowers containing methyl eugenol (Shelly 2001a) or a methyl eugenol-like compound (this study). The only exception involved tests with methyl eugenol-containing flowers of the golden shower tree where signal attractiveness was enhanced but the overall level of male signaling was not (Shelly 2000a). As noted above, the increase in signal attractiveness may result from the incorporation of breakdown products of methyl eugenol into the pheromone (Nishida et al. 1997). This scenario resembles that described for various Lepidoptera, where adult males acquire plant compounds (pyrollizidine alkaloids) and use them as pheromone precursors

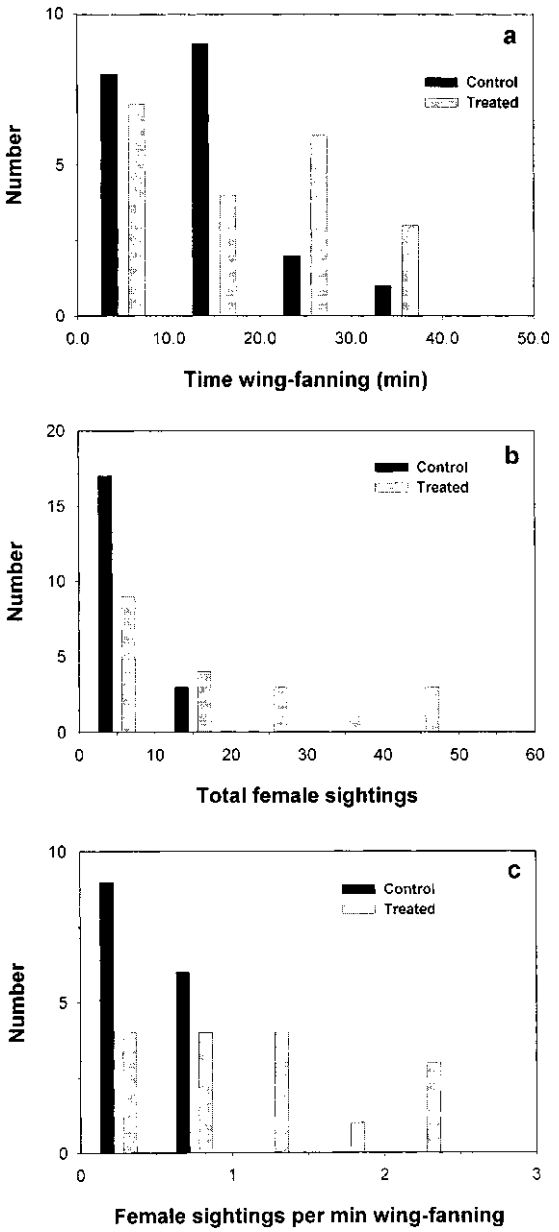

Fig. 4. Results of the laboratory test comparing (treated) males exposed to puakenikeni flowers 7 d before use with (control) males not given access to the flowers. (a) Frequency distribution of signaling activity among individual males (n = 20 per treatment). (b) Frequency distribution of female sightings among individual males. (c) Frequency distribution of female: signaling effort ratios among individual males. Axes are the same as Fig. 3.

(Landolt & Phillips 1997). In contrast, exposure of male Mediterranean fruit flies, *Ceratitis capitata* (Wied.), to a natural attractant (ginger root oil) enhances signaling activity but has no effect on the attractiveness of the signal produced (Shelly 2001b). Unlike the oriental fruit fly, however, *C. capitata* males do not feed on this attractant.

Although there is a strong female preference for methyl eugenol-fed males of *B. dorsalis*, its adaptive basis, if any, remains unknown. The preference does not appear to arise from any direct benefits of mating: egg production and hatch rate do not differ between females mated to methyl eugenol-fed or unfed males (Shelly 2000b). Alternatively, incorporation of metabolites of methyl eugenol in the sex pheromone may elicit a strong, pre-existing sensory bias that has evolved in a different context (e.g., food searching). This notion is supported by reports that male pheromones in other tephritid species contain certain compounds that mimic food and host odors (Baker et al. 1990; Robacker & Warfield 1993). Thus, the methyl eugenol-bearing pheromone may represent a sensory trap (West-Eberhard 1984) or a case of sensory exploitation (Ryan 1990). A final (and not mutually exclusive) hypothesis is that pheromone composition indicates male ability to locate natural sources of methyl eugenol in the environment. As such, by selecting males whose pheromone contains methyl eugenol metabolities, females may increase the probability that their sons will have a high ability to locate methyl eugenol sources and hence enjoy a high mating success. If true, this scenario represents a case of runaway selection (Andersson 1994), where female preference is based on a trait that is arbitrary with respect to offspring viability but does confer an advantage to male progeny in mating competition.

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DISTRIBUTION AND MOVEMENT OF ADULT *DIAPREPES ABBREVIATUS* (COLEOPTERA: CURCULIONIDAE) IN A FLORIDA CITRUS GROVE

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Abstract

Over 10 weeks, 765 adult, feral *Díaprepes abbreviatus* were captured from 750 young citrus trees by dislodging them into inverted umbrellas. Newly captured weevils were distributed evenly among plots throughout the experimental site. Five hundred eighty of these weevils were marked and released; 146 were recovered. Recaptured (marked) weevils tended to stay close to the release point. Because recaptured weevils were not homogenously distributed, a mark-release method for a population estimation was untenable. Weevils were recaptured at distances up to 120 m from the release point, the farthest distance checked. There were no differences between males and females in the numbers and distances moved. Marked females were recovered at the experimental site over a longer time period than marked males. Weevils were recaptured within 6 weeks of marking, but none after 6 weeks from first capture. Over the 10 week experimental period, Malaise and Tedders traps captured 0 and 2 weevils, respectively, compared to the 765 weevils captured with the beat method. Average adults per tree ranged from 0.016 to 0.376 per week with an overall average of 0.172 ± 0.140, enough adult weevils to thoroughly infest all trees with larvae.

Key Words: Population distribution, mark and release, Tedders trap, Malaise trap

Resumen

Durante un período de 10 semanas, se recolectaron 765 ejemplares adultos del tipo silvestre de gorgojo *Diaprepes abbreviatus,* a partir de 750 árboles cítricos, para lo cual se agitaron los mismos, recogiéndose los individuos desprendidos en una sombrilla invertida. Los individuos recolectados se distribuyeron al azar en toda el area experimental. Quinientos cincuenta de los mismos fueron debidamente marcados para su posterior identificación y liberados a continuación; de éstos, 146 fueron recuperados, en la mayoria de los casos en las proximidades de los puntos en que fueron dejados en libertad. Teniendo en cuenta que los individuos recuperados no fueron distribuidos de forma homogénea, no es aplicable un metodo para el cálculo de la población a partir de los datos de marcado y liberación de los individuos. Los gorgojos fueron recapturados a distancias de mayores de 120 m de los puntos en que fueron liberados. No se encontraron diferencias entre individuos femeninos y masculinos en cuanto a las distancias que se desplazaron y el número de los mismos. Las hembras marcadas fueron recuperadas en los puntos experimentales al cabo de períodos mas prolongados que en el caso de los machos. Los gorgojos fueron recapturados en un plazo no mayor de seis semanas a partir del momento de su marcaje. Al cabo del período experimental de 10 semanas, las trampas de tipo "Malaise" y "Tedders" solo permitieron capturar 0 y 2 individuos, respectivamente, en contraste con los 765 ejemplares capturados mediante el método aplicado en el experimento. El número promedio de individuos adultos por árbol osciló entre 0.172 y 0.376 por semana, para un promedio total de 0.172 ± 0.140, lo que significa una cantidad de gorgojos adultos suficiente para infestar todos los árboles con las larvas correspondientes.

Citrus is the most valuable agronomic crop in Florida, covering an estimated 850,000 acres and having an estimated annual value of approximately $8.6 billion in 1998 (R. Barber, Florida Citrus Mutual, Lakeland, FL, pers. comm.). *Diaprepes abbreviatus L.* (Coleoptera: Curculionidae) (ESA approved common name, Diaprepes) is a polyphagous herbivore whose most economically important host in Florida is *Citrus* spp. (Beavers et al. 1979b; Simpson et al. 1996). Since its discovery in Florida in 1964, *D. abbreviatus* has spread to 20 Florida counties, where it currently infests approximately 164,000 acres (66,420 ha) (Anonymous 1997). This area con-

tains approximately 30,000 acres (12,150 ha) of infested commercial citrus. For some citrus growers, the first indication of infestation may be the sighting of adults and feeding damage on the leaves; however, lack of tree vigor may be the first sign that larvae of *D. abbreviatus* have been feeding on roots (Griffith 1975).

The female oviposits an average of 5,000 eggs over her lifetime, with 50-150 eggs per mass (Wolcott 1933, 1936, Simpson et al. 1996). An egg mass is laid between two leaves (generally mature leaves); the neonate larvae hatch and drop to the ground to feed on roots. Adult weevils feed on young citrus leaves. This cycle from egg to adult may take from 3 months to 2 yr for eggs from the same egg mass.

The adult weevil is secretive. That is, a citrus grower probably would not notice an initial infestation of a few beetles. Females reproduce themselves about 30 times, with a 1:1 sex ratio (Beavers & Selheime 1975). With this geometric progression, weevils should be numerous enough to be noticed in the third or fourth year of an infestation.

The larva is the damaging stage. Larval root feeding damage will cause a grove to become unprofitable within an estimated 5-7 yr after the initial infestation. To prevent large larval infestations from developing, it is essential that adult weevils in citrus groves be detected early, especially when the adult population is low. Various methods have been evaluated as surveillance tools for *D. abbreviatus* populations, although none appear to have been effective (Beavers et al. 1979a, 1984; Schroeder & Jones 1983, 1984; Jones & Schroeder 1984; Schroeder & Beavers 1985). Currently, modified pecan weevil traps (Tedders traps) (Tedders & Wood 1994) are used for monitoring the presence and seasonal abundance of *D. abbreviatus* adults by some researchers and citrus growers (J. L. Knapp, Univ. of Florida, pers. comm.). *D. abbreviatus* may also be collected by dislodging them from foliage onto ground cloths or into inverted umbrellas using a beating stick (Jones 1915; Nigg et al. 1999), a common collection method for some insects (Borror et al. 1981).

The movement and dispersal of D. *abbreviatus* are not understood. There appear to have been at least three introductions of Diaprepes into Florida since 1964 (Bas et al. 2000), but this weevil does not infest every acre of citrus. We have many grower reports of finding Diaprepes on mower decks, spray machines, and other equipment. This weevil has been reported in loads of fruit, and loads of fruit may move many miles between a citrus grove and a packing plant. In a genetic study, our data indicated man as the primary mover of this pest (Bas et al. 2000). Although we are beginning to understand the artificial movement of Diaprepes by man, we do not understand its natural movement and dispersal in a commercial citrus planting.

Also, there have been many reports of a single tree in a commercial citrus planting where many weevils congregate (Beavers et al. 1982; Jones & Schroeder 1984), a phenomenon we have personally observed. In addition to the population level, how this weevil distributes itself then may be important for treatment. That is, absence of adults in a portion of a planting could lead to treatment only where adults are present.

The objectives of this experiment were 1) to determine the distribution of D. *abbreviatus* over time in a commercial citrus grove, 2) to determine if a mark-release method could be used to estimate the population level, and 3) to relate the beat method weevil capture numbers with the numbers captured using the Malaise trap and the Tedders trap.

Materials and Methods

Experimental

An experiment was conducted in a red navel orange *(Citrus sinensis* (L) Osbeck) grove (2.27 ha) planted in 1994 in Astatula sand with a 5-12% slope (Furman et al. 1975) in Mt. Dora, Florida (Lake County). Trees (0.9-1.2 m tall) were irrigated by a microsprinkler system and were in excellent horticultural condition. No pesticides had been applied to this grove for 8 months before starting this experiment, nor were any pesticides applied during the experiment. The experimental grove was surrounded on the north, east and west by mature citrus groves of trees approximately 3.5 m in height and on the south by an access road.

A 750 tree planting was divided into 25 plots; each 25 m × 41.5 m plot consisted of 30 trees planted in five rows of six trees (Fig. 1). A rain gauge and a platform (20.3 cm × 20.3 cm) for release of marked adult *D. abbreviatus* were placed in the center plot of the 25 experimental plots (Fig. 1). Fourteen Tedders traps (2.8 traps/acre, 6.2 traps/ha) with enlarged cone holes and 4 Malaise traps (0.6 traps/acre, 1.3 traps/ha) (Golden Owl Publishers, Lexington Park, MD) were arranged in each designated plot as shown in Fig. 1. Linear distances from the trap in each plot to the central release platform were measured. Tedders traps were also placed inside the dripline of every fourth tree in the second row of each citrus grove surrounding at a density of 28 traps/acre (62 traps/ha). These traps were placed to understand weevil emergence from the soil in the older groves surrounding the experimental site. Data of this type might have given an indication of the immigration into our site from older Diaprepes-infested groves. All traps were monitored weekly.

In addition to traps, weevils were also collected throughout the 25 plots with the beat method (Nigg et al. 1999). For beat samples, 1.3 m diameter, straight handled golf umbrellas were placed

Fig. 1. Experimental design and trap locations in each of 25 plots containing 30 trees (750 trees total). Weevils were collected in even or odd weeks as indicated. ★ 1 m high release platform; ● Malaise trap; ▲ Tedders trap (linear distance to release platform).

under the tree to cover the distance from trunk to dripline and the foliage was beaten with a 0.5 in. × 4 ft. oak dowel rod. The foliage directly over the umbrella was beaten from top to bottom. The umbrella then was moved to a new and contiguous area under the tree, the foliage was beaten, and this process was repeated until all of the foliage had been beaten. Weevils were removed from the

umbrella by hand, were sexed based on a pointed (female) or a rounded (male) abdomen, and were placed in a vial with a polyurethane plug for a closure. Five people took these data: four to beat and one to immediately record data. In the first week, (week 0) all 750 trees at our test site were sampled for weevils by the beat method. All trees within the central plot were sampled weekly with the beat method. All the trees in the remaining plots were sampled by the beat method on a biweekly basis with half of the plots being sampled each week in an alternating pattern (Fig. 1). In week 9, all 750 trees (all 25 plots) were sampled by the beat method, so each tree was sampled a total of six times.

All collected weevils were moved to the release platform, removed from their cage individually, and marked on the elytra with colored enamel paint (Testors, No. 9146, The Testor Corp., Rockford, IL). Different colors were used for each week. This method was adapted from Cross & Mitchell (1964) and was a durable, non-toxic marking method for D. *abbreviatus* adults (HNN et al., unpublished data). Recaptured, previously marked weevils were re-marked at a different location on the elytra with the current week's color. Weevils were placed on the release platform after being marked and were not further disturbed.

Data were collected from May 30, 1996 to Aug. 1, 1996. The last sampling was at the grower's request due to the number of weevils being detected in the experimental site.

Data Analysis

The Kruskal-Wallis test was used to examine the radial symmetry of the population distribution among plots (Hollander & Wolfe 1973; SAS Institute 1989). Weevil capture status was categorized as either newly captured (unmarked) or recaptured (previously captured and marked) (Figs. 2 and 3). Poisson regression models were used to examine variables and their interactions (McCullagh & Nelder 1989). Estimates for these models were obtained using PROC GENMOD (SAS Institute 1996). Inferences for Poisson models were made with Wald Chi-Square tests (Agresti 1990). Statistical analysis of the population distribution was performed as follows Kruskal-Wallis tests were used to examine whether weevils tended to appear more often in one section of the experimental region. Plots in the northern half of the region were compared to southern plots, eastern plots were compared to western plots, and the four corners were compared. Newly captured and recaptured weevils were examined separately. The center plot was not used in these analyses. P-values were calculated from the Kruskal-Wallis test (Hollander & Wolfe 1973). No significant differences among the directions were found (P = 0.05). Because tests did not show any general asymmetry of counts in the grid, plots in the grid which were equidistant from the center were regarded as replicates.

The weevil counts in each plot were regarded as functions of the following variables:

1. Week (1, 2, . . . , 9)—Week 0 was not considered since recaptures were not present in that week.
2. Plot position from center - one center plot, four inner center plots, four inner corner plots, four outer center plots, eight knight plots (a chess knight's move from the center), and four outer corner plots. Their distances from the center are 0, 1, 1.41, 2, 2.24, and 2.83 units, respectively, where a unit is the length of one plot. For example, the Kruskal-Wallis tests showed that no adjustments for northern and southern plots were necessary, so the two southern outer corner plots could be regarded as replicates of the two northern outer corner plots.
3. Sex—male, female.
4. Capture Status—newly captured, recaptured.

An initial Poisson regression model was constructed with the four main effects and their two and three-way interactions, except for the interactions involving weeks and positions (McCullagh & Nelder 1989). For example, outer corner plots were counted only every other week, so the week*outer corner interaction was not estimable. This is the complex model in Table 2.

The simplified Poisson regression model was obtained by deleting nonsignificant terms and simplifying plot position effects by considering only their distances from the center. In the first model, a knight plot and an outer corner plot were regarded to be at two different positions in the grid, but their relative positions with respect to each other were not used. In the simplified model, the difference between a knight plot and an outer corner plot is not regarded as a difference in classifications; instead, the knight plot is regarded to be (2.83-2.24) = 0.59 units closer to the center. The fit of the simplified model was not significantly worse than the fit of the initial model (Chi-square = 24.59, df = 26, p = 0.54), but its terms were much easier to interpret. A summary for the simplified model appears in Table 2. Note that all terms in the simplified model were significant at the 0.05 level.

Distances from the release platform that weevils were recaptured were calculated by triangulation and were divided into three distance categories: 0-24 m, 24-72 m, and 73-120 m. These correspond generally to the central plot and the inner eight plots around the central plot and the outer 16 plots. Differences in recapture distance were compared by the GLM procedure and Tukey's HSD test (SAS 1996).

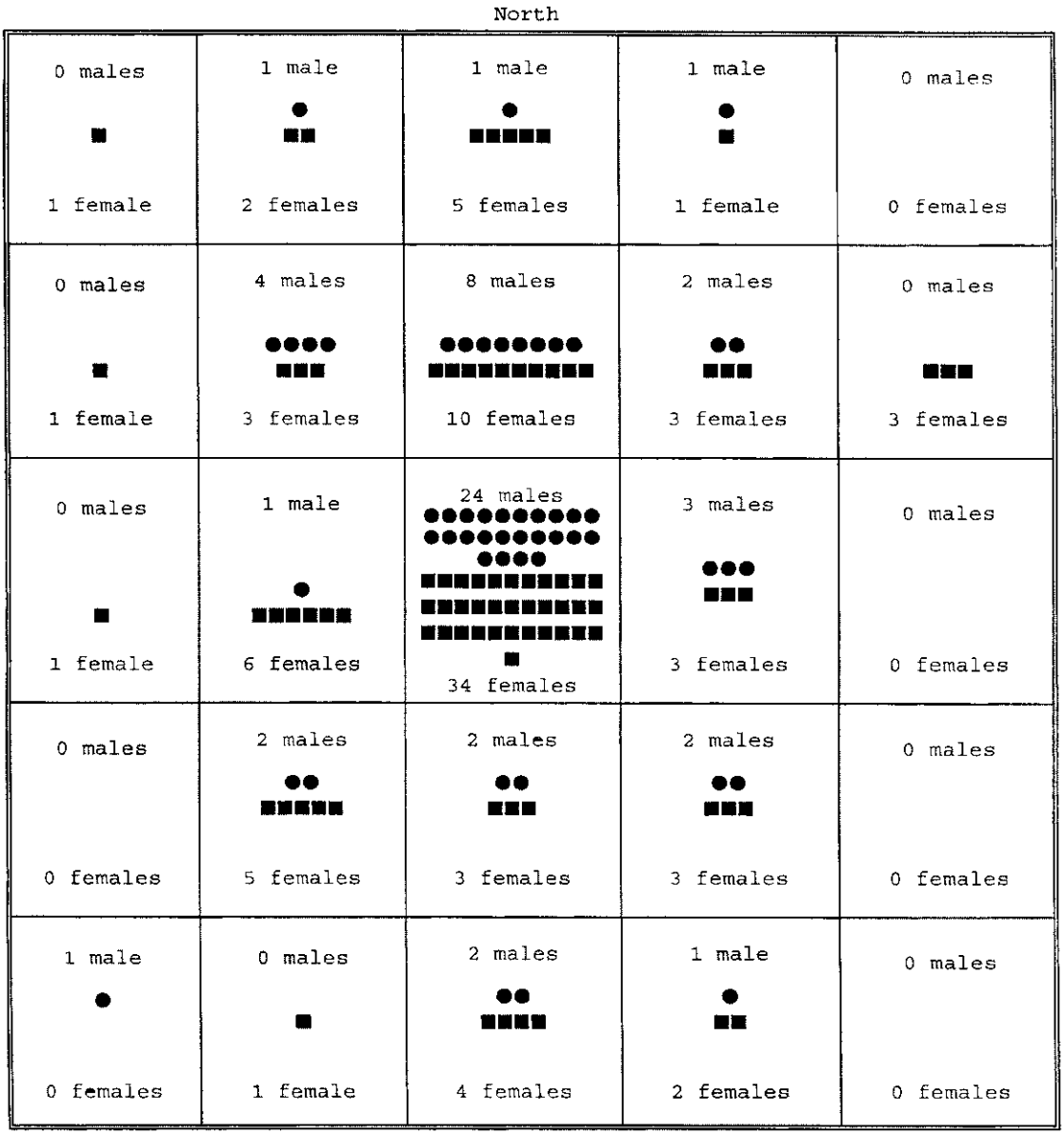

Fig. 2. Distribution of recaptured males (●) and recaptured females (■) from May 30, 1996 to August 1, 1996 in a red navel orange grove, Mount Dora, Florida (146 total weevils).

Results and Discussion

Statistical Analyses and Models

The fit of the Poisson regression models were evaluated by examining their standardized deviance residuals. These were calculated by comparing observed counts from those predicted by the model. Even though the general model does not assume a normal distribution of the counts, the standardized deviance residuals should appear to have a normal distribution with mean 0 and variance 1. There were no obvious departures from that distribution, indicating that the assumptions of the model were met closely enough for the estimates to be valid.

Simplified Model Interpretation

Since the interactions were significant, numerical interpretations were made from the interaction terms rather than the main effects (Table 2). Our estimates are based on this model constructed from all of the data.

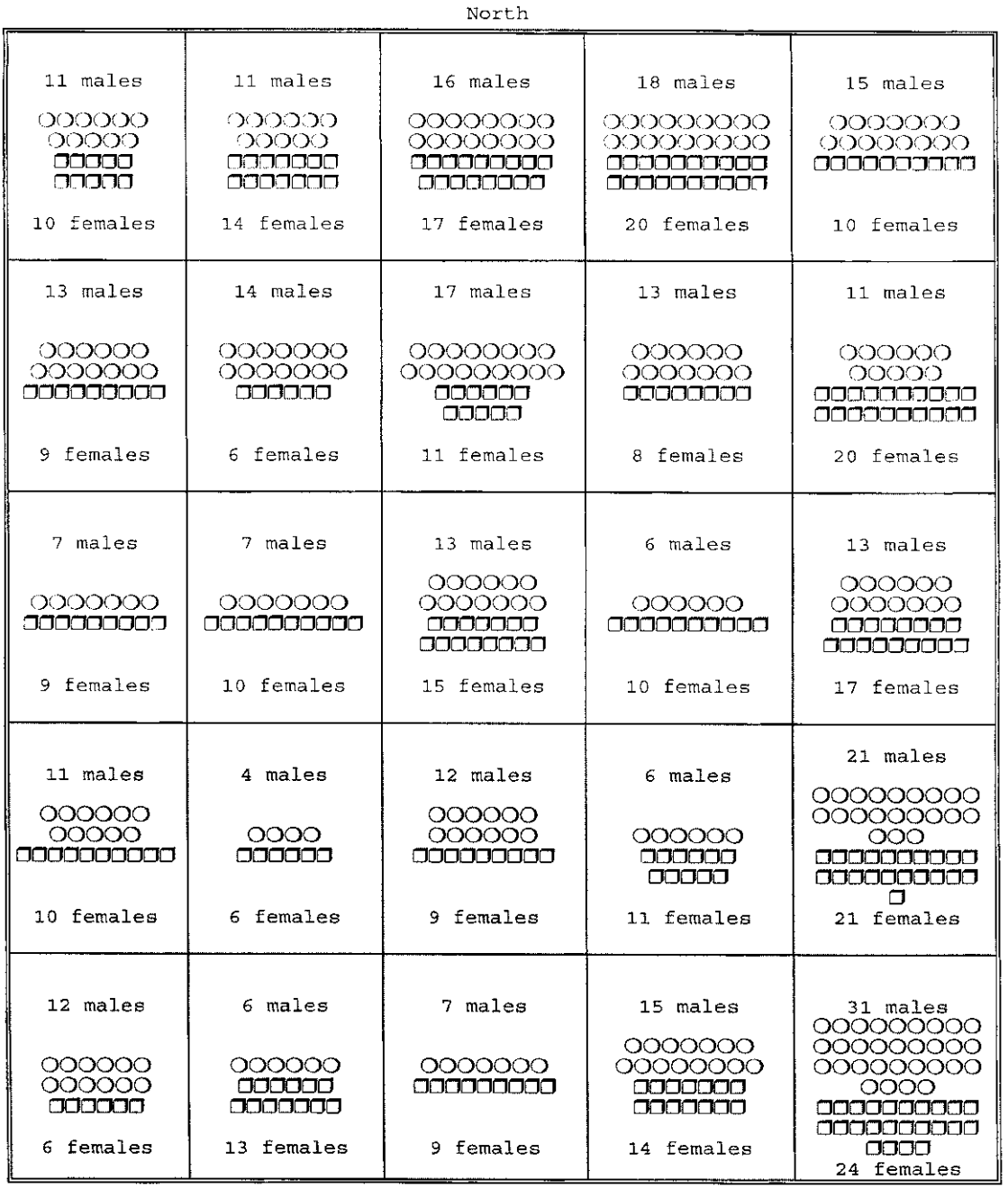

Fig. 3. Distribution of newly captured males (○) and newly captured females (□) from May 30, 1996 to August 1, 1996 in a red navel orange grove, Mount Dora, Florida (619 total weevils).

The capture status*plot position interaction can be explained as follows. Within the same week and gender, the number of newly captured weevils tended to increase by a factor of 1.30 for every additional unit from the center, so there was a slight tendency to capture more new insects on the periphery than in the center. For example, starting with the reference value of 0.21 newly captured males in the center plot in week 1, we would have expected to see 0.21 (1.30) = 0.27 newly captured males in an inner center plot in week 1 and 0.21 (1.302) = 0.35 newly captured males in an outer center plot in week 1. However, the average number of recaptured weevils tended to decrease by a

factor of 0.26 for every additional unit from the center. For example, the center plot had, on average, $(1/0.26)^1 = 3.85$ times more recaptured weevils than an inner center plot and $(1/0.26)^2 = 14.8$ times more recaptured weevils than an outer plot. These numbers show that the newly captured weevils tended to be captured away from the center, while marked weevils which were recaptured had not migrated far from the center.

The capture status*sex interaction was also significant. Within any particular plot in one week, the average number of recaptured males was 2.21 times higher than the average number of newly captured males. For example, in the center plot in week 1, we would have expected to see 0.21 (2.21) = 0.46 recaptured males. For females, the average number of recaptured females was 3.73 times higher than the average number of newly captured females. In simpler terms, there were more recaptures than newly captured captures for both genders, but the tendency to recapture females was stronger than the tendency to recapture males. The difference between 2.21 and 3.73 provides the significant interaction. The same results showed that, among recaptured weevils, the average ratio of females to males was 1.60:1; among newly captured weevils, the average ratio of females to males was only 0.95:1. The model predicted 0.21 newly captured males in the center in week 1, so the estimated number of newly captured females in the center in week 1 was 0.21 (0.95) = 0.20.

The capture status*week interaction can be explained as follows. At week 1, the average number of recaptured weevils in a plot was 4.65 times higher than the average number of newly captured weevils, which was a significant difference (Chi-square = 9.83, df = 1, p = 0.0017). At week 2, the newly captured weevils outnumbered the recaptured weevils by a ratio of 2.44:1, but that difference was not significant. In fact, from weeks 2 to 9, the effects of time did not differ significantly between newly captured weevils and recaptured weevils; this difference occurred only in week 1. For both newly captured weevils and recaptured weevils, from weeks 2 through 9, the counts tended to increase by a factor of 1.28 each week. That rate of increase was significant (Chi-square = 173.67, df = 1, $p < 0.0001$). This estimate is supported by the beat method numbers. The beat method has a numbers efficiency of about 65% and a detection efficiency of 75% (Nigg et al., 1999). The weevil numbers for June 6, 13, and 20 might be attributable to a 35% inefficiency of the beat technique; thereafter, weevil absolute numbers increased each week.

We attempted to estimate the population by the mark and release method (Southwood 1966; Carothers 1973; Seber 1982). However, the fact that marked insects did not mix freely and homogeneously with the unmarked population (Fig. 2), would not allow a population estimate using a mark and release method (Southwood 1966; Carothers 1973).

General Observations

Over the 10 weeks of this experiment (May 30-Aug. 1), we captured 765 weevils (Table 1). We released 580 marked weevils and recovered 146 of these for a recovery rate of about 25% (Table 1, Fig. 2). The difference between 765 and 580 is the sum of weevils captured in week 9 (170) (not marked and released) plus 15 weevils that escaped before being marked in other weeks. The percent recapture varied from week to week (Table 1). In any week, we recaptured an average of 21% of weevils marked in the previous week. For weevils marked 3 weeks previously, only about 5% were recaptured at the experimental site. Over the course of the experiment, 17 weevils with two marks were recaptured; three weevils with three marks were recaptured, but none with four marks. Marked weevils were detected in the experimental site for no more than 6 weeks after being marked and released.

In week 1, recaptured weevils were 4.6-fold greater than newly captured weevils in all plots. However, in weeks 2-9, there were no significant differences between newly captured weevils and recaptured weevils in each plot. During the last 8 weeks, both recaptured weevils and newly captured weevils increased by the same factor of 1.28 each week.

Newly captured males outnumbered recaptured males by about a 5:1 ratio; the same ratio was about 3:1 for newly captured and recaptured females (Table 1). The ratio of recaptured males to recaptured females overall was 0.5:1. For newly captured weevils, the sex ratio was 1.2:1, males to females. These ratios are different because marked females were recaptured in the experimental site in greater numbers compared to marked males. Beavers & Selheime (1976) observed field captured *D. abbreviatus* sex ratios of 0.79: 1 ♂:♀ in 1972 and 0.69: 1 ♂:♀ in 1973.

Adult weevils per tree ranged from a low of 0.016 in week 3 to a high of 0.339 in week 7 (Table 1). Stated on a tree basis, in week 3 a weevil was captured about every 58 trees; in week 7 one weevil was captured about every 2.5 trees. Based on these population levels, the distribution of newly captured weevils (Fig. 3), and their reproductive potential, there were enough weevils present to infest all 750 trees of this experiment. Based on the distribution of newly captured weevils throughout the experimental site, spot pesticide treatment for this weevil appears unlikely.

Movement

The central release plot had the highest number of recaptured weevils (Fig. 2). The second

TABLE 1. *DIAPREPES ABBREVIATUS* ADULT UMBRELLA CAPTURE, MAY 30-AUG 1, 1996.

		Newly captured adults			Recaptured adults					
Week	(date)	New captures	Males/females	Ratio	Recaptures	Males/females	Ratio	Overall total captures	Released	Weevils/tree[a]
0	(5/30)	74	29/45	0.64	N/A	N/A N/A[b]	N/A	74	65	0.098
1	(6/06)	10	6/4	1.50	11	3/8	0.38	21	20	0.059
2	(6/13)	7	2/5	0.40	1	1/0	N/A	8	8	0.021
3	(6/20)	4	3/1	3.00	2	0/2	0.00	6	6	0.016
4	(6/27)	20	9/11	0.82	4	1/3	0.33	24	24	0.064
5	(7/C3)	61	35/26	1.35	9	3/6	0.50	70	69	0.187
6	(7/11)	96	44/52	0.85	22	6/16	0.38	118	118	0.315
7	(7/18)	106	48/58	0.83	34	13/21	0.62	140	137	0.376
8	(7/25)	104	57/47	1.21	30	10/20	0.50	134	133	0.357
9	(8/01)	137	77/60	1.28	33	18/15	1.20	170	0	0.227
Overall		619	310/309	1.19 + 0.72	146	55/91	0.49 + 0.34	765	580	0172 + 0.140

[a]Actual weevils collected with the umbrella divided by the number of trees sampled.
[b]N/A = Not applicable.

TABLE 2. STATISTICAL SUMMARY OF POISSON REGRESSION MODELS OF *DIAPREPES ABBREVIATUS* BEAT METHOD CAPTURES AND INTERACTION WITH PLOT POSITION FROM CENTER, SEX, WEEK AND CAPTURE STATUS.

Effect	df	Wald Type III Chi-square	P
	Complex model		
Week	8	162.8	<0.0001
Capture status[a]	1	54.4	<0.0001
Plot position from center	5	66.3	<0.0001
Sex	l	2.3	0.13
Capture status*plot position[a]	5	121.6	<0.0001
Capture status*sex[a]	1	3.1	0.079
Capture status[a]*week	8	21.2	0.0066
Plot position*sex	5	3.8	0.57
Sex*week	8	8.1	0.42
Plot position*sex*capture status[a]	5	1.2	0.94
	Simplified model		
Week	8	164.2	<0.0001
Capture status[a]	1	18.4	<0.0001
Plot position from center	1	85.9	<0.0001
Sex	1	4.8	0.029
Capture status*plot position	1	188.3	<0.0001
Capture status*sex	1	7.4	0.0066
Capture status*week	8	22.5	0.0040

[a]Capture status = newly captured or recaptured after marking.

highest plot for recaptures was the plot immediately north of the central release plot with 18 recaptures or 12.3% of the recaptured weevils (Fig. 2). There were no statistical differences in the movement categories between sexes (Table 3). However, males appeared to be less represented in the 73-120 m category (Table 3). Beavers & Selheime (1978) found 10 of 100 marked weevils 3-26 m from their release point 4 days after release. After 50 days, one female and three males were found 18-228 m from the release point. In a second experiment, 11 of 122 released weevils were found 11-148 m from the release point after 7 days; after 52 days, 12 weevils were found 18-208 m from the release point (Beavers & Selheime 1978). What is not clear from our data and from Beavers & Selheime (1978) was the fate of the unrecovered weevils.

One explanation for marked weevils not being recaptured at our site is simply that they were not in the sampling zone when we sampled. Upon release, many marked weevils flew off-site to a mature grove, sometimes within seconds, an observation also made by Beavers & Selheime (1978). We agree with Beavers & Selheime (1978) that *D. abbreviatus is* capable of strong flight of short duration and distance. Another explanation for the low recovery of marked weevils is that the marking paint may have worn off. We believe this is unlikely as we recaptured weevils marked three weeks previously. Death is also a possible explanation for the rapid decline in marked wee-

TABLE 3. MARKED DIAPREPES ABBREVIATUS RECAPTURE DISTANCE FROM THE CENTRAL RELEASE POINT BY SEX.

Sex	Category	Recapture total	Average recaptured weevils/week	
Females	0-24 m	34	3.9	±3.3 a
	25-72 m	36	4.0	±4.5 a
	73-120 m	21	2.3	±3.8 a
Male	0-24 m	24	2.7	±2.8 a
	25-72 m	24	2.7	±3.7 a
	73-120 m	7	0.8	±1.1 a

Means ± SD Means followed by the same letter are not different at $\alpha = 0.5$ by Tukey's HSD test.

vils; however, we recovered only one dead marked weevil during the course of this experiment.

Distribution

Although the raw numerical data indicated that the population increased with time in the east and southeast plots, this trend was not statistically significant. According to the Poisson models, insect counts followed steady gradients from the center to the exterior plots. The simplified model was not statistically inferior to the complex full model (Wald chi-square = 24 6, df = 26, P = 0.54) (Table 2). In the simplified model, the interactions of capture status and plot position, capture status and sex, and capture status and week were significant (P = <0.01, Wald chi-square tests) (Table 2). Counts of newly captured weevils increased by a factor of 1.09 for every 10 m removed from the center plot. The peripheral plots averaged about 28 newly captured weevils per plot; interior plots averaged 20 newly captured weevils per plot. More newly captured weevils on the periphery of our site might be due to emergence of adults from a peripheral infestation in the first year after planting, i.e., in 1994-95.

Weevils may have immigrated into our site. The grove was 2-yr-old, and based on a 1 yr field life cycle (Simpson et al. 1996), perhaps only a few weevils had reached the adult stage in our experimental plots. However, the Tedders traps placed under the tree dripline in the surrounding groves caught only one weevil, indication that movement of a large population of weevils into our test site from surrounding groves was unlikely.

Trap Capture

The Malaise traps, which were designed to trap flying insects, caught only one unmarked weevil. One unmarked weevil was captured in a Tedders trap in the west adjoining mature grove in week 1. Two (one marked, one unmarked) weevils were captured in a Tedders trap in the experimental area in weeks 7 and 8 after releases of 118 and 137 weevils in the previous weeks, respectively. In our experiment, the Tedders traps were placed between trees in the experimental site. Our catches with this trap might have been greater with another trap placement, e.g., under the tree canopy. When used as described, the Tedders trap and Malaise traps were much less effective than the beat method for detecting *D. abbreviatus,* capturing two weevils and one weevil, respectively, compared to 765 total weevils with the beat method (Table 1).

In conclusion, over 10 weeks newly captured weevils were distributed evenly throughout the experimental site. Recaptured weevils were unevenly distributed thus preventing a population estimate with a mark-release method. The Malaise and Tedders traps captured one and two weevils, respectively, compared to 765 weevils with the beat method. Based on these results, we conclude that the beat method is much more accurate in determining population levels. Adult weevils per tree ranged from 0.016 to 0.376 per week, enough adult weevils to infest all trees at the experimental site.

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DESCRIPTION OF *CHOREBUS DENTICURVATUS* SP. NOV. AND THE EXUVIAE OF ITS FINAL LARVAL INSTAR (HYMENOPTERA: BRACONIDAE: ALYSIINAE)

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ABSTRACT

The imago and exuviae of the final larval instar of a new species of Dacnusini found in Spain are described and drawn: *Chorebus denticurvatus* sp. nov., an endoparasitoid of *Chromatomyia horticola* (Goureau). The morphological structures of phylogenetic value are discussed and keys are offered for the determination of the imagines.

RESUMEN

Se describen el imago y la exuvia, del último estado larvario, de una nueva especie de Dacnusini de España endoparasitoide de *Chromatomyia horticola*: *Chorebus denticurvatus* n. sp. Se discuten sus afinidades filogenéticas y se elaboran claves para la determinación de los adultos.

The subfamily Alysiinae, which has traditionally been subdivided into the tribes Alysiini and Dacnusini, is characterized, among the Braconidae, by having exodont mandibles. All of its members are endoparasitoids of cyclorrhaphous Diptera.

Chorebus Haliday, with approximately 215 Holarctic species, is the largest genus of the Dacnusini. Many of its species are morphologically characterized by displaying a densely setose metapleuron and, usually, a sculptured precoxal sulcus. From the biological point of view, they can be said to be endoparasitoids of Agromyzidae and Ephydridae (Diptera), although there is a species that attacks *Psila rosae* (F.) (Diptera: Psilidae).

The imagines of the Dacnusini have been treated, both at morphological and biological levels, by Griffiths (1964, 1966, 1968, 1984) and Tobias (1986, Summary of the Palearctic taxa with keys to genera and species, translated into English, 1995). The immature instars of the Alysiinae, together with those of other Hymenoptera Parasitica, have been studied by several authors, the most important works being the now classic ones of Clausen (1940) and Hagen (1964), together with the keys for the taxonomic separation of the mature larvae offered by Beirne (1941), Short (1952, 1959, 1970, 1976, 1978), Finlayson (1967, 1975), Finlayson and Hagen (1979) and Čapek (1970).

Within this broad set, the final larval instars of the Dacnusini have received little attention. Only six species of the genus *Chorebus* have been described: *C. aquaticus* Muesebeck, 1950; *C. avesta* (Nixon, 1944) [Čapek 1970]; *C. gracilis* (Nees von Esenbeck, 1834) [Wright, Geering & Ashby 1946; Short, 1952]; *C. merella* (Nixon, 1937); *C. nana* (Nixon, 1943) [Čapek 1970], and *C. nydia* (Nixon, 1937) [Čapek 1970]. Of these six species, the structures which allow characterization of the preimaginal instars of the Hymenoptera Parasitica have been described only in *C. gracilis* (Short 1978; Finlayson 1987). Diagnostic features can be found on the head (sclerotized mouthparts and supporting rods), spiracles (usually the prothoracic) and integument.

Here we describe the male and female imagines and the cast skin of the final larval instar of a new species of Dacnusini: *Chorebus denticurvatus* sp. nov. This species is an endoparasitoid of *Chromatomyia horticola* (Goureau, 1851), a very common agromyzid species in the Regional Community of Valencia (Spain) on cultivated plants (Docavo et al. 1987).

The terms for the body morphology, the biometric data and wing venation of the imago follow Griffiths (1964), van Achterberg (1993) and Wharton (1977, 1986). The methodology used for opening the puparium and preparing the exuviae is that proposed by Wahl (1984). The terminology used to refer to the different cephalic sclerites and other body structures of the final larval instar is that of Finlayson and Hagen (1979), Short (1978), and Sime and Wahl (1998). All of the material ex-

amined (imagines and prepared exuviae) is deposited at the "Torres Sala" Entomological Foundation (Valencia, Spain). The following abbreviations have been used in the descriptions: d= diameter; h = height; l = length and w = width.

Chorebus denticurvatus **sp. nov.**

Female

Head (Fig. 1a)—Transverse, 1.94 times wider than long, 1.36 times higher than long, 1.12 times wider at temples than at eyes, 1.75 times wider than mesosoma; ocelli oval, in an equilateral triangle; back of head very sparsely setose; face setose; eyes in lateral view 0.66 times as long as temples; width of head/distance between eyes/ width of clypeus: 2.12/1/1.37; antennae with 21 antennomeres, length first /second /third flagellomere: 1.10/1/1.0, third flagellomere ca 3.2 times as long as wide, tenth flagellomere ca 2.3 times as long as wide; mandibles (Fig. 1a) not expanded, 4-toothed, 1st tooth weakly expanded, blunt, 2nd tooth relatively long, pointed, curved upwards, 3rd and 4th teeth pointed, small; width of mandibles/length of head: 3.0; maxillary palpi short: length third/ fourth/fifth/sixth segments:1.3/2/1/1.3.

Mesosoma—Elongate, 2.17 times longer than width between tegulae, 1.4 times longer than high; sides of pronotum practically bare; mesonotal disc dotted (punctate), rough, setose, with setae extending across entire surface, except around the posterior half of the lateral lobes; notauli scarcely visible, represented by a fine line of punctures that seem to reach midpit; precoxal sulcus well developed, long, crenulated, extending to posterior border of mesopleuron; posterior mesopleural furrow smooth; mesopleuron smooth, shiny, without setae on central part; metapleuron and propodeum densely setose (of the derived type), coarsely punctate; base of hind coxae punctate, rough, with fairly dense setae, with a tendency to form tufts; posterior tibiae about 1.3 times longer than their corresponding tarsus, with fairly dense pubescence at apex of upper inner side; setae of these pubescences from 0.5 to 0.75 times as long as the middle width of the hind tibia; length of hind leg: femur/ tibia/ tarsus: 0.5/1/0.7, length first/ second/ third/ fourth/ fifth hind tarsal segments: 1.6/1/0.6/0.5/0.5.

Wings (Fig. 1c)—Long, 1.08 times longer than body. Pterostigma short and wide, little darkened, 1.4 times longer than the metacarpus; 1st radial segment slightly shorter than both the length between its insertion and the parastigma and the width of the pterostigma; remainder of radius slightly sinuous; Radial cell not reaching tip of wing; n. rec. antefurcal; 3rd discoidal segment (cu1b) absent, so that cell B is open at its lower distal corner. Fore wing length: 2.7 mm.

Metasoma—First tergite 1.7 times longer than wide apically, almost parallel-sided, practically evenly setose, although slightly more densely pubescent on posterior and lateral parts; length of first tergite/metasoma: 3.8; tergite 2 with a few setae near its base; ovipositor sheath robust, extending slightly beyond last tergite in resting position.

Color and size—Head, mesosoma and metasoma shiny black; labrum reddish-brown; antennae dark, with exception of scapus, pedicellus, and first two antennomeres of flagellum, which are yellowish-brown; center of mandibles reddish-yellow; legs yellow with exception of hind coxae (black), posterior tarsi and last tarsomere of all tarsi (dark). Body length: 2.5-2.8 mm.Wing span: 5.9 mm.

Male—Essentially as in female but with antennae yellow-brown and longer, with 24 antennomeres.

Host: *Chromatomyia horticola* (Goureau, 1851)

Material examined [deposited at the "Torres-Sala" Entomological Foundation (Valencia, Spain)]: Holotype: 1 female from puparium of *C. horticola* 8.VII.1997 in leaf of *Lactuca sativa* L., Cullera, Valencia, Spain, emerged 10.VII.1997. Paratypes: 1 male from puparium of *C. horticola* 8.VII.1997 in leaf of *L. sativa*, Cullera, Valencia, Spain, emerged 7.VII.1997; 1 female Cullera, Valencia, Spain, 27.IX.1984.

Etymology: The specific name of this species refers to the peculiar morphology of its mandibles.

This new species belongs to the group that Griffiths (1964) has described as the "*ovalis* / *lateralis* complex". It is similar to *C. fallax* (Nixon, 1937) from which it differs in the following respects: a) fewer antennomeres; b) coloring of the labrum (reddish-yellow), antennae (dark, with exception of scapus, pedicellus, and first two antennomeres of flagellum, which are yellowish-brown), mandibles (reddish-yellow at center), legs (yellow with exception of hind coxae (black), posterior tarsi and last tarsomere of all tarsi (dark), and metasoma (shiny black); c) mandibles (Fig. 1a) not expanded, 4-toothed, 1st tooth weakly expanded, blunt, 2nd tooth relatively long, pointed, curved upwards, 3rd and 4th teeth pointed, small; d) mesonotal disc dotted (punctate), rough, setose, with setae extending across entire surface, except around the posterior half of the lateral lobes; e) more poorly developed notauli; f) posterior tibiae about 1.3 times longer than their corresponding tarsi. It should also be noted that *C. fallax*, according to the available information, has a different host (see the following amended Tobias key).

The most important characteristic for recognizing this species lies in the conformation (morphology) of the mandibles (Fig. 1a). Although the second tooth is long and pointed, it does not reach

the length observed in *C. fallax* (Fig. 1b), and it is curved upwards.

From puparia of the same species of agromyzid from which the newly described species emerged, collected at the same location, on the same date and on the same plant species, the following species of Chalcidoidea were obtained at the laboratory: Eulophidae: *Diglyphus isaea* Walker, 1838**,** 2 females, VII. 1997; *Pediobius acantha* (Walker, 1839), 1 female, VII.1997. Pteromalidae: *Halticoptera* sp**,** 1 female, VII.1997. Tetracampidae: *Epiclerus nomocerus* Masi, 1934**,** 1 male, 2 females, VII.1997. Since *P. acantha* and *Halticoptera* sp. have been reported as hyperparasitoids of braconids (Herting 1977), it is possible that they are hyperparasitoids of *C. denticurvatus*.

So far, six species of Dacnusini had been observed parasitizing *C. horticola* in Spain (Docavo, Jiménez, Tormos & Verdú 1987; Docavo and Tormos 1997; Docavo and Tormos 1988, Docavo, Tormos, Asís & Gayubo 1992; Garrido, Tormos & Beitia 1992; Francés and Jiménez 1989;Tormos, Asís, Gayubo & Sendra 1991; Tormos and Gayubo 1990, Tormos; Gayubo & Asís 1989; Tormos, Gayubo, Asís & Vacas 1989): *Dacnusa sibirica* Telenga, 1934; *Dacnusa areolaris* (Nees von Esenbeck, 1812); *Dacnusa laevipectus* Thomson, 1895; *Dacnusa rodriguezi* Docavo & Tormos, 1997; *Chorebus misellus* (Marshall, 1895) and *Chorebus sativi* (Nixon, 1943). The peculiar conformation of the mandibles allows *C. denticurvatus,* the species recently discovered on this host, to be distinguished from the rest of species previously found.

This species can be inserted in the keys of Griffiths[1] (couplet VI, 1968:126) and Tobias[2] (couplet 56, 1995 (III): 189) as follows:

[1]43 Mandibles with tooth 2 very long, about 0.36 times as long as total length of mandible, and curved outwards (Fig. 136) . . . . . *C. fallax* (Nixon)

Mandibles with tooth 2 long, about 0.29 times as long as total length of mandible, and curved upwards (Fig. 1) . . . . . C. *denticurvatus* sp. nov.

Mandibles with tooth 2 not so long and not curved (Fig. 131) 44

[2]157 (157a) Head noticeably broadened behind eyes, wider than mesosoma. Second denticle on mandibles long, about 0.36 times as long as total length of mandible, curved outwards, denticles weakly developed (Fig. 116: 9). Setae at apex of upper side of hind tibiae much shorter than width of tibia in middle. Hind coxae dark brownish. Body: 2.7-2.9 mm. Parasite of *Phytomyza cardui* Hering. Western Europe . . . . . *C. fallax* Nixon

157a (158) Head noticeably broadened behind eyes, wider than mesosoma. Second denticle on mandibles relatively long, about 0.29 times as long as total length of mandible, curved upwards, denticles weakly developed (Fig. 1). Setae at apex of upper side of hind tibiae much shorter than width of tibia in middle. Hind coxae black. Body: 2.5-2.8 mm. Parasite of *Chromatomyia horticola* (Goureau) . . . . . *C. denticurvatus* sp. nov.

158 (157) Head not broadened behind eyes. Second denticle on mandibles less long, not uncinate, 3rd and 4th denticles distinctly developed. Setae at apex of upper side of hind tibiae almost as long as width of tibia in middle. Hind coxae yellow. Body 2.1-2.3 mm. Center; Sweden . . . . . *C. oritias* (Nixon)

Cast skin of final instar larva (Figs. 2, 3)

An exuviae was obtained from a puparium of *C. horticola* in a leaf of *L. sativa*. The puparium was collected on 8.VII.1997 at Cullera (Valencia, Spain) and a female imago emerged on 10.VII.1997.

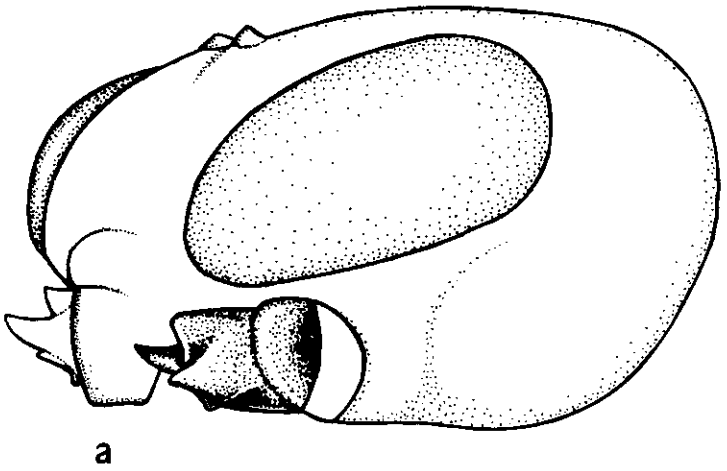
Description of final larval instar. Integumental structures of the body (except head) include scattered small setae (s) (l = 3 µm) and bluntly conical papillae (p) (h = 3 µm; w = 3 µm) (Fig. 2). Spiracles with small atrium (d = 11 µm).

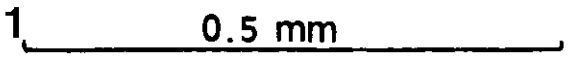
Cranium (Fig. 3). Antennae (a) (d = 30 µm) situated in dorsolateral position represented by two circular and slightly protruding areas, without sensilla (ss); epistomal suture (es) unsclerotized; pleurostoma (pt) sclerotized, with distinct mandibular processes (mp1 = superior, mp2 = inferior); hypostoma (h) sclerotized without hypostomal spur; stipital sclerite (sc) very sclerotized, long; setae, sensilla and papilla of head capsule small.

Mouthparts. Mandibles (m) (l = 51 µm) with slightly sclerotized and wide base, and blade relatively long and sclerotized; labial sclerite (ls) slightly sclerotized; maxillary (mp) (d = 7 µm) and labial palpi (pl) (d = 10 µm) disc-like, with two sensilla, one large and one very small; salivary orifice (so) very well defined, as a transverse slit; setae, sensilla and papillae of mouthparts like those of head, very small.

Overall, the subfamily Alysiinae shows great variation in the differentiation of the morphological characters of the final larval instar (Short 1952, 1978; Čapek 1970, 1973). In this sense, it is possible to observe a continuous succession from the condition in *Alysia* Latreille and *Phaenocarpa* Foester, where almost all of the cephalic sclerites are seen, to the condition in *Aspilota* Foester, *Coelinidea* Viereck, *Coelinius* Nees von Esenbeck and *Polemochartus* Schulz, where the structures are obliterated, with the exception of the epistoma and mandibles, or the mandibles and the palpi.

From scrutiny of the descriptions made, *Chorebus* seems to be a fairly homogeneous genus as regards its larval morphology. The final larval





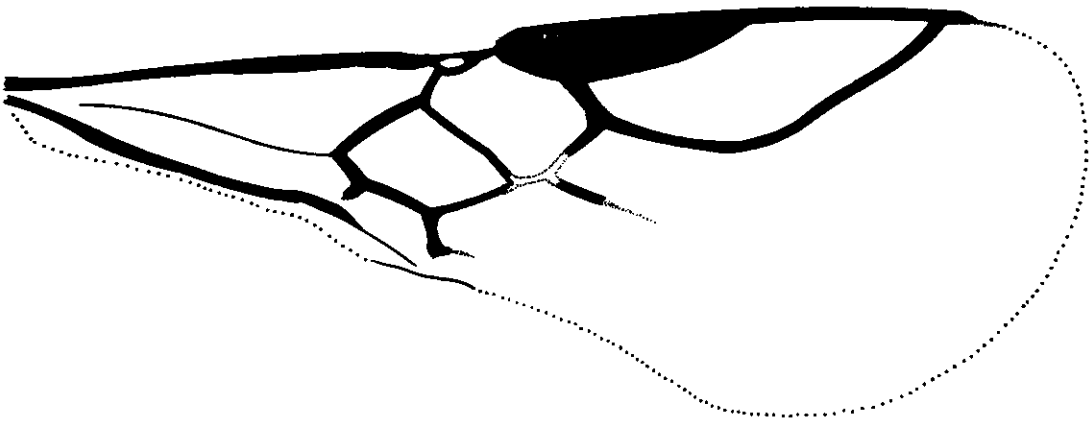
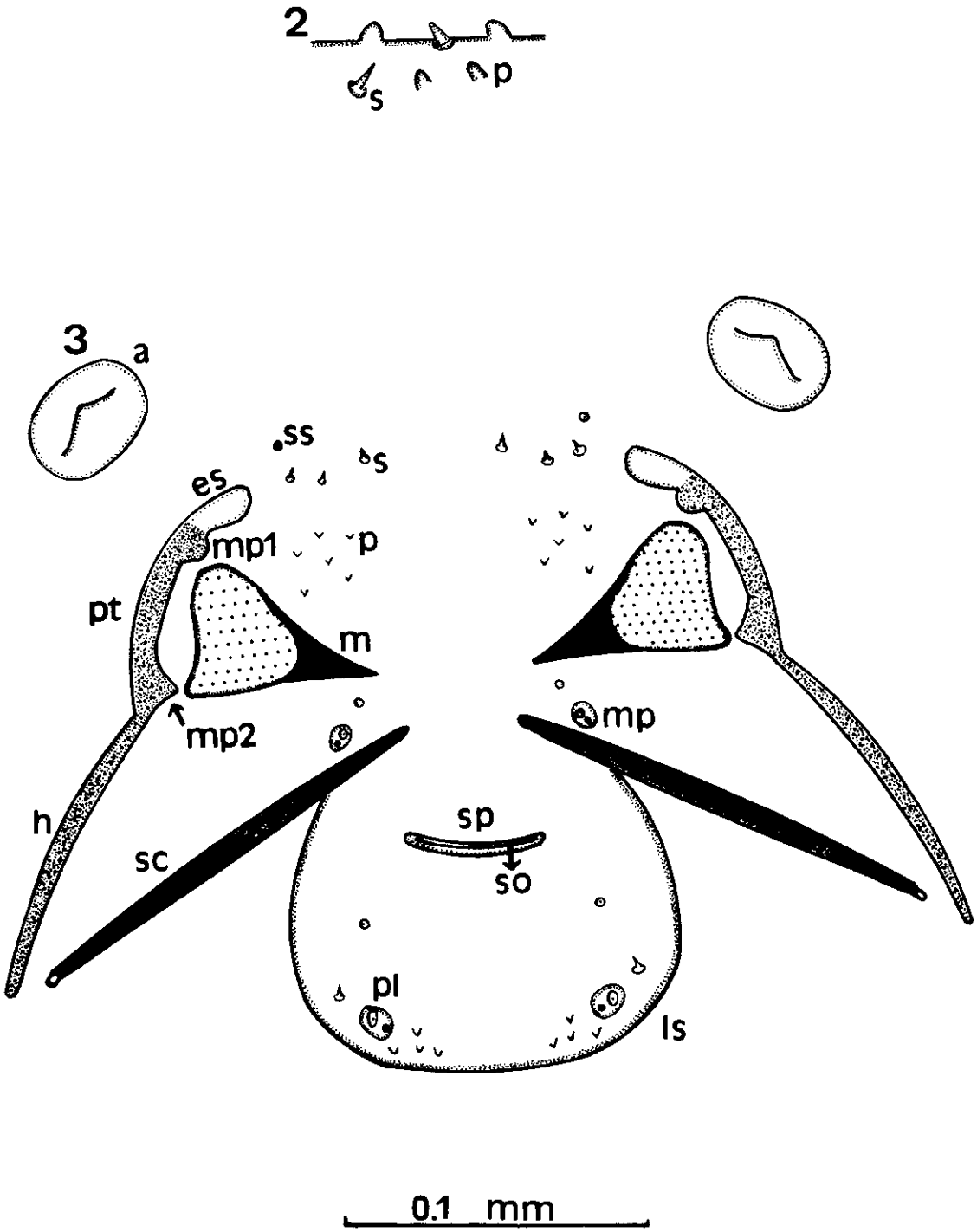


Fig. 1. *Chorebus denticurvatus* sp. nov.: (1a) Head of imago, in lateral view, showing the left mandible; (1c) Right fore wing. *Chorebus fallax*: (1b) Left mandible.



Figs. 2 and 3. *Chorebus denticurvatus* sp. nov.: (2) and (3) Final larval instar: (2) setae (s) and papillae (p) of integument (detail); (3) Cranium in frontal view: antennae (a), epistomal suture (es), hypostoma (h), labial sclerite (ls), mandible (m), mandibular processes (mp1 = superior, mp2 = inferior), palpi (maxillary (mp), labial (pl)), papillae (p), pleurostoma (pt), salivary orifice (so), sensilla (ss), setae (s), silk press (sp), stipital sclerite (sc).

instar of *C. denticurvatus*, like all of those described for the Dacnusini, has simple and unarmed mandibles and the labial sclerite is reduced (Čapek 1970, 1973). Like larvae of the genera *Dacnusa* Haliday, *Laotris* Nixon and *Synelix* Foerster, it shares a pleurostoma with well differentiated mandibular processes and a long stipital sclerite.

The only appreciable differences with *C. gracilis* (the only species whose larva have been described, although not in depth) lie in the number and arrangement of the setae and sensilla of the head capsule.

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EVALUATION OF COMMERCIAL PHEROMONE LURES AND TRAPS FOR MONITORING MALE FALL ARMYWORM (LEPIDOPTERA: NOCTUIDAE) IN THE COASTAL REGION OF CHIAPAS, MEXICO

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ABSTRACT

Commercially available sex pheromone lures and traps were evaluated for monitoring male fall armyworm (FAW), *Spodoptera frugiperda*, in maize fields in the coastal region of Chiapas, Mexico during 1998-1999. During the first year, Chemtica and Trécé lures performed better than Scentry lures, and there was no difference between Scentry lures and unbaited controls. In regard to trap design, Scentry *Heliothis* traps were better than bucket traps. In 1999, the pattern of FAW captured was similar to that of 1998, although the number of males captured was lower. The interaction between both factors, traps and lures, was significant in 1999. Bucket traps had the lowest captures regardless of what lure was used. Scentry *Heliothis* traps with Chemtica lure captured more males than with other lures or the controls. Delta traps had the greatest captures with Chemtica lure, followed by Trécé and Pherotech lures. Several non-target insects were captured in the FAW pheromone baited traps. The traps captured more non-target insects than FAW males in both years. Baited traps captured more non-target insects than unbaited traps.

Key Words: *Spodoptera frugiperda*, sex pheromone, monitoring, maize, Mexico

RESUMEN

Se evaluaron feromonas y trampas comercialmente disponibles para el monitoreo del gusano cogollero *Spodoptera frugiperda* en cultivo de maíz en la costa de Chiapas, México durante 1998-1999. El patrón de captura de machos del gusano cogollero fue muy similar para ambos años, aunque el número de machos capturados en el segundo año fue muy bajo. En el primer año, la trampa Scentry *Heliothis* fue mejor que la bucket. En cuanto a los cebos, la feromona de Chemtica y Trécé fueron mejores que la Scentry. La captura obtenida con la feromona de Scentry fue muy similar al control. En 1999, la interacción de trampas-cebo fue significativa. La trampa bucket tuvo las más bajas capturas independientemente del cebo usado. La trampa Scentry *Heliothis* capturó mejor con los cebos Chemtica que los otros cebos. La trampa delta tuvo las más altas capturas con el cebo Chemtica, seguido de los cebos Trécé y Pherotech. En las trampas, también se capturaron otros insectos con la feromona del gusano cogollero y se observó que la entomofauna asociada capturada fue mayor que la captura de gusano cogollero en ambos años. Las trampas cebadas con feromona capturaron significativamente más entomofauna asociada que las trampas que no contenían feromona.

The fall armyworm (FAW), *Spodoptera frugiperda* (J. E. Smith), is a generalist noctuid moth that is distributed from Brazil northward, throughout Central and North America (Mitchell 1979). FAW larvae feed on more than 60 different species of plants, particularly graminaceous hosts, such as maize, sorghum and Bermuda grass (Mitchell 1979). *S. frugiperda* is one of the most important constraints to maize production throughout Mexico, where this crop plays a principal role in both farming production and human diet. Chemical insecticides are routinely employed as control agents against this insect pest in Mexico, although recently, some alternatives to chemical control have begun to be explored, particularly the use of entomopathogenic agents (e.g., Williams et al. 1999). However, complementary strategies of pest management remain to be tested, including the use of pheromones. Lepidopteran pheromones have been successfully used for insect monitoring, mass trapping, and mating disruption of a diversity of insect pests (Wyatt 1998).

The FAW sex pheromone was reported by Tumlinson *et al*. (1986), as a mixture of (*Z*)-9-tetradecen-1-ol acetate, (*Z*)-9-14:Ac; (*Z*)-7-dodecen-1-ol acetate, (*Z*)-7-12:Ac; (*Z*)-9-dodecen-1-ol acetate, (*Z*)-9-12:Ac and (*Z*)-11-hexadecen-1-ol acetate, (*Z*)-11-16:Ac in the ratio of 81: 0.5: 0.5: 18, respectively. These four components have been formulated and this mixture has been quite effective in monitoring populations of *S. frugiperda* from the USA and the Caribbean Basin (Mitchell et al. 1985). Commercially available FAW sex pheromones have been used in the USA, and have

been shown to be a useful tool for monitoring FAW males (Adams et al. 1989; Mitchell et al. 1989; Gross & Carpenter 1991). The efficacy of these commercial sex pheromones towards Mexican populations of FAW is largely unknown. Gutiérrez-Martínez et al. (1989) evaluated lures but did not report the source of lures. This study was therefore undertaken to evaluate the capture of commercial pheromone formulations and trap designs as a first step for developing a system for monitoring FAW in Mexican maize crops.

Materials and Methods

Study Area

Trials were performed during the late summer growing cycle of 1998 and 1999. Both trials were conducted in the municipality of Suchiate (14°42'N, 92°16'W), Chiapas, in maize fields planted with Cristiani Burkard hybrid (1998) or TACSA 2000 hybrid (1999) sown at the usual density of 50,000 plants per ha with a 0.75 m row spacing.

1998 Trial

Three commercially available FAW sex pheromone lures and two trap designs were evaluated in a 2 × 4 factorial design. The treatments were arranged in a fully randomized block design with four replicates of each treatment. The replicate blocks were arranged in parallel lines approximately 30 m apart within the field (5 ha). The lures tested were Scentry (Scentry Inc., Buckeye, Ariz.), a grey rubber septum dispenser; Trécé (Trécé Inc., Salinas, Calif.) a red rubber septum dispenser, obtained through Gempler's Inc., Belleville, WI, (USA); and Chemtica, a bubble cap (Chemtica, Heredia, Costa Rica). Traps without lures were used as a control. The traps evaluated were the Scentry *Heliothis* trap, a white double cone collapsible plastic net (Ecogen Inc. Billings, MT); and a green reusable bucket trap (Gempler`s, Belleville, WI). Traps with the lures were hung approximately 1.5 m above the ground on wooden stakes placed at 30 m intervals along planted rows. The traps were placed on 18 July, when the maize plants were 15 d old, and they remained in place over the two- month trial. All lures were changed monthly. Trap captures were recorded every 3-4 d from 18 July to 3 September, a total of 16 observation dates. However, at end of the trial, male capture was very low (3 FAW males in total), and for this reason the last two observation dates were not included in the statistical analysis. On each date, we emptied the traps and recorded the numbers of FAW males and non-target insects captured. All non-target insects captured were identified to order (Borror et al. 1989). Voucher specimens were placed in the insect collection held at El Colegio de la Frontera Sur, Tapachula, Mexico.

1999 Trial

The second experiment evaluated four commercial FAW pheromone lures, which were Scentry, Trécé, Chemtica and Pherotech (Pherotech, Delta, BC) and three trap designs, Scentry *Heliothis*, bucket and white delta plastic (Pherotech, Delta, BC) arranged in a 3 × 5 factorial design. The traps were placed one day after planting at 1 m above the ground in the first month, at 1.5 m in the second month and at 2 m in the third month. Traps were checked as described above and a total of 14 observation dates were recorded, although the last three observation dates were not analyzed because no FAW males were caught.

Collection of Volatiles

Volatiles emitted by the pheromone lures were collected by using the dynamic headspace (air-entrainment) technique (Heath & Manukian 1992). New lures (unaged) were individually confined in a 100 ml glass entrainment container (4.8 cm ID × 12.5 cm height). Volatiles were drawn from the container, using purified air that had previously passed through an activated charcoal trap, onto a glass volatile collection trap (4 mm ID × 40 mm long) containing 50 mg of Super Q adsorbent (Alltech Associates, Deerfield, IL, USA) (Heath & Manukian 1992). Air was drawn through the trap at a rate of 1 liter/min by a vacuum pump. The volatiles were collected for a period of 5 h. Volatiles were eluted from the adsorbent with 100 µl of methylene chloride (Baker, HPLC grade), and 100 ng of octyl acetate was added as an internal standard for subsequent quantification. The collection of volatiles was replicated 5 times.

Chemical Analysis

Gas chromatographic-mass spectrometry (GC-MS) was performed with a Varian Saturn III, equipped with a DB5-MS column (30 m × 0.25 mm). Gas chromatographic conditions were as follows: Injector temperature, 200°C; column temperature, isothermal at 80°C for one minute, then increasing to 250°C at 8°C/min and held at this temperature for 3 min. The mass spectrum was obtained at 70 eV by electronic impact. The chemical identification was made by comparing the spectra and the retention times of the natural products with those of authentic synthetic standards.

Statistical Analysis

The number of FAW males captured per trap per sample period in both years were converted to percent of moths captured by each trap and lure combination within each block (Mitchell et al. 1985). Percentage values were arcsine of square root transformed to increase the homogeneity of

variance and normality. Data were analyzed by two-way ANOVA (trap × lure), and treatments means were compared by least significant difference (LSD) ($P = 0.05$).

Results

The total capture of FAW males for all traps pooled throughout the 1998 study was 703 males, with a mean of 1.37 FAW moths per trap per observation date (0.37 male/trap/night) (Fig. 1a). The number of males captured steadily decreased until 14 September when trapping ceased due to damage caused by a tropical storm. A greater number of males were captured at the beginning of the experiment than at the end ($r^2 = 0.48$, $P < 0.01$). Scentry *Heliothis* traps captured significantly more FAW males than bucket traps ($F = 38.25$; df = 1, 21; $P = 0.0001$) (Fig. 2). Chemtica and Trécé lures captured significantly more FAW males than Scentry lures or the controls ($F = 4.16$; df = 3, 21; $P = 0.01$) (Fig. 2). The interaction between traps and lures was not significant ($F = 1.75$; df = 3, 21; $P = 0.18$).

A similar pattern of captures to that in 1998 was observed in the second year, although the overall number of males captured was substantially lower (only 380 males) in 1999 (Fig. 1b). As in 1998, a greater number of male FAW were captured at the beginning of the trial than at the end ($r^2 = 0.60$, $P < 0.05$). There were differences in capture rates among traps ($F = 36.6$; df = 2, 42; $P = 0.0001$) and lures ($F = 7.59$; df = 4, 42; $P = 0.0001$). In this year, the interaction between trap type and lure was significant ($F = 2.72$; df = 8, 42; $P = 0.01$). Bucket traps had the lowest captures no matter what lure was used. Scentry *Heliothis* traps captured more males with Chemtica lure than with other lures and control. Delta traps had the greatest captures with Chemtica lure, followed by Trécé and Pherotech lures (Fig. 3).

Many non-target insects also were captured in the FAW pheromone traps. The traps captured more non-target insects than FAW males in both years. In 1998, 67.7% of the total insects captured were non-target insects, while in 1999, the percentage of non-target species captured was 86.6 (Fig. 4). The insects captured included non-target moths such as *Diatraea lineolata;* Hymenoptera (mainly honey bees, *Apis mellifera*, and bumble bees); and species of Diptera, Coleoptera, and Homoptera (Fig. 4). The bucket traps with pheromone (all lures) captured 2.5 times more non-target insects than the same unbaited trap in 1998 and 1.5 times more in 1999. Baited Scentry *Heliothis* traps captured three times more than control traps in 1998 and 4.5 times more in 1999. Baited delta traps caught four times more than unbaited delta traps in 1999 (Table 1).

Chemical analysis of the commercial unaged pheromone lures indicated the presence of (Z)-9 tetradecen-1-ol acetate as the major component in all lures (Table 2). With respect of the minor components, (Z)-7 dodecen-1-ol acetate was found in all lures, with a release rate ranging from 2.9 ng/h/lure (Trécé) to 14.1 ng/h/lure (Chemtica). In addition, (Z)-11 hexadecen-1-ol acetate was found in quantifiable amounts (12.2 ng/h/lure) only in the Chemtica lure, while in the other lures it was found only in trace quantities.

Discussion

The number of males caught was very low in comparison with other studies where FAW sex pheromone lures have been evaluated (Mitchell et al. 1985; Adams et al. 1989; Gonzalez & Caballero 1990; Gutiérrez-Martínez et al. 1989). For example, Gutiérrez-Martínez et al. (1989) reported captures as high as 150 moths/trap/night in the central area of Chiapas State, Mexico. The reason of the low capture in our study is not known, but several factors may be involved. One possibility is that the low capture may reflect the low FAW population during the study. There is no published data about seasonal abundance of *S. frugiperda* in the region where the study was conducted. Another possibility may be that the traps used in this study were not efficient in catching FAW males. However, the same traps performed well elsewhere (Mitchell et al. 1985; Gutiérrez- Martínez et al. 1989). Still another possibility may be that FAW males from this region respond less to the commercial sex pheromone lures compared with populations elsewhere. In Costa Rica, sex pheromone lures from North America and England gave erratic capture rates under field conditions (Andrade et al. 2000). A re-examination of four acetates for *S. frugiperda* from Costa Rica showed that (Z)-7-dodecen-1-ol acetate and (Z)-9-dodecen-1-ol acetate were highly attractive to FAW males when present alone. The binary combination of (Z)-7-dodecen-1-ol acetate (0.6%) and (Z)-9-tetradecen-1-ol acetate (99.4%) was at least 10 times more attractive to *S. frugiperda* in Costa Rica than North American or English lures (Andrade et al. 2000).

The good performance of Chemtica and Trécé lures can not be explained by qualitative difference in its components because all lures had the same active components. Also, the type of dispenser used for releasing the pheromone did not explain the better performance of Chemtica and Trécé because the pheromone of Trécé was loaded into rubber septa, whereas the Chemtica lure was in a bubble cap. Other studies have shown that the type of substrates used for releasing the pheromone can influence trap captures. For example, Mayer & Mitchell (1999) have shown that more *Plutella xylostella* males were captured with pheromone mixtures loaded into grey septa than with red septa.

Scentry *Heliothis* traps captured more FAW males compared with bucket traps. These results

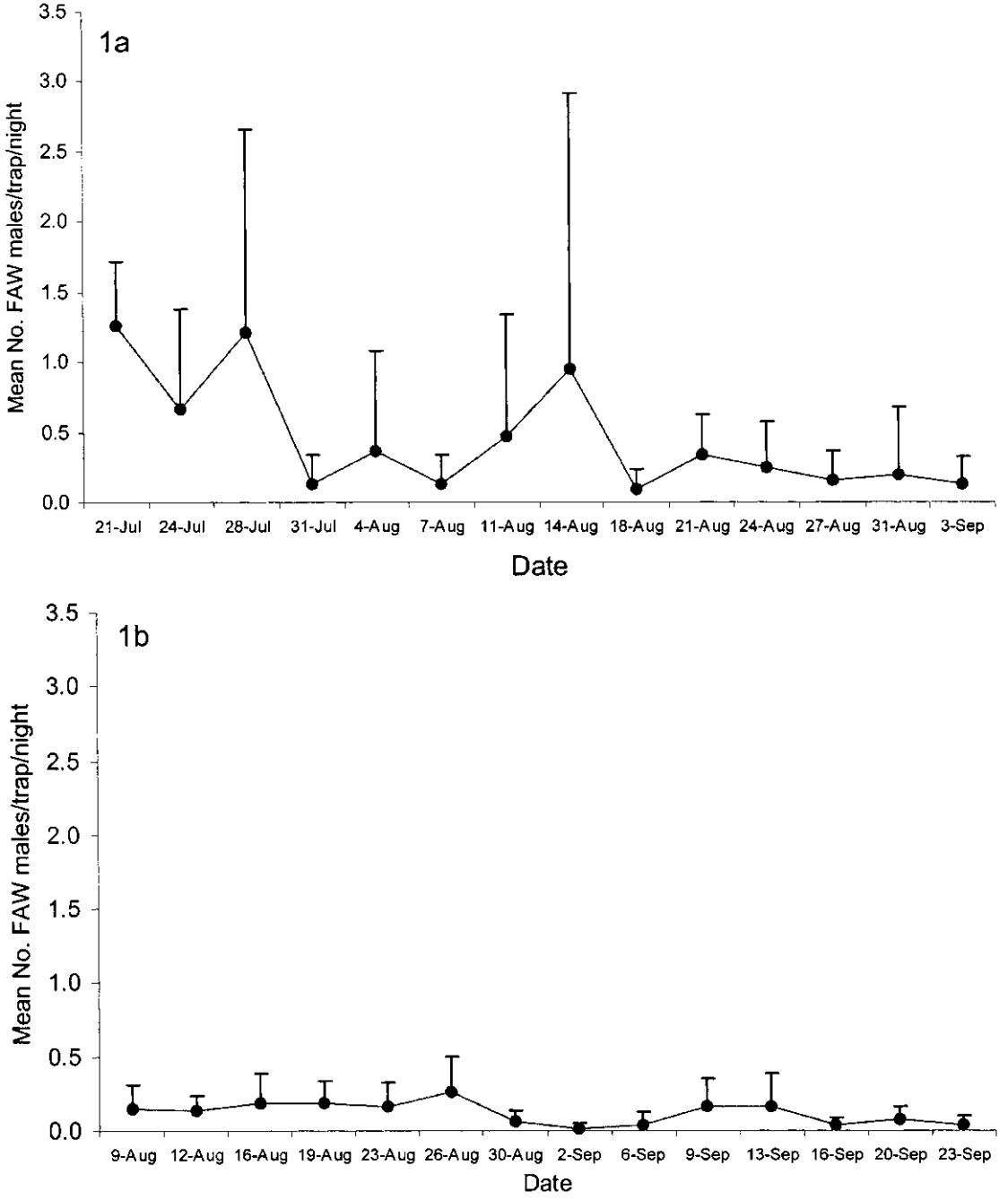

Fig. 1. Seasonal mean number (+SEM) of captures of male *Spodoptera frugiperda* with sex pheromone traps in a maize field in southern Mexico. a) 1998, b) 1999.

are in agreement with Mitchell et al. (1985), who reported that Scentry *Heliothis* traps performed better than bucket traps. However, other studies have shown that FAW capture was the same with Scentry *Heliothis* traps, multi-pher, bucket and pherocon traps (Adams et al. 1989).

Un baited traps, mainly Scentry *Heliothis* traps, captured 9% of all FAW males caught in both years. Others have reported that unbaited control traps caught few or no moths (Mitchell et al. 1985). However, the differences between our results and those of Mitchell et al. (1985) may be

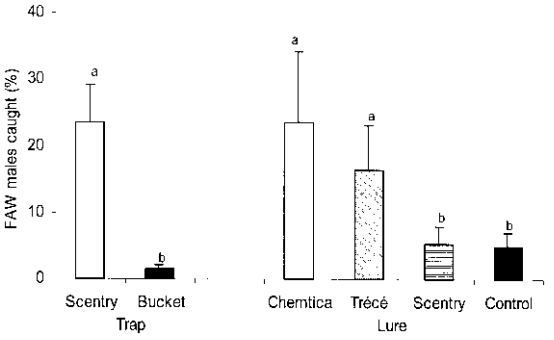

Fig. 2. Percent capture of male fall armyworm (+SEM) in different traps and lures evaluated during 1998. Significant differences within trap and lures are shown by different letters over the bars (LSD test, $P = 0.05$).

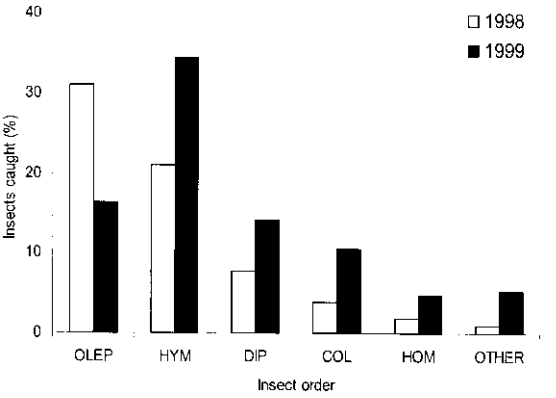

Fig. 4. Percentage non-target and target insects captured in fall armyworm traps during 1998 and 1999 in a maize field in southern Mexico. (OLEP = Other Lepidoptera; HYM = Hymenoptera; DIP = Diptera; COL = Coleoptera; HOM = Homoptera; Other = Hemiptera + Orthoptera + Neuroptera + Dermaptera).

due to the type of trap used. They utilized bucket traps, a trap that in our study captured only very few males. It is not known why males were attracted to unbaited traps. Mitchell et al. (1989) have reported that color and design of traps may influence trap capture, although the sex pheromone is fundamental for attracting males.

Baited traps caught more non-target insects than unbaited traps, suggesting that some of the pheromone components may attract non-target insects. In the case of other moth species, this is not surprising because some of these non-target moths may use similar or identical pheromone components to those of *S. frugiperda*. For example, Weber & Ferro (1991) reported that the noctuids *Leucania phragmitidicola*, *Sideridis rosea* and *Eurois occulta* were commonly captured in FAW traps in Massachusetts, USA. Several studies have documented the phenomenon that baited traps attract non-target and even beneficial insects (Adams et al. 1989; Mitchell et al. 1989; Gauthier et al. 1991; Gross & Carpenter 1991; Meagher & Mitchell 1999). Apparently, trap color may play a role in the attraction of insects. For instance, several studies have documented that white or yellow traps attracted large numbers of *Bombus* spp. (Hamilton et al. 1971; Mitchell et al. 1989). However, Gross & Carpenter et al. (1991) and the results of our study, where a control trap was used, suggest that chemical compounds from pheromones may be involved in the attraction of non-target insects captured. In the case of *Bombus* spp., Gross & Carpenter (1991) reported that insects approached only the yellow traps, but they did not enter the traps unless olfactory stimuli were present. Meagher & Mitchell (1999) speculated that *Bombus* spp. are attracted to any of the FAW sex pheromone components. The problem of capturing non-target insects has been discussed in detail elsewhere (Adams et al. 1989; Weber & Ferro 1991).

In conclusion, the results of this study showed that some lures and traps performed better than

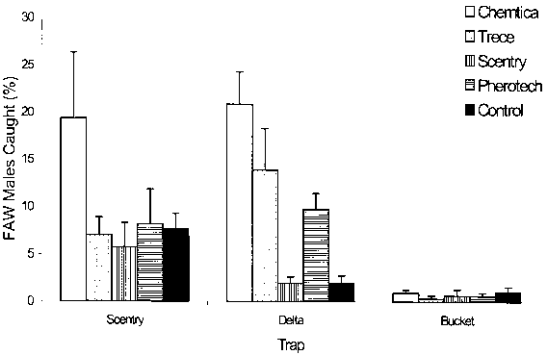

Fig. 3. Percent capture of male fall armyworm in three traps with four different lures during 1999 in a maize field in southern Mexico.

TABLE 1. TOTAL NUMBER OF NON-TARGET INSECTS CAPTURED IN TRAPS IN MAIZE FIELDS IN SOUTHERN MEXICO.

	Year	
Trap type	1998	1999
Unbaited bucket	38	50
Baited bucket	99	78
Unbaited Scentry	366	332
Baited Scentry	1078	1497
Unbaited delta	*	98
Baited delta	*	392

*Not tested.

Total numbers of non-target insects were 1581 in 1998 and 2447 in 1999.

TABLE 2. RELEASE RATES (MEAN ± SEM, N = 5) OF PHEROMONE COMPONENTS IN UNAGED COMMERCIAL LURES COLLECTED BY DYNAMIC HEADSPACE AND DETERMINED BY GAS CHROMATOGRAPHIC-MASS SPECTROMETRY.

Pheromone component	Mean (±SEM) Lure Release Rate (ng/h/lure)			
	Chemtica	Trécé	Scentry	Pherotech
(Z)-7-12: Ac	14.1 ± 11.5	2.9 ± 2.0	6.4 ± 3.0	4.1 ± 1.9
(Z)-9-14: Ac	92.4 ± 54.2	21 ± 7.5	46 ± 20.0	71 ± 42.0
(Z)-11-16:Ac	12.2 ± 9.2	1.28 ± 0.68	0.6 ± 0.01	0.08 ± 0.04

others. However, we found that the abundance of FAW populations may affect the results obtained. Therefore future studies with high density populations of *S. frugiperda* will be necessary to confirm these results.

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We thank Antonio Santiesteban for his help with the chemical analysis of pheromone lures, Alvaro Garcia-Ballinas for his advice in the identification of the nontarget insects. Trevor Williams for reading an early draft of the manuscript and the comments of three anonymous reviewers. We especially thank Don Fortino Galvez Toledo for the use of his land and Chemtica for giving us the lures used in the first year of this study. This study was supported by PIAFECH-ZONA SUR, A.C. (Patronato de Investigación Agropecuaria y Forestal) and SIBEJ (Sistema de Investigación Benito Juárez, project number 980501024).

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EGG LAYING BEHAVIOR OF MEDITERRANEAN FRUIT FLIES (DIPTERA: TEPHRITIDAE): IS SOCIAL FACILITATION IMPORTANT?

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ABSTRACT

In a set of three experiments, we were unable to verify earlier reports of social facilitation of oviposition-associated behavior in Mediterranean fruit flies, *Ceratitis capitata* (Wiedemann). In our first 2 experiments, we placed a focal fly on a kumquat (Experiment 1) or artificial fruit (Experiment 2) either occupied by an ovipositing resident fly or alone. The frequency of oviposition attempts by the focal fly was slightly, but not significantly, *lower* in the social than solitary case. In the third experiment, which was carried out in a large field enclosure, we found that focal flies did not prefer to alight on a kumquat occupied by an ovipositing fly compared with a similar but unoccupied kumquat. Our results suggest that social facilitation of oviposition-associated behavior may not be a ubiquitous phenomenon in medflies.

Key Words: Conspecific attraction, Mediterranean fruit fly, *Ceratitis capitata,* Fruit flies, Egglaying behavior

RESUMEN

En una serie de tres experimentos, no pudimos verificar reportes previos de la facilitación social del comportamiento asociado con la oviposición en la mosca frutera del Mediterráneo, *Ceratitis capitata* (Wiedemann). En los 2 primeros experimentos, colocamos a una mosca focal en una fruta kumquat (Experimento 1) o en una fruta artificial (Experimento 2) ya sea ocupada por una mosca residente ovipositante o sola. La frecuencia de los intentos de oviposición por la mosca focal fue ligeramente, pero no significativamente, más baja en el caso social que en el caso solitario. En el tercer experimento, el cual se llevó a cabo en un cercado grande de campo, encontramos que las moscas focales no prefirieron posarse en una kumquat ocupada por una mosca ovipositante en comparación con una kumquat similar pero no ocupada. Nuestros resultados sugieren que la facilitación social del comportamiento asociado a la oviposicion tal vez no sea un fenómeno ubicuo en la mosca del Mediterráneo.

The presence and behavior of conspecifics sometimes enhances an individual's likelihood of exploiting resources such as feeding grounds, hosts or mates. For example, hunters and wildlife managers have successfully employed conspecific decoys or playback-audio-tapes to attract individuals of various bird and mammal species at their feeding or breeding grounds (Reed and Dobson 1993). Further, Alatalo et al. (1982), using taped playback of pied flycatchers, demonstrated that these birds preferentially settled in areas where songs were played even though the species is strongly territorial. Other examples include tendencies of various insects to lay more eggs per female when held in groups than alone (Hilker 1989; Chess et al. 1990; Abernathy et al. 1994), and increases in time spent per host patch and amount of superparasitism with increasing numbers of female *Leptopilina* and *Asobara* parasitoids in patches of host *Drosophila* larvae (Visser et al. 1900, 1992a,b; van Alphen et al. 1992).

Recently, it has been reported that female Mediterranean fruit flies, *Ceratitis capitata* (Wiedemann), are more likely to alight on fruit occupied by conspecific females (Prokopy et al. 2000) than on unoccupied fruit and to express heightened propensity to oviposit in the presence than absence of an ovipositing conspecific female on a fruit (Prokopy and Duan 1998). Moreover, other reports have suggested that other species of tephritid flies also are more likely to oviposit in host fruit when in the presence than absence of a conspecific ovipositing fly (Robertson et al. 1995; Prokopy and Reynolds 1998; Prokopy et al. 1999). These studies are of ecological interest because social facilitation of egg laying can create non-linear patterns of individual distribution with far reaching effects on population dynamics (Fretwell

1972; Reed and Dobson 1993; Sutherland 1996; Stephens and Sutherland 1999; Courchamp et al. 1999). For tephritid flies, a thorough understanding of such non-linear population dynamics may also be of economic importance.

Our intent here was to verify the phenomenon of socially facilitated oviposition-associated behavior in medflies reported by Prokopy et al. (2000) and Prokopy and Duan (1998) in experiments conducted under a broader range of conditions than characterized in these previous reports.

Materials and Methods

We conducted all experiments at the University of Hawaii Research Center in Kauai, Hawaii. Prior to the experiments, we initiated a colony of wild medflies from infested coffee berries collected from a commercial grove. All flies used in the experiments developed as larvae in papaya in the laboratory. Following eclosion, adults of both sexes were held together in groups of about 50 females and 50 males at about 25°C, 60% relative humidity and natural day length of 13 hours in 30 $\times$ 30 $\times$ 30 cm screen cages supplied with water and food consisting of a mixture of enzymatic yeast hydrolysate and sucrose. All flies tested were 1 to 3 weeks old, sexually mature, presumably mated, and carried a moderate egg load of 20-30 eggs (see below). Except for the "experienced" flies in experiment 2, the flies were not exposed to fruit prior to testing. A fly was used only once in the experiments.

We conducted Experiments 1 and 2 inside a large screen house with a transparent plastic roof, which provided ample natural light and protection from frequent brief showers. The test arena consisted of a 1 m tall, 70 cm wide and 50 cm deep screen enclosure, which contained a small potted non-fruiting coffee plant.

Experiment 1: The Tendency to Bore in Occupied Kumquats

In the first experiment, we followed the methods of Prokopy and Duan (1998). We hung a single kumquat fruit (*Fortunella japonica*, family Rutaceae*)* using a coated wire twist attached to the coffee plant. The kumquats were essentially the same size as those used by Prokopy and Duan (1998). On average, they weighed 13.5 ± 0.3 g (mean ± SE), were 35.8 ± 0.6 mm long and 25.3 ± 0.3 mm wide (n = 10). They were shipped from California, were uninfested, and were washed and dried prior to use. A fresh fruit was used for each trial. Because medflies cannot readily penetrate a kumquat skin, we followed Prokopy and Duan (1998) and used a pin to generate a single 0.5 mm diameter hole at the center of the kumquat prior to placing a fly on the fruit. The flies used were 14 days old, with an average load of 22.9 ± 3.8 eggs (based on a sub-sample with n = 10 flies).

Each trial, we randomly selected a new, experimentally naïve focal fly from the cage, and using a small plastic cup, placed her on the fruit. To test whether a focal fly was more likely to oviposit or oviposited more quickly when another fly was present, we compared the behavior of focal flies in two treatments detailed below. We ran 50 trials of each treatment in haphazard order. We used chi square tests or log linear models to analyze frequency data and ANOVA's for latency data.

Treatment 1: Resident Present

A trial of this treatment began with puncturing a single hole in the fruit and then placing on the fruit a first fly, the resident. Shortly after the resident initiated oviposition, we punctured a second hole approximately 1 cm to her rear and placed the focal fly about 1.5 cm to her side. We recorded interactions between the flies, whether the focal fly initiated oviposition, and the latency from introducing the focal fly to initiation of oviposition.

Treatment 2: Resident Absent

Here we initiated a trial by puncturing the fruit and then placing the focal fly at the center of the fruit approximately 1.5 cm from the hole. We recorded whether or not the focal fly initiated oviposition, as well as the latency from introducing the focal fly to initiation of oviposition.

Based on the results of Prokopy and Duan (1998), we predicted that the frequency of boring by focal flies would be higher, and the latency to bore would be shorter in the resident present than resident absent treatment.

Results

In the 'resident present' treatment, the resident and focal flies were within less than fly length in 80% of the trials, but we observed clear interactions between the flies only in 20% of the trials. Such interactions typically involved head waggling and wing waving, and sometimes also head butting and foreleg kicking. Following such an exchange, focal and resident flies departed the fruit in 4% and 2% of the trials respectively.

The presence of an ovipositing resident fly did not affect the propensity of focal flies to initiate an oviposition bout: focal flies started boring in 74% of the 'resident present' trials and in 84% of the 'resident absent' trials (χ^2 = 0.5, df = 1, P > 0.4), and their latency to bore was similar in either treatment, 55.7 ± 6.7 s in the 'resident present' trials and 53.6 ± 9.1 s in the 'resident absent' trials ($F_{1,77}$ = 0.03, P > 0.5).

Experiment 2: The Tendency to Bore in Occupied Artificial Fruits

Focal flies in the 'resident absent' treatment of Experiment 1 bored in 84% of the trials compared to only 34% in the comparable treatment of Prokopy and Duan (1998). One may argue that in our experiment, there was relatively little opportunity for a resident to facilitate the boring propensity of the focal fly, which was already very high in the absence of a resident. Hence we conducted a more elaborate experiment, using a less acceptable 'fruit' and a variety of resident and focal flies. Our general motivation was to try to generate a favorable condition for the expression of social facilitation.

We created spherical artificial fruits 30 mm in diameter by mixing 6% agar and 1% green food coloring in water, boiling the mixture and pouring into spherical molds (Boller, 1968). After the spheres cooled, we wrapped them with parafilm, leaving a short 'stem' used to hang the sphere with a plastic coated wire twist from the coffee plant.

We used two types of flies in this experiment: naïve flies, which were 8-10 days old with no prior exposure to fruit; and experienced flies, which were 3 weeks old and had been exposed to artificial fruit in their cage for 2 days. The average egg load of a sample cohort of naïve flies was 31.9 ± 5.8 and that of a sample cohort of experienced flies was 26.1 ± 2.9 (n = 10) for each sample. Overall, there were 3 conditions of the resident fly (resident absent, naïve resident, or experienced resident), and 2 conditions of the focal fly (naïve or experienced). We ran trials of the 6 combinations in haphazard order within blocks of 6 trials for a total of 180 trials. Here, no fruit punctures were necessary, so in 'resident absent' trials we simply placed the focal fly at the center of a fruit. In trials with a naïve or experienced resident, we introduced the focal fly to the side of the resident after she had initiated boring.

Results

In trials with a resident present, the resident and focal flies were within less than fly length in 92.5% of the trials; the flies showed clear interactions in 72% of the trials. Such interactions typically involved head waggling and wing waving, and sometimes also head butting and foreleg kicking. Following such an exchange, focal and resident flies departed the fruit in 10% and 11% of the trials respectively.

The presence of either a naïve or experienced resident fly did not affect the propensity of focal flies to initiate oviposition bouts ($\chi^2 = 1.0$, df = 2, $P > 0.4$, Fig. 1a). The only notable trend was a slightly higher propensity to bore by experienced than naïve focal flies ($\chi^2 = 3.0$, df = 1, $P = 0.08$, Fig. 1a). Similarly, the average latency to bore by focal flies was similar among the 3 resident-type treatments ($F_{2,87} = 0.09$, $P > 0.5$, Fig. 1b).

Experiment 3: The Tendency to Alight on Occupied Fruits

In this experiment, we tested whether flies preferred to land on a fruit already occupied by a fly over an unoccupied fruit. The experiment was conducted in a cylindrical nylon-screen field enclosure 4 m wide and 2.5 m high containing 2 large potted coffee plants creating a canopy ca. 1 m wide and ca. 2 m high. At the start of each of the four days of the experiment we released approximately 200 naïve 10-14 day old flies (males and females in approximately equal numbers) inside the enclosure. Using coated wire twists, we hung 2 kumquats matched for size from a thin copper wire stretched between 2 branches. The 2 fruits were 20 cm apart.

Prior to the start of a trial, we punctured 2 holes on opposite sides of each kumquat. We then

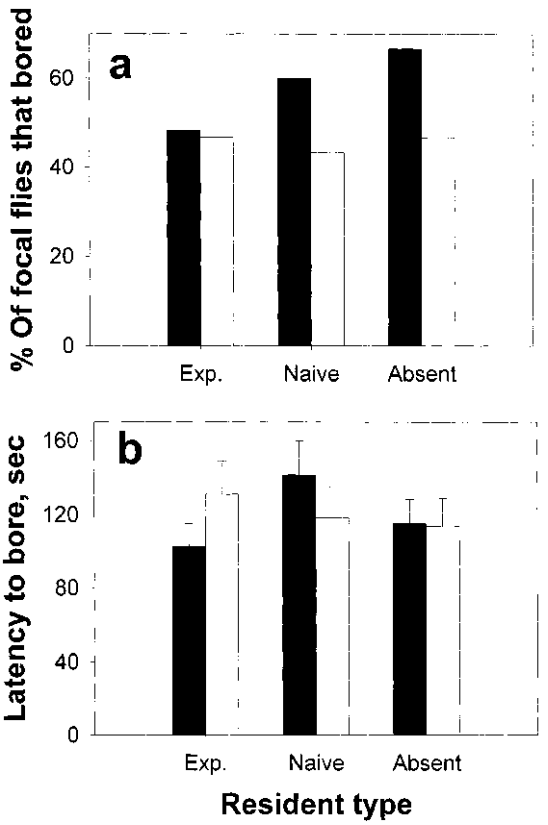

Fig. 1. (a) The proportion of experienced (dark bars) and naïve (clear bars) focal flies that initiated boring in a kumquat occupied by an experienced, naïve or no fly, and (b) the average latency from placement on a fruit to initiation of boring by those focal flies that bored.

placed a resident fly on one of the 2 kumquats and watched for alighting flies. The resident fly typically initiated inspection of the fruit, followed by boring and egg laying. We noted the choice of the first alighting fly and her behavior after landing on a fruit. At the end of each trial, we removed the resident and any alighting fly from the enclosure except for a few occasions where these flies flew off a fruit and could not be located. We conducted a total of 100 trials, while haphazardly alternating the side of the occupied fruit within each block of two successive trials (i.e., the occupied fruit was on the right side in one trial and on the left side in the other trial within a block).

RESULTS

The flies showed no side preference, landing in identical proportions (0.5:0.5) on the left and right fruits. Neither did the flies preferentially land on the fruit occupied by a resident fly, which they chose in only 54% of the trials ($\chi^2 = 0.6$, df = 1, $P > 0.5$). The proportion of flies that initiated egg laying was similar for flies that landed on fruit with or without a resident, 57% and 60% respectively. Finally, the latency to bore was similar for the 2 fly categories, 95.3 ± 10.8 s for flies landing on the fruit occupied by a resident and 90.3 ± 11.4 s for the flies that landed on an unoccupied fruit ($F_{1, 57} = 0.1$, $P > 0.5$).

DISCUSSION

Social Facilitation?

A focal fly placed on a fruit with a boring fly was not more likely to initiate egg laying than a focal fly placed alone (Experiments 1 and 2; Fig. 1). Moreover, in Experiment 3, we found that flies were not more likely to land on a kumquat occupied by another fly than on a fruit with no fly. These findings are in contrast to findings of social facilitation of alighting and post-alighting behavior of medfly females reported by Prokopy et al. (2000) and Prokopy and Duan (1998).

With respect to social facilitation of alighting behavior, it is relevant to recognize that Prokopy et al. (2000) used artificial fruit-mimicking spheres or hemispheres each occupied by at least four conspecific females (held in place by sticky adhesive), whereas we used punctured kumquats each occupied by just a single conspecific resident female. In our study, the value of odor from punctures in real fruit may have outweighed the value of the presence of a single resident female as information signaling a fruit as a potentially quality resource to a focal female. In the study by Prokopy et al. (2000), the presence of multiple resident females may have overridden the value of other information emanating from artificial fruit. In our judgment, therefore, the propensity of a medfly female to alight on a fruit occupied by one or more conspecific resident females may be influenced by a variety of fruit chemical or visual stimuli whose informational value may or may not exceed that of a resident.

With respect to social facilitation of post-alighting behavior, it is possible that the results reported by Prokopy and Duan (1998) were unique to a set of biotic and abiotic conditions different from the ones in our experiments. Alternatively, some details of experimental protocol may explain the positive results obtained by Prokopy and Duan (1998). First, in the experiment of Prokopy and Duan (1998), as in our experiment 1, 2 punctures were provided per fruit occupied by a resident and only 1 puncture was available in "resident absent" trials. It is possible that under the specific conditions existing during their test, this confounding factor resulted in higher boring propensity in two-than single-punctured fruit. Neither they nor we could find such a positive effect of an additional puncture in separate experiments, but a few other studies have documented positive effects of punctures on oviposition in medflies (Papaj et al. 1989, 1992; Papaj & Messing 1996). The methods we employed in experiments 2 and 3 resolved this possible confound. In experiment 2, we used artificial fruit, which does not require punctures, and in experiment 3, we provided 2 punctures each per occupied and unoccupied fruit. Second, Prokopy and Duan (1998) worked in a relatively exposed location under highly variable weather conditions typical of east coasts of the Hawaiian islands. For example, on a typical morning, there were a few brief showers, a few cloudy and windy periods, and breaks of intense sunshine. Medflies are highly sensitive to such weather fluctuations, with a strong preference to oviposit during calm and sunny times. A "resident absent" trial can be conducted at any moment even if the weather is "bad". In contrast, a precondition for performing a 'resident present' trial is that the weather is above a critical threshold allowing a resident fly to initiate boring. That is, while the weather has to be "good" for all 'resident present' trials, this condition does not necessarily have to be met for "resident absent" trials. An inherent bias of this sort could have led to a finding of apparent social facilitation by Prokopy and Duan (1998). Our experiment 3 addressed this issue because we employed a choice test, simultaneously presenting a 'resident present' and "resident absent" fruit. However, in our experiment 3, there were relatively favorable conditions for boring (60% of focal females on fruit lacking a resident female bored), so it is still possible that social facilitation occurs under less favorable conditions for boring.

These inconsistent results for social facilitation of oviposition-associated behavior in medflies are troubling and strongly suggest that positive re-

sults must be taken with extra caution until repeatedly replicated in meticulously conducted experiments. Moreover, because some of the inconsistencies may be artifacts of laboratory rearing conditions and experimental protocols, we suggest that, in this unusual case, social facilitation ought to be studied in 'natural' field settings. Ultimately, to make a case for the ecological significance of social facilitation in egg-laying behavior, one must demonstrate that females in the field commonly encounter each other on host fruit and that such encounters consistently and significantly increase the tendency for females to lay eggs. Such future demonstration must control for potential confounding factors such as fruit location and damage (see Papaj et al. 1989; Papaj 1994).

The Nature and Adaptive Significance of Fly Interactions on Fruit

In our study, the interactions between resident and focal flies varied between experiments. The frequency of interaction between the resident and focal fly was just 20% in Experiment 1 but 72% in Experiment 2. In Experiment 1, resident females frequently proceeded to oviposit, rather than engage in interactions with the focal female. In Experiment 2, by contrast, interactions were the norm. The difference in frequency of interactions may reflect a difference between the experiments in the acceptability of oviposition substrates. In Experiment 1, we used kumquats, which are highly acceptable fruits in terms of oviposition. In Experiment 2, we used artificial fruits, which are considerably less acceptable for oviposition than kumquats. In contrast to resident flies on kumquats (Experiment 1), resident flies on the less acceptable agar spheres (Experiment 2) were evidently more likely to abort boring, thus providing opportunity to interact with focal flies. A pattern in which ovipositing resident medflies ignored intruders, as in Experiment 1, was noted by Prokopy and Duan (1998) and Papaj and Messing (1998), again on real fruit. Two possible explanations for this behavior are, first, that a female engaged in egg laying does not attend to her surrounding (see Dukas 1998), and second, that the ovipositing female notices the intruder but prefers to continue oviposition rather than confront the intruder, because of the higher expected fitness benefits from the former.

The exact motivation for and effects of interactions between resident and focal females are not fully clear to us. However, many interactions seemed to be aggressive in nature. Indeed, aggressive interactions by female medflies on coffee berries have been described by Papaj and Messing (1998) and female-female aggression has been documented in other tephritids as well (e.g., Prichard 1969; Fitt 1989; Prokopy et al. 1999). At the ultimate level, it is probably easier to understand causes underlying aggression than social facilitation. In small fruits, which are the preferred fruit size by medflies (Katsoyannos 1989), a second egg clutch per fruit may reduce fitness due to larval competition for resources. Such competition reduces survival and growth rate (Debouzie 1989). Results of larval competition experiments in kumquats about 30% smaller than those used in our experiments (R. Dukas, R. J. Prokopy and J. J. Duan, in press) indeed suggest that laying a second clutch per small fruit reduces fitness. Hence a resident fly's attempt to chase away an intruding fly from a small fruit can potentially increase the resident's fitness.

It is not obvious, however, how an intruding fly should respond to either an aggressive or a nonresponding ovipositing resident. First, our observations of fly-fly interactions on fruit revealed that rather than escalating into fighting, aggressive interactions quickly ended either with one fly leaving the fruit, or the two flies staying and ovipositing (see also Papaj and Messing 1998). This suggests that an intruding fly does not risk injury or other costs if she decides to stay. Second, one can imagine some proximate mechanism, such as a stimulating odor emitted by the ovipositing resident, that increases a focal fly's laying propensity under certain conditions. Such odor may simply be fresh fruit volatiles emitted during the boring activity of the resident. The ultimate explanation for a stimulating effect of fruit odor is that punctures usually allow faster oviposition (Papaj 1994).

We believe that a suite of environmental and physiological factors such as fly density, age, nutrition, egg load, fruit size and ripeness, existence of punctures, and even weather should guide a fly's egg laying decisions. An ultimate approach, which seeks to define female fitness in the context of such factors, has been successful in explaining other oviposition decisions in medflies (e.g., Prokopy et al. 1989, 1994; Papaj et al. 1990; Papaj and Messing 1996). In our experiments, focal flies (except for the "experienced" ones in Experiment 2) had no prior experience with fruit, but they had encountered numerous conspecifics in their cage. The perception of high fly density during caging should diminish a fly's tendency to avoid fruits occupied by ovipositing flies, egg infested fruits, and fruits of low quality, because unoccupied, uninfested fruits of high quality are less likely to be found at high fly density. Indeed, several insect studies have documented a higher egg laying propensity per individual under social than solitary conditions (e.g., Prokopy and Bush 1973; Chess et al. 1990; Prokopy and Reynolds 1998). However, these studies, and the body of theory motivating them, do not lead us to predict that a focal fly would *prefer* a fruit occupied by an ovipositing fly over an uninfested fruit of similar quality, as long as laying a second clutch in a fruit is costly in terms of larval competition.

Probably the best explanation for numerous reports on social facilitation in various taxa including nest site selection in birds (Alatalo et al. 1982) and mate choice in fish (Dugatkin 1992) involves issues of information: the focal individual, which is inexperienced, mimics another individual (the model) on the assumption that the model has made an informed choice. By copying the model, the focal individual presumably avoids paying a cost associated with gathering information. Applied to our protocol, this argument implies that a focal fly may be more likely to oviposit after watching a resident ovipositing than when alone because the savings in terms of information-gathering raise the relative value of that fruit to the focal fly. However, the occurrence of such savings is not itself sufficient to favor social facilitation. Rather, the benefit of copying in terms of information-gathering must exceed the cost of competition that a fly's larvae would suffer if deposited into a fruit that is being exploited by another fly. Whether the benefit of copying exceeds this cost is, at present, unclear.

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EFFICACY OF SPINOSAD BAIT SPRAYS TO CONTROL MEDITERRANEAN AND CARIBBEAN FRUIT FLIES (DIPTERA: TEPHRITIDAE) IN COMMERCIAL CITRUS IN FLORIDA

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ABSTRACT

A serious infestation of Mediterranean fruit fly in Florida in 1997 and 1998 led to the widespread aerial and foliar application of malathion-bait sprays. Public concerns over property damage, environmental impact and public health led to the immediate need and acceptability of alternative pesticide/bait combinations. Preliminary work with spinosad, a derivative of a soil microorganism developed by Dow AgroSciences, in combination with a new bait (SolBait) showed promise. To ensure that this product would be effective in Florida for fruit fly control, three field tests were conducted using aerial and/or foliar applications. Results indicated that sprays with spinosad-SolBait provided comparable and significant control levels for sterile Mediterranean and Caribbean fruit flies in comparison to standard malathion with NU-LURE® or SolBait treatments by aerial or foliar application. In one test, honey bees and hives were exposed to sprays in the treatment area and no significant treatment differences were observed in hive condition or brood. Insufficient data on effects of treatments on naturally occurring and introduced beneficial insects were collected for statistical analysis but it appears no harmful effects were observed.

Key Words: Spinosad, Bait spray, Mediterranean fruit fly, Caribbean fruit fly

RESUMEN

Durante los años 1997 y 1998 ocurrió en Florida una infestación de impotancia de la mosca del Mediterráneo, que trajo como consecuencia una amplia aspersión aérea y foliar de la mezcla malathion-cebo. Debido a la preocupación pública por daños a la propiedad privada, el impacto ambiental, y la salud pública fue posible la aceptación necesaria e inmediata de alternativas a las combinaciones de pesticida/cebo. Los trabajos iniciales con Spinosad, el cual es un derivado de microorganismos del suelo, con un cebo nuevo (SolBait) y producido por la compañía Dow AgroScience fueron prometedores. Para asegurar la efectividad del producto en el control de la mosca de la fruta en Florida, se efectuaron tres pruebas de campo usando aspersión aérea y foliar. Los resultados indicaron que las aspersiones de Spinosad combinado con SolBait produjeron un nivel de control de las moscas del Mediterráneo y del Caribe, comparable y significativo en comparación con los estándares de los tratamientos usando Malathion con NU-LURE® o SolBait aplicados por aspersión aérea o foliar. En una de las pruebas, colmenas de abejas fueron expuestas a las aspersiones en el (rea de tratamiento y no se observó diferencia significativa en las condiciones de las colmenas o las crías. Los datos acerca del efecto de los tratamientos en los insectos benéficos fueron insuficientes, pero no se observaron efectos dañinos.

Since 1956, malathion-bait sprays have been used extensively for the control of Mediterranean fruit fly (Medfly), *Ceratitis capitata* (Wiedemann) and, more recently, Caribbean fruit fly (Caribfly), *Anastrepha suspensa* (Loew) (Steiner et al. 1961). Ten serious infestations of Medfly were eradicated successfully in Florida using malathion-bait spray mixtures applied by ground and/or air (Clark et al. 1996). The same strategy was used to eradicate Medfly from Brownsville, Texas in 1966 (Stephenson & McClung 1966). California has had a similar history of Medfly infestations since 1975 and has used malathion-bait spray in all or part of their eradication efforts (Carey et al. 1999).

In 1997, the detection of 749 Medflies in a five-county area in Florida led to the widespread aerial and ground application of the malathion-bait spray mixture over a heavily populated urban environment. Subsequent reports of vehicle paint discoloration, fish kills and public complaints about the use of organophosphate insecticides led to increased emphasis on identifying

alternative insecticides and attractants with reduced environmental and public health impact.

Several materials with insecticidal properties in conjunction with an improved bait attractant have been tested against several species of economic tephritid fruit flies. Phloxine B is a photoactive dye which is toxic to certain insect species (Heitz 1987, 1995). Moreno and Mangan (1995) and Liquido et al. (1995) reported that phloxine B added to an attractant bait could evoke a high degree of mortality in Medfly and other fruit fly species.

Shortly thereafter, a new species of actinomycetes, *Saccharopolyspora spinosa* (Mertz and Yao 1990) was shown to produce compounds, primarily spinosyns A and D, which had insecticidal properties. Spinosad, a mixture of spinosyns A and D, has shown activity against several insect orders including Diptera. It acts as a stomach and contact poison and degrades rapidly in the environment. Preliminary laboratory tests by King and Hennessey (1996) and Adan et al. (1996) indicated mortality of Caribfly and Medfly fruit flies at low concentrations.

An initial field test by Moreno et al. (2000) with spinosad and other compounds in a new bait material, SolBait (Moreno and Mangan 2000), against sterile, dyed Mediterranean fruit flies, showed efficacy comparable to the standard, malathion-NU-LURE®. This test in Florida indicated that aerial sprays by helicopter and foliar spot sprays of spinosad-SolBait in commercial citrus groves were equal to or better than malathion-NU-LURE® in reducing fruit fly populations. However, additional field trials were needed to confirm the efficacy of spinosad-SolBait against Caribfly and Medfly using aerial and ground application techniques.

Non-target effects of materials tested were evaluated by releasing the fruit fly parasitoid *Diachasmimorpha longicaudata* (Ashmead), and by placing honey bee hives in treatment blocks during the first test.

Materials and Methods

Three replicated field tests were conducted in commercial orange groves in Florida in spring and fall, 1999 and spring, 2000. Test 1 consisted of ground applications of foliar sprays of spinosad and malathion in SolBait at higher volumes compared to the malathion-NU-LURE® standard of 20% malathion ULV with 80% NU-LURE® at 12 oz of mix per acre. Test 2 was also a ground application of foliar sprays of spinosad-SolBait versus malathion-NU-LURE® plus water at the standard dosage but at the same volume per acre as spinosad-SolBait. Test 3 compared aerial application of spinosad-SolBait at two rates to the malathion-NU-LURE® standard and to ground application of spinosad-SolBait. Tests 1 and 3 were conducted against both sterile Caribflies and Medflies while Test 2 was conducted against sterile Medfly only.

Treatments

Test 1 (22 March 1999-03 May 1999). Each treatment was applied to 3.2 ha plots replicated four times in a commercial orange grove in DeSoto County, Florida. Blocks had about 309 trees per ha. Treatment blocks were separated by a minimum buffer of 91.4 m. Treatments were also replicated in time by separation of applications at two week intervals for three applications. The treatments in the experiment were (1) a check (SolBait only) at 21.5 l/ha, (2) spinosad at 80 ppm (0.28 g AI/ha) in SolBait at 21.5 l/ha, and (3) malathion (Fyfanon® 96.8%) (208.3 g AI/ha) at 175.4 ml/ha in SolBait at 21.3 l/ha; and (4) malathion (Fyfanon® 96.8%) (208.3 g AI/ha) at 175.4 ml/ha, was applied with NU-LURE® bait at 700.9 ml/ha as spot sprays on 30 trees per ha at 30 ml per tree. Each of the first three treatments was applied as a foliar spot spray at a rate of 60 ml per tree. Foliar spot sprays for treatments 1,2, and 3 were applied to about a one square meter area of each tree at about tree height using Spraying Systems Co.© 5500 cone jet nozzles attached to a 0.6 m wand and a GunJet #43 hand held spray gun. Working pressure of 862.5 kPa was generated by a Hypro D-30 diaphragm pump and Honda GX 160 5.5 hp engine mounted on a John Deere "Gator™" (4 × 2, 10 hp) utility vehicle. Treatment four was applied by using 11.4-l (3 gallon) hand held pump up sprayers on every 10th or 12th tree of each row.

Test 2 (08 November 1999-06 December 1999). Three treatments were applied to four 4.0 ha blocks of mature orange trees in a commercial grove in Highlands County, Florida. Blocks had about 309 trees per ha and were separated by a minimum buffer of 91.4 m. The application was repeated one time with a two-week interval between applications. Treatments consisted of (1) a control (untreated), and foliar spot sprays at 60 ml per tree of either (2) spinosad 80 ppm (1.57 g AI/ha) in SolBait at 18.7 l/ha or (3) malathion 5 EC (MICRO FLO© 56%) (187.2 g AI/ha) at 312.5 ml/ha with NU-LURE® at 700.9 ml/ha and water at 17.7 l/ha. Foliar spot spray was applied to trees at about tree height using hand held nozzles attached to the same pressure spray equipment described in Test 1.

Test 3 (20 March 2000-08 May 2000). Treatments were applied to 24, 4.0 ha plots in a commercial orange grove in Hendry County, Florida. A minimum buffer of 122 m separated treatment blocks. Treatments were replicated four times and replicated in time by separation at two-week intervals for three treatment dates. Treatments consisted of (1) a control (untreated), (2) a SolBait check applied aerially at 3.5 l/ha, (3) malathion

(Fyfanon® 96.8%) (208.3 g AI/ha) at 175.4 ml/ha with NU-LURE® at 700.9 ml/ha applied aerially, (4) spinosad 80 ppm (0.13 g AI/ha) in SolBait applied aerially at 1.75 l/ha, (5) spinosad 80 ppm (0.28 g AI/ha) in SolBait applied aerially at 3.5 l/ha, and (6) spinosad 80 ppm (3.37 g AI/ha) in SolBait applied as a foliar spot spray at 90 ml per tree (40.2 l/ha) using hand held nozzles attached to the same pressure spray equipment described in Tests 1 and 2.

For the first and third treatment dates, all treatments were applied. For the second treatment date, no check treatment was included.

Insects

Test 1. Sterile, dyed Medfly pupae were received from the El Pino rearing facility in Guatemala at the USDA Preventative Release Program facility at MacDill AFB, Tampa, Florida. The flies were eclosed in plastic adult rearing containers (PARC), held for five days, and transported to the test site in an air-conditioned van. The dyed Caribfly pupae were shipped from the Caribfly rearing facility in Gainesville, Florida to Ft. Pierce for eclosion one week before release. Flies were also transported in air-conditioned vans to the test site. Sterile, dyed Medflies and Caribflies with about equal numbers of males and females were released at the rate of 17,300 flies/ha in each treatment block the day before treatment. Flies were released statically at two equidistant release points along the central row of each test plot.

The braconid parasitoid, *Diachasmimorpha longicaudata* (Ashmead) was released at the rate of 10,000 per treatment plot one day after treatment application for one test date only. Nylon stocking exposure traps containing sterile larvae of Caribfly in larval diet were placed in host trees for 5 days to monitor *D. longicaudata* activity.

Brood and hive condition of the honey bee,*Apis mellifera* L. was observed by placing two hives in the center of each treatment block one week before the first treatment. Hive condition was rated individually by experienced apiary personnel on a scale of 1-5 (dead-strong) and recorded as the average of two hives in each block. Brood was measured by counting the number of frames of brood for each hive and averaging the results from the two hives in each block. Hives were evaluated three times at two-week intervals.

Test 2. Sterile, dyed Medflies with about equal numbers of males and females were released at the rate of 23,700 flies/ha in each treatment block the day before treatment. Flies were released statically from three equidistant release points along the central row of each block.

Test 3. Sterile, dyed Caribflies with about equal numbers of males and females were released at the rate of 17,300/ha in each treatment block for the first treatment date. Medflies and Caribflies were released at 17,300/ha for the second and third treatment dates. Medflies were released statically from two central release points and Caribflies were released from three release points along the central row of each treatment block.

Data Collection and Analysis

In test 1, 10 plastic International Pheromone (South Wirral, UK) IPM (Liquibaitor®) traps with Concept™'s Medfly Biolure® (ammonium acetate, putrescine, trimethylamine) were placed in each plot for the first treatment date. Ten Jackson traps containing trimedlure (TML) plugs were added for subsequent treatments to attract male flies in addition to the predominantly female attractive IPM trap with Biolure®. Traps were placed about 72 h after treatment application, checked and removed 6 d after application. Data were collected on the number of flies trapped by species and treatment for each date interval. For test 2, 10 Multi-Lure® traps with the Medfly Biolure® were placed in each plot for each treatment date. Traps were managed as in Test 1. For test 3, 10 Multi-Lure® traps were placed in each plot for each treatment date. For the first treatment date in which only Caribflies were released, traps contained a prepared solution of torula yeast and borax (4-5 g tablets/500 ml water). For succeeding treatment dates in which Caribflies and Medflies were released, a Concept™'s trimethylamine lure was added to each trap. Traps were managed as in test 1.

Environmental monitoring of water and soil was done for all tests but most extensively for Test 3. Pre and post-treatment water and soil samples were taken as well as 4" × 4" swab cards for aerial and ground application. Direct samples of all mixed treatment materials were taken before application. Split samples were evaluated by the Division of Agricultural Environmental Services, FDACS and the USDA, APHIS, PPQ laboratory in Gulfport, MS.

A randomized complete block experimental design (Little and Hills 1975) consisting of four, three or five treatments, with four replicates was used for tests 1,2, and 3, respectively. Fly recoveries were combined where two trap types occurred at trap locations. Data were analyzed by dates using Statistix® ANOVA, and means separated using Tukey's HSD (P = 0.05).

Results

Large plot sizes of 3-4 ha repeated over space and time were used to reduce the variability inherent in field trials. Buffers of 91-122 m minimized migration of flies between plots. No difference was indicated by statistical analysis among application dates for either Caribfly or Medfly for each of the three tests.

In test 1, there was a difference between the check and the three ground application pesticide treatments for both Caribfly (F = 5.73, df = 3,42, P = 0.0022) and Medfly (F = 11.22, df = 3,42, P = <0.0001). There were no differences among insecticide treatments (Fig. 1) although the malathion-SolBait treatment had the lowest mean number of flies trapped for both fly species (Table 1). For the average of the three test dates, spinosad-SolBait, malathion-NU-LURE® and malathion-SolBait reduced Medfly populations by 80, 76 and 91%, respectively compared to the check. Likewise, Caribflies were reduced 87, 94 and 91% for the same treatments.

No adverse or measurable effect was shown by any of the treatments on the number of frames of honey bee brood (Table 2). No significant differences in hive condition were observed (Table 3).

Due to the small numbers of recaptures of established beneficial insects in test plots including the checks, the data could not be analyzed statistically. Similarly, few recaptures of adult *D. longicaudata* and small numbers of larval-traps resulted in insufficient data but suggest that pesticide treatments had no effect.

In test 2, spinosad-SolBait was compared to an equal volume of malathion, NU-LURE® and water mixture applied with ground application equipment. Only sterile Medflies were used in this test. Treatment effects were observed (F = 29.69, df = 2,20, P = <0.0001) and comparison of means (Fig. 2) indicates that spinosad-SolBait and the malathion-NU-LURE®-water mixture provided comparable control (Table 1). Medfly populations were reduced by about 90 and 89% for the spinosad-SolBait and malathion-NU-LURE®-water treatments, respectively.

Aerial and foliar spot spray applications of spinosad-SolBait at two different rates were compared to the malathion-NU-LURE® standard by aerial application in test 3. For Medfly, there were treatment effects (F = 18.90, df = 6,34, P = <0.0001). The SolBait check and untreated control were different from the insecticide treat-

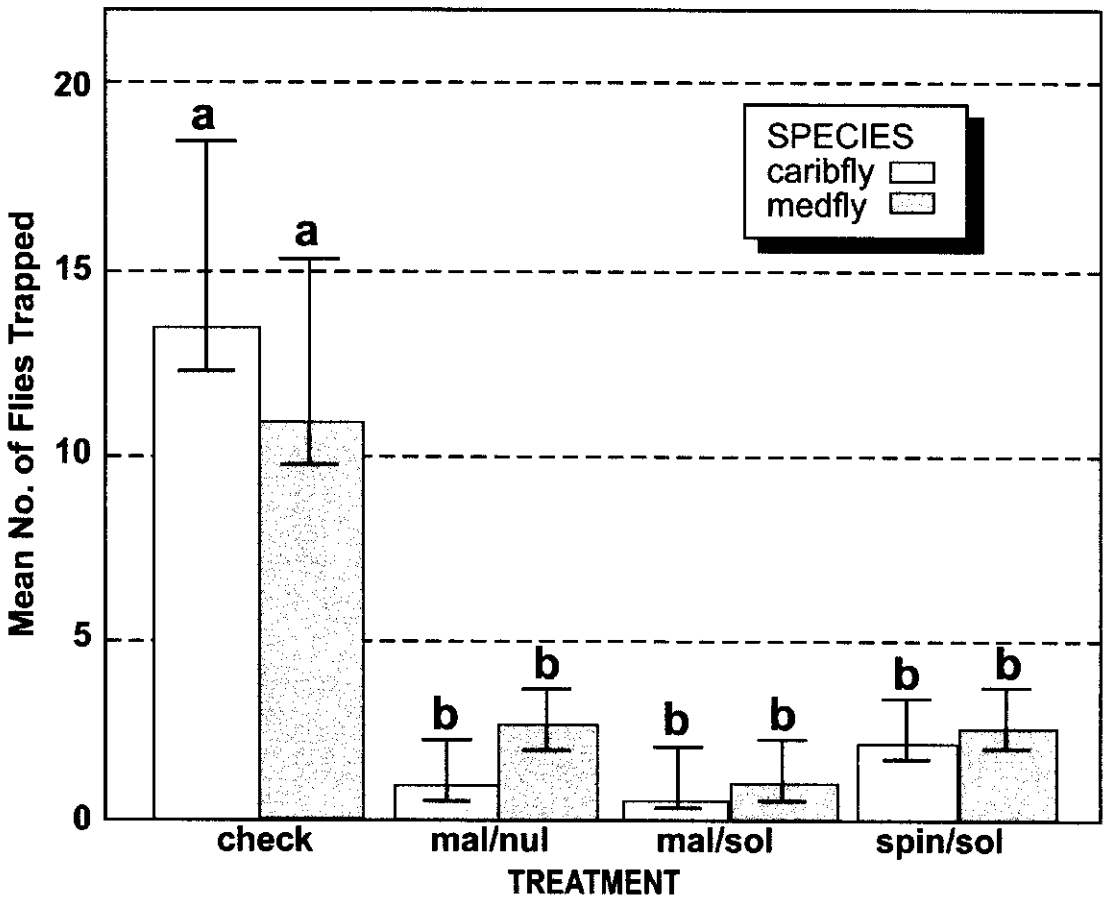

Fig. 1. Mean numbers (±SE) of sterile Caribflies and Medflies recovered following ground applications in Test 1. For each species, bars with the same letter are not significantly different from each other according to Tukey's HSD (P = 0.05).

TABLE 1. EFFECT OF SPINOSAD AND MALATHION TREATMENTS ON STERILE RELEASED CARIBBEAN AND MEDITERRANEAN FRUIT FLIES.

Treatments	Mean no. Caribfly/trap		Mean no. Medfly/trap	
	n	x ± SE	n	x ± SE
Test 1[1]—Foliar Spot				
Check	12	13.75 ± 5.16 a[2]	12	12.33 ± 2.89 a
Spinosad/SolBait	12	2.16 ± 0.90 b	12	2.50 ± 0.71 b
Malathion/NuLure	12	1.08 ± 0.56 b	12	3.00 ± 0.66 b
Malathion/SolBait	12	0.67 ± 0.40 b	12	1.08 ± 0.45 b
Test 2—Foliar Spot				
Control		not released	8	115.38 ± 17.75 a
Spinosad/SolBait			8	10.78 ± 3.10 b
Malathion/NuLure			8	11.38 ± 5.23 b
Test 3				
Control	12	937.83 ± 108.81 a	7	109.14 ± 24.42 a
Aerial				
Check	8	759.38 ± 155.26 ab	3	149.00 ± 72.67 a
Spinosad/SolBait-1.8 l/ha	12	468.08 ± 141.18 bc	7	4.29 ± 1.06 b
Spinosad/SolBait-3.5 l/ha	12	233.83 ± 66.01 cd	7	2.14 ± 0.83 b
Malathion/NuLure	12	44.17 ± 32.97 d	7	0.00 ± 0.00 b
Foliar Spot				
Spinosad/SolBait	12	21.92 ± 9.69 d	7	0.14 ± 0.14 b

[1]Mean separation is distinct for each species and test date.
[2]Means within a column followed by the same letter are not significantly different (P = 0.05, Tukey's HSD).

ments, but there was no difference among the three pesticide treatments (Table 1). Treatment effects were also observed for Caribfly (F = 14.66, df = 6,63, P = <0.0001). Spinosad-SolBait applied at 1.8 l/ha by air was not different from the check, while only the 3.5 l/ha spinosad-SolBait applied by air was statistically similar to the malathion-NU-LURE® standard. Figure 3 illustrates the treatment differences for both species.

Compared to the untreated control, Medfly populations aerially treated with malathion-NU-LURE® at 0.876 l/ha, spinosad-SolBait at 1.8 l/ha, and spinosad-SolBait at 3.5 l/ha reduced Medfly populations by 100, 96, and 99% respectively. Foliar spot spray applications of spinosad-SolBait reduced Medfly by 99%. Likewise, the same aerial treatments reduced Caribfly populations by 95, 54, and 73%, respectively. Ground applications of spinosad-SolBait reduced Caribfly by 97%.

Environmental monitoring results indicated all mixed treatment materials were at or below established percentages. No pre-water or soil samples indicated detectable levels of any treatment material. The highest post-treatment levels of treatment materials were: soil-malathion = 640 ppb, spinosad = not detected; water-malathion = 0.65 ppb, spinosad = not detected; swab-malathion = not sampled, spinosad = 0.00015 $\mu g/cm^2$.

TABLE 2. BROOD NUMBERS OF HONEY BEES EXPOSED TO SPINOSAD/MALATHION TREATMENTS IN TEST 1.

Treatments	n	24 h pre-treatment[1]	14 d post 1st treatment	14 d post 2nd treatment	14 d post 3rd treatment
Check	8	6.25 ± 0.56 a[2,3]	7.00 ± 0.68 a	6.12 ± 0.72 a	5.62 ± 0.86 a
Spinosad/SolBait	8	7.25 ± 0.62 a	7.88 ± 0.74 a	7.25 ± 1.08 a	6.75 ± 0.80 a
Malathion/NuLure	8	6.25 ± 0.66 a	7.25 ± 0.59 a	7.00 ± 0.91 a	5.88 ± 1.19 a
Malathion/SolBait	8	7.62 ± 0.65 a	6.50 ± 0.76 a	6.12 ± 1.09 a	6.25 ± 1.25 a

[1]Successive treatments were cumulative.
[2]Mean and SE of avg. no. of frames of brood.
[3]Means within a column followed by the same letter are not significantly different (P = 0.05, Turkeys HSD).

TABLE 3. HIVE CONDITION OF HONEY BEES EXPOSED TO SPINOSAD/MALATHION TREATMENTS IN TEST 1.

Treatments	n	24 h pre- treatment[1]	14d post 1st treatment	14d post 2nd treatment	14d post 3rd treatment
Check	8	3.88 ± 0.40 a[2,3]	3.62 ± 0.42 a	3.75 ± 0.37 a	3.50 ± 0.19 a
Spinosad/SolBait	8	4.12 ± 0.40 a	4.25 ± 0.25 a	4.38 ± 0.38 a	3.75 ± 0.31 a
Malathion/NuLure	8	3.75 ± 0.53 a	3.75 ± 0.37 a	3.75 ± 0.41 a	3.50 ± 0.33 a
Malathion/SolBait	8	4.25 ± 0.41 a	3.62 ± 0.42 a	3.75 ± 0.45 a	3.25 ± 0.37 a

[1]Successive treatments were cumulative.
[2]Mean and SE of avg. no. of frames of brood.
[3]Means within a column followed by the same letter are not significantly different (P = 0.05, Turkeys HSD).

DISCUSSION

Aerial applications of a spinosad-SolBait material at the rate of 3.5 l/ha compared to either a bait only check or an untreated control and the standard malathion-NU-LURE® mix provided acceptable control of sterile Medflies and Caribflies released in commercial citrus groves. Similar results were reported by Moreno et al. (2000) comparing spinosad-SolBait to 10 and 20% rates of malathion in NU-LURE®. Likewise, comparable results have been observed for wild Medflies in a recent eradication program in Guatemala and Mexico (Rendon et al. 2000).

Spinosad-SolBait at 1.8 l/ha applied by air in test 3 did not provide an adequate measure of control for Caribflies possibly due to differences in foraging behavior. The reduction in Caribfly population was 54% compared to the control and a 96% reduction in Medflies. The aerially applied 3.5-l/ha rate of spinosad-SolBait was significantly different than the control and reduced Caribflies by 73% compared to 99% for Medflies.

Applications of spinosad-SolBait applied as foliar spot sprays on individual trees in a commercial grove setting at 90 ml of mix per tree provided excellent reduction of both Medflies and Caribflies. There were no differences observed among Spinosad-SolBait treatments and malathion-NU-LURE® treatments at 876.8 ml/ha or at 90 ml per tree. Application of 90 ml per tree is equivalent to about 21.5 l of mix per ha. Lower recapture rates of flies in this test compared to tests 2 and 3 may be attributed to a prior pesticide application in this grove.

Honey bees exposed to foliar spot sprays in test 1 exhibited no effects either in number of frames of brood produced or in overall hive condition. SolBait has been shown to be repellent to the European honey bee (Tarshis Moreno 2001), which may explain the absence of any effect of the foliar spot sprays. Likewise, the larval-trap data from release of the braconid parasitoid, *Diachasmimorpha longicaudata*, suggests that neither of the insecticide treatments affects parasitism though the number of replicates for this measure was inadequate (J. M. Sivinski and T. C. Holler, pers. comm.).

Costs of aerial application and materials were compared at the 3.5 l/ha rate for spinosad-SolBait and 876.8 ml/ha for the standard malathion-NU-LURE® bait mix. Spinosad-SolBait derived from

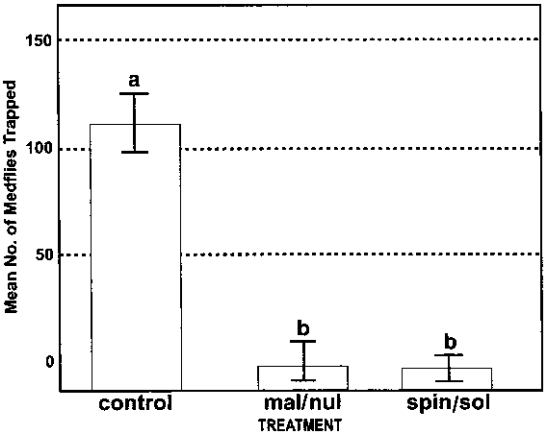

Fig. 2. Mean numbers (±SE) of Medflies recovered following ground applications in Test 2. Bars with the same letter are not significantly different from each other according to Tukey's HSD (P = 0.05).

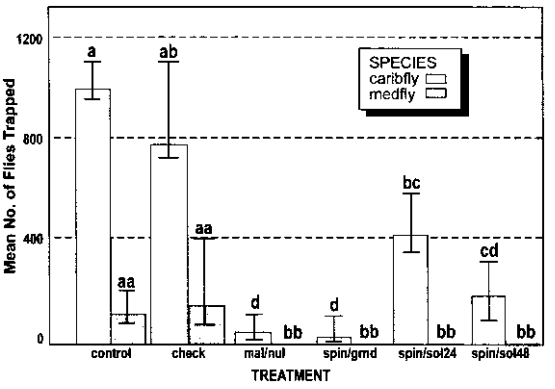

Fig. 3. Mean numbers (±SE) of sterile Caribflies and Medflies recovered following ground (spin/grnd) and aerial applications in Test 3. For each species, bars with the same letter are not significantly different from each other according to Tukey's HSD (P = 0.05).

the GF 120 formulation (Dow AgroSciences) would cost about $18.53/ha ($7.50/acre) based on current private applicator costs in Florida. Malathion-NU-LURE® costs are $12.36/ha ($5.00/acre). Due to variability of equipment used and rates of material for ground application, no cost estimates were determined.

The results of this series of tests indicate that spinosad-SolBait bait materials may be used as an alternative tool for control of fruit fly pests in Florida. Further studies are needed on relative response of fruit fly species to the SolBait-based toxins, application techniques and equipment, dosage of spinosad, rate of application, incorporation into bait stations and any effect on non-target organisms in commercial citrus groves.

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ROLES OF PUTRESCINE AND 1-PYRROLINE IN ATTRACTIVENESS OF TECHNICAL-GRADE PUTRESCINE TO THE MEXICAN FRUIT FLY (DIPTERA: TEPHRITIDAE)

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ABSTRACT

Laboratory experiments were conducted to determine if 1-pyrroline, present as a contaminant of putrescine, was responsible for the observed attractiveness of putrescine to the Mexican fruit fly, *Anastrepha ludens* (Loew) (Diptera: Tephritidae). Technical-grade putrescine contained 0.025% 1-pyrroline measured by gas chromatography. Putrescine purified by high performance liquid chromatography contained 0.0000053% 1-pyrroline, constituting a 99.98% reduction compared with technical-grade putrescine. Purified putrescine was more attractive than technical-grade putrescine over a range of concentrations. The amount of 1-pyrroline found in technical-grade putrescine was attractive, but less so than technical-grade putrescine at 2 concentrations. Either purified putrescine or an amount of 1-pyrroline equivalent to that in technical putrescine could substitute for technical putrescine in combinations with 2 other attractive chemicals, ammonium bicarbonate and methylamine HCl. Results indicate that putrescine more so than 1-pyrroline accounts for the attractiveness of technical putrescine but that either chemical enhances the attractiveness of ammonia and methylamine about equally.

Key Words: *Anastrepha ludens*, attractants, lures, putrescine, 1-pyrroline

RESUMEN

Experimentos de laboratorio fueron conducidos para determinar si 1-pirrolina, la cual está presente como un contaminante en la putrescina, fue responsable de la atracción a la putrescina observada para la mosca mejicana de las frutas, *Anastrepha ludens* (Loew) (Diptera: Tephritidae). La putrescina de grado técnico tuvo un contenido de 1-pirrolina de 0.025%, medida por cromatografía de gases. La putrescina purificada por cromatografía liquida de alto rendimiento tuvo un contenido de 0.0000053% de 1-pirrolina, constituyendo una reducción de 99.98% en comparación con la putrescina de grado técnico. La putrescina purificada fue más atractiva que la putrescina de grado técnico sobre una gama de concentraciones. La cantidad de 1-pirrolina encontrada en la putrescina de grado técnico fue atractiva, pero menos que la putrescina de grado técnico a 2 concentraciones. Ya sea la putrescina purificada o una cantidad de 1-pirrolina equivalente a la que se encuentra en la putrescina técnica pudiera sustituir la putrescina técnica en combinaciones con 2 otros químicos atractivos, el bicarbonato de amonio y el HCl metilamino. Los resultados indican que la putrescina mas que la 1-pirrolina explica la atracción de la putrescina técnica ya que cualquier químico aumenta la atracción del amonio y el metilamino casi igualmente.

Independent research conducted by three different groups has implicated putrescine as an important attractant for fruit flies. Wakabayashi & Cunningham (1991) first reported putrescine as a component of a four-chemical mixture attractive to the melon fly, *Bactrocera cucurbitae* (Coquillett). Robacker & Warfield (1993) provided evidence that putrescine was attractive to the Mexican fruit fly, *Anastrepha ludens* (Loew), both by itself and as part of a three-chemical mixture. Finally, Heath et al. (1995) demonstrated that a combination of ammonium acetate and putrescine was more attractive than ammonium acetate by itself to the Mediterranean fruit fly, *Ceratitis capitata* (Wiedemann), and the Mexican fruit fly.

1-Pyrroline was identified as a component of male-produced pheromone of the Mediterranean fruit fly (Baker et al. 1985) and was shown to be slightly attractive to sexually active female Mediterranean fruit flies, and to synergize attractiveness of other pheromone components (Jang et al. 1994). Robacker & Bartelt (1997) found 1-pyrroline in volatiles produced by bacterial fermentations attractive to the Mexican fruit fly, and Robacker et al. (1997) demonstrated that 1-pyrroline not only was attractive to the Mexican fruit fly but also synergized attractiveness of a mixture of ammonium carbonate, methylamine HCl, and putrescine.

Amoore et al. (1975) reported that technical-grade putrescine contains a small amount of

1-pyrroline that is produced by spontaneous oxidation of putrescine. The presence of 1-pyrroline is easily verifiable by gas chromatography. Because everyone who 'demonstrated' the attractiveness of putrescine to fruit flies used technical putrescine, it was never actually proven that putrescine itself, without 1-pyrroline present as a contaminant, is attractive to fruit flies. Three facts that suggest the possibility that 1-pyrroline is responsible for the observed attractiveness of technical putrescine are: 1) 1-pyrroline is attractive to fruit flies at low concentrations (Jang et al. 1994; Robacker et al. 2000); 2) emissions of putrescine and 1-pyrroline were equal from a lure that contained technical putrescine by design and 1-pyrroline only as a contaminant of technical putrescine (Robacker & Bartelt 1996); and 3) 1-pyrroline is responsible for the perceived odor of technical putrescine in human olfaction (Amoore et al. 1975), a fact that has significance here because of mounting evidence of similarities in neural functioning in humans and insects (Hildebrand & Shepherd 1997).

The purpose of this work was to determine whether putrescine or 1-pyrroline is responsible for the reported attractiveness of technical putrescine to fruit flies. Our method was to remove 1-pyrroline from technical putrescine and test attractiveness of a range of concentrations of purified putrescine to the Mexican fruit fly. Attractiveness of 1-pyrroline at concentrations equal to those present in various technical putrescine solutions was also tested. Finally, attractiveness of mixtures of ammonium bicarbonate and methylamine HCl with either purified putrescine or 1-pyrroline was tested to determine if purified putrescine and 1-pyrroline could substitute for technical putrescine.

Materials and Methods

Chemistry Methods

Technical-grade putrescine was purified by high performance liquid chromatography (HPLC) using a Waters 717plus Autosampler and 600E Multisolvent Delivery System with 60F Pump (Waters Corp., Milford, MA). The system was controlled by a NEC Image 466es computer with Millennium™ 2010 Chromatography Manager Software. The HPLC column was a Waters µ-Bondapak C18 (3.9 mm × 30 cm, 125 A, 10 µm particle size). Mobile phase was water at 1 ml/min. Technical-grade putrescine (98%; Sigma Chemical Co., St. Louis, MO) was dissolved in water (100 mg/ml), and 200 µl was injected. Detection of putrescine eluting from the column was done by measuring pH elevation of the eluant with a pH meter (Fisher Accumet Model 805, Fisher Scientific Co., Pittsburgh, PA) and by gas chromatographic (GC) analysis of fractions (see below). Both purified putrescine and technical putrescine were kept at -20°C when not in use.

Sampling of 1-pyrroline and putrescine for GC quantitation was done by solid-phase microextraction (SPME) using a polydimethylsiloxane fiber (100 µm coating) (Supelco, Inc., Bellefonte, PA). Introduction of chemicals from the SPME fiber onto the GC was by thermal desorption for 0.5 min into a 10 cm deactivated fused silica retention gap (0.53 mm ID) in an on-column injector at 210°C. The retention gap was connected to the analytical column by a GlasSeal connector (Supelco). A DB-1 column (60 m × 0.32 ID, 5 µm film) (J & W Scientific, Folsom, CA) was used in a Shimadzu GC-17A gas chromatograph (Shimadzu Scientific Instruments, Inc., Columbia, MD) with flame ionization (FID) and flame thermionic (FTD) (Model FTD-17) detectors, and a cool on-column injector.

1-Pyrroline was synthesized by acid hydrolysis of 4-aminobutyraldehyde diethylacetal (Aldrich Chemical Co., Inc., Milwaukee, WI) using the method of Schopf & Oechler (1936). 1-Pyrroline reaction product was kept at -20(C when not in use. The concentration of 1-pyrroline in the reaction product was determined using a calibration curve prepared with pyrrolidine (99%, Sigma). Pyrrolidine solutions and 1-pyrroline reaction product dilutions were adjusted to pH >12 with NaOH. For GC analysis, the SPME fiber was inserted through a septum into the headspace above 1 ml of the solutions in sealed 4 ml vials at room temperature for 5 min. Analyses were at 100°C and carrier gas (He) linear velocity of 30 cm/sec. Detection was by FID.

For preparation of various solutions for bioassay, it was necessary to quantify putrescine in HPLC purifications of technical putrescine, and 1-pyrroline both in technical putrescine and in putrescine purified by HPLC. Concentrations of putrescine in HPLC collections were determined using a FID calibration curve constructed from several concentrations of technical putrescine. The concentration of 1-pyrroline in a 10 mg/ml aqueous solution of technical putrescine was determined using a FID calibration curve for pyrrolidine in 10 mg/ml aqueous solutions of technical putrescine. The pyrrolidine calibration solutions were prepared in solutions containing putrescine to compensate for effects of putrescine on SPME analysis of 1-pyrroline (Robacker & Bartelt 1996). The concentration of 1-pyrroline in purified putrescine was determined by comparing FTD peak areas of 1-pyrroline in purified putrescine (HPLC fractions, approximately 2-5 mg/ml of putrescine), with 1-pyrroline areas measured using previously determined concentrations of 1-pyrroline in dilutions of technical putrescine. FTD was used for 1-pyrroline in purified putrescine because concentrations were low and FTD is 35× more sensitive than FID to 1-pyrroline. All solu-

tions were adjusted to pH >12 for SPME samplings. For GC analyses, the SPME fiber was inserted through a septum into 2 ml of the solutions in sealed 4 ml vials at room temperature for 5 min. GC analyses of putrescine were at 180°C and analyses of 1-pyrroline were at 100°C. Linear velocity of He carrier gas was 30 cm/sec.

Various concentrations of technical putrescine, purified putrescine, and 1-pyrroline were prepared in water at pH 9, to determine attractiveness of purified putrescine and 1-pyrroline relative to attractiveness of technical putrescine containing equivalent amounts of putrescine and 1-pyrroline. Test solutions were prepared by dilution of stock solutions each day bioassays were performed. Before preparations, the stock solution of purified putrescine was checked for purity by GC. Concentration of 1-pyrroline in purified putrescine stock solution did not increase for the duration of these experiments. Also, the stock solution of 1-pyrroline was calibrated by GC each day before test solutions were made. The concentration of 1-pyrroline in the stock solution decreased by about 10% over the course of these experiments.

Because putrescine is known to oxidize to 1-pyrroline, an experiment was conducted to determine if 1-pyrroline that formed during bioassay of purified putrescine could be sufficient to affect attraction of flies to the filter papers. Ten microliters of a technical putrescine solution (1 mg/ml in water, pH 9) were put onto a 2×2 cm piece of filter paper inside a 4 ml vial with a cap containing a septum. Headspace inside the vial was sampled for 1 min by SPME by inserting the fiber through the septum. A vial with technical putrescine was sampled once, either immediately after the putrescine was applied to the paper or 10 min later, then discarded. 1-Pyrroline was analyzed by GC-FTD at 100°C using the Shimadzu instrument, DB-1 column and procedure described above.

Insects and Test Conditions

Flies were from a culture that originated from yellow chapote fruit (*Sargentia greggii* S. Wats.) collected in Nuevo Leon, Mexico, in 1997. Flies were sugar-fed and protein-starved since eclosion, because this physiological state facilitates attraction to AMPu, a lure that contains putrescine (Robacker 1998). Flies were tested when 2-12 days old. Within this range, age does not affect attraction to bacterial odors that contain 1-pyrroline and other attractive amines (Robacker & Garcia 1993). Laboratory conditions for holding and testing flies were 22 ± 2°C, 50 ± 20% relative humidity, and photophase from 0630 to 1930 h.

Bioassay Method

Attractiveness of test chemicals and mixtures was evaluated using cage-top bioassays as described in Robacker & Warfield (1993). Briefly, the bioassay was conducted by placing 2 filter paper triangles containing test chemicals or mixtures (treatment papers) and 2 papers containing water or control mixtures (control papers) on the top of an insect cage ($30 \times 30 \times 30$ cm) and counting the number of flies beneath each paper once each minute for 10 min. The 2 treatment papers were positioned diagonally across from each other on the cage top as were the 2 control papers. The filter papers were raised 5 mm above the cage top using plastic rings. Each bioassay cage contained 180-200 flies (sex ratio approximately 1:1). A cage of flies was used once per day for up to 3 days before it was discarded.

Bioassays of Putrescine and 1-Pyrroline Individually

The purpose of these tests was to determine if amounts of purified putrescine and 1-pyrroline equivalent to those in technical putrescine could account for the attractiveness of technical putrescine. Four quantities of technical putrescine and equivalent quantities of purified putrescine and 1-pyrroline were tested. Amounts tested are shown in Tables 1-2. Each bioassay evaluated one quantity of one test chemical against water as the control. Samples of test chemicals or water were applied to filter papers in 10 µl aliquots.

Two experiments were conducted, one to test purified putrescine and the other 1-pyrroline. In the first experiment, the 4 quantities of purified putrescine were tested along with the 4 quantities of technical putrescine. The second experiment was conducted the same way using 1-pyrroline instead of purified putrescine.

Bioassays of Combinations

The purpose of these tests was to determine if purified putrescine and/or 1-pyrroline could substitute for technical putrescine in the attractive mixture of ammonium bicarbonate, methylamine HCl and technical putrescine (AMPu) published by Robacker & Warfield (1993). The method was to compare attractiveness of combinations of ammonium bicarbonate and methylamine HCl with either technical putrescine, purified putrescine or 1-pyrroline. In all bioassays, 10 µl of a solution of ammonium bicarbonate (>99%, Sigma) and methylamine HCl (>99%, Sigma) in water at pH 9, was applied both to the treatment papers and the control papers, resulting in 10 µg of each chemical on all papers. In addition, treatment papers received 10 µl of one of the following, each in water at pH 9: 1 µg of technical putrescine; 1 µg of purified putrescine; 0.25 ng of 1-pyrroline; or 0.30 pg of 1-pyrroline. The first 1-pyrroline amount, 0.25 ng, is equivalent to the amount found in 1 µg of technical putrescine. The latter 1-pyrroline amount, 0.30 pg, was intended to be equivalent to the amount in 1 µg of

purified putrescine, but was approximately 6× higher due to miscalculation. Testing of the actual equivalent amount of 1-pyrroline was deemed unnecessary based on bioassay results with 0.30 pg. Control papers received an additional 10 µl of water. The additional 10 µl aliquots put onto treatment and control papers were placed near to, but not overlapping, the 10 µl of ammonium bicarbonate and methylamine HCl solution.

The combinations were tested in a series of 3 experiments. In each experiment, bioassays of technical putrescine combinations were paired with bioassays of combinations containing one of the other 3 chemicals (Table 3).

Test of Observer Bias and/or pH

An experiment was conducted to test observer bias and/or effect of pH on bioassay results. The additional experiment was conducted like the other combination experiments except that water at pH 9, the same pH as all bioassay test solutions in previous experiments, was applied to treatment papers instead of a test chemical. In this last experiment, the observer was unaware that the test chemical was water.

Statistical Analysis of Bioassays

Bioassay count differences were obtained by subtracting the total count at the control papers from the total count at the treatment papers. Paired t-tests were performed to determine attractiveness of chemicals or combinations on treatment papers relative to control papers by testing whether bioassay count differences were significantly different from 0. Student's t-tests or analyses of variance (ANOVA) were used to determine attractiveness of various chemicals or combinations relative to other chemicals or combinations by testing whether their bioassay count differences were significantly different from each other. SuperANOVA (Abacus Concepts 1989) was used to perform ANOVA's.

Results and Discussion

HPLC Purification of Putrescine

Peak elution of putrescine from the HPLC column was between 7-9 min but elution occurred over at least 30 min. No attempt was made to improve column efficiency by addition of stabilizers to the mobile phase because I wanted the purified putrescine in water only. Concentrations of putrescine in 2 HPLC collections were 2.2 and 5.3 mg/ml (1 determination of each).

Concentrations of 1-Pyrroline in Putrescine

The mean concentration of 1-pyrroline in a 10 mg/ml solution of technical putrescine was calculated as 2.5 ± 0.12 (SE) µg/ml (n = 3 determinations). This is approximately 0.025% w/w relative to putrescine. The mean concentration of 1-pyrroline measured in 2 concentrations of HPLC purified putrescine (2.2 and 5.3 mg/ml) was calculated as 0.20 ± 0.015 ng/ml (n = 2 determinations, one for each putrescine concentration), or 0.0000053% w/w. The reduction of 1-pyrroline in purified putrescine relative to technical putrescine was 99.98%.

Formation of 1-Pyrroline from Technical Putrescine in Vials

1-Pyrroline peak areas obtained from samples 10 min after application of technical putrescine solution onto filter papers in vials were 96 ± 2.2% (mean ± SE, n = 3 replications) as great as those sampled immediately. This indicates that the amount of 1-pyrroline in the vials did not increase during the 10 min test. Note that this does not prove that 1-pyrroline did not form from putrescine in the vial. It is possible that 1-pyrroline both formed and degraded inside the vial. However, the result indicates that no net increase in the amount of 1-pyrroline should occur from oxidation of purified putrescine during bioassays.

Attractiveness of Putrescine and 1-Pyrroline

Technical putrescine and HPLC purified putrescine were significantly more attractive than water at the 1 and 10 µg test quantities, and purified putrescine was also significantly more attractive than water at the 0.1 µg quantity (smallest $t = 3.4$, df = 11, $P < 0.01$, for 0.1 µg purified putrescine vs. water) (Table 1). There were no significant differences between responses to technical putrescine and purified putrescine at any of the 4 test quantities by *t*-tests. ANOVA also indicated that purified putrescine and technical putrescine did not differ in attractiveness, summed over all concentrations. However, an ANOVA that included data from only the 3 highest test quantities showed that purified putrescine was significantly more attractive than technical putrescine ($F = 6.4$; df = 1,50; $P < 0.05$). The results suggest that something removed from technical putrescine by purification, perhaps 1-pyrroline, inhibited attractiveness of putrescine.

Technical putrescine and 1-pyrroline were significantly more attractive than water at the 2 highest technical putrescine test quantities and the 3 highest 1-pyrroline quantities (smallest $t = 3.1$, df = 11, $P < 0.05$, for 25 pg of 1-pyrroline vs. water) (Table 2). There were no significant differences between responses to technical putrescine and 1-pyrroline at any of the 4 equivalent test quantities. ANOVA also indicated that 1-pyrroline and technical putrescine did not differ in attractiveness, summed over all concentrations.

TABLE 1. ATTRACTIVENESS OF TECHNICAL-GRADE PUTRESCINE AND PURIFIED PUTRESCINE TO MEXICAN FRUIT FLIES IN CAGE-TOP BIOASSAYS.[1]

Test chemical applied to T paper[2]	Total putrescine	Total 1-pyrroline	Mean ± SE Count at T	Mean ± SE Count at C[3]	Ratio T/C
Technical putrescine	0.010 µg	2.5 pg	51.2 ± 4.6	46.0 ± 5.8	1.11
Purified putrescine	0.010 µg	0.53 fg	56.4 ± 4.2	49.9 ± 5.0	1.13
Technical putrescine	0.10 µg	25 pg	57.8[4] ± 8.3	51.5 ± 4.6	1.12
Purified putrescine	0.10 µg	5.3 fg	63.9[4,5] ± 4.2	50.2 ± 4.0	1.27
Technical putrescine	1.0 µg	250 pg	77.8[4,5] ± 9.0	54.8 ± 6.8	1.42
Purified putrescine	1.0 µg	53 fg	75.3[4,5] ± 6.1	48.4 ± 4.6	1.56
Technical putrescine	10 µg	2.5 ng	71.3[4,5] ± 3.1	52.7 ± 4.9	1.35
Purified putrescine	10 µg	530 fg	80.2[4,5] ± 5.1	51.5 ± 4.0	1.56

[1]Six replications of the experiment were conducted. Each replication included 2 bioassays of each purified putrescine quantity and 1 of each technical putrescine quantity, conducted in random order.
[2]T (treatment) paper contains amounts of test chemicals shown in table.
[3]C (control) paper contains water.
[4]Purified putrescine was more attractive than technical putrescine by ANOVA including only the highest 3 test quantities.
[5]The count at T was significantly greater than the count at C by paired t-test ($P < 0.05$).

An ANOVA that included data from only the 2 highest test quantities showed that technical putrescine was significantly more attractive than 1-pyrroline (F = 4.3; df = 1,33; $P < 0.05$). The results show that 1-pyrroline does not completely account for the attractiveness of technical putrescine, at least at some concentrations.

Attractiveness of Putrescine and 1-Pyrroline with Ammonium Bicarbonate and Methylamine HCl

Combinations of ammonium bicarbonate and methylamine HCl with 1µmg of either technical putrescine or purified putrescine were significantly more attractive than ammonium bicarbonate and methylamine HCl alone (t = 3.8, df = 19, $P < 0.01$, for each chemical) (Table 3, Pair 1). Moreover, both chemicals increased the attractiveness of the combinations equally. These results indicate that purified putrescine can account for the increase in attractiveness that occurs when technical putrescine is added to a mixture of ammonium bicarbonate and methylamine HCl.

Combinations with either 1 µg of technical putrescine or 0.25 ng of 1-pyrroline, the amount present in 1 µg of technical putrescine, were also significantly more attractive than combinations without these chemicals (smaller t = 2.5, df = 23, $P < 0.05$ for 1-pyrroline) (Table 3, Pair 2). Again, both chemicals increased the attractiveness of the combinations equally. These results indicate that the amount of 1-pyrroline equal to that in technical putrescine can account for the increase in attractiveness that occurs when technical putre-

TABLE 2. ATTRACTIVENESS OF TECHNICAL-GRADE PUTRESCINE AND 1-PYRROLINE TO MEXICAN FRUIT FLIES IN CAGE-TOP BIOASSAYS.[1]

Test chemical applied to T paper[2]	Total putrescine	Total 1-pyrroline	Mean ± SE Count at T	Mean ± SE Count at C[3]	Ratio T/C
Technical putrescine	0.010 µg	2.5 pg	45.8 ± 5.6	43.2 ± 6.7	1.06
1-pyrroline	nd[4]	2.5 pg	45.0 ± 3.5	45.7 ± 3.9	0.98
Technical putrescine	0.10 µg	25 pg	51.7 ± 7.3	45.2 ± 6.0	1.14
1-pyrroline	nd[4]	25 pg	50.6[5] ± 3.5	43.8 ± 3.0	1.15
Technical putrescine	1.0 µg	250 pg	66.0[5,6] ± 8.4	43.8 ± 5.2	1.51
1-pyrroline	nd[4]	250 pg	53.2[5,6] ± 4.0	42.0 ± 2.9	1.27
Technical putrescine	10 µg	2.5 ng	74.3[5,6] ± 7.6	40.8 ± 8.3	1.82
1-pyrroline	nd[4]	2.5 ng	63.7[5,6] ± 5.6	43.8 ± 4.0	1.45

[1]Six replications of the experiment were conducted. Each replication included 2 bioassays of each 1-pyrroline quantity and 1 of each technical putrescine quantity, conducted in random order.
[2]T (treatment) paper contains amounts of test chemicals shown in table.
[3]C (control) paper contains water.
[4]nd, not detected by GC/FTD.
[5]The count at T was significantly greater than the count at C by paired t-test ($P < 0.05$).
[6]Technical putrescine was more attractive than 1-pyrroline by ANOVA including only the highest 2 test quantities.

TABLE 3. ATTRACTIVENESS OF MIXTURES CONTAINING AMMONIUM BICARBONATE, METHYLAMINE HCl AND EITHER TECHNICAL-GRADE PUTRESCINE, PURIFIED PUTRESCINE OR 1-PYRROLINE TO MEXICAN FRUIT FLIES IN CAGE-TOP BIOASSAYS.

Pair[1]	Test chemical applied to T paper[2]	Total putrescine	Total 1-pyrroline	Mean ± SE Count at T	Mean ± SE Count at C[3]	Ratio T/C
1	technical putrescine	1.0 µg	0.25 ng	99.2[4] ± 3.7	84.4 ± 4.4	1.18
	purified putrescine	1.0 µg	0.053 pg	102.0[4] ± 4.2	86.2 ± 3.5	1.18
2	technical putrescine	1.0 µg	0.25 ng	112.2[4] ± 4.1	95.5 ± 3.8	1.17
	1-pyrroline	nd[5]	0.25 ng	114.4[4] ± 4.6	100.3 ± 3.5	1.14
3	technical putrescine	1.0 µg	0.25 ng	109.2[4,6] ± 4.8	88.9 ± 4.4	1.23
	1-pyrroline	nd[5]	0.30 pg	92.1 ± 3.7	87.4 ± 3.7	1.05
4	technical putrescine	1.0 µg	0.25 ng	110.7[4,6] ± 2.7	90.9 ± 3.4	1.22
	water (pH 9)	nd[5]	nd[5]	93.1 ± 1.9	89.7 ± 2.9	1.04

[1]Replications: Pair 1, 20; Pair 2, 24; Pair 3, 36; Pair 4, 18.
[2]T (treatment) paper contains 10 µg of ammonium bicarbonate, 10 µg of methylamine HCl, and amounts shown in the table of technical putrescine, purified putrescine, and 1-pyrroline.
[3]C (control) paper contains 10 µg of ammonium bicarbonate and 10 µg of methylamine HCl.
[4]The count at T was significantly greater than the count at C by paired t-test ($P < 0.05$).
[5]nd, not detected by GC/FTD.
[6]The T-C count difference was significantly greater for combinations with technical putrescine than with 1-pyrroline or water, respectively.

scine is added to a mixture of ammonium bicarbonate and methylamine HCl.

The combination with 0.30 pg of 1-pyrroline, an amount greater than that present in 1 µg of purified putrescine but less than that in 1 µg of technical putrescine, was not significantly more attractive than ammonium bicarbonate and methylamine HCl alone (Table 3, Pair 3). As in previous experiments, the combination with 1 µg of technical putrescine was significantly more attractive than ammonium bicarbonate and methylamine HCl alone ($t = 6.6$, df = 35, $P < 0.001$). The combination containing technical putrescine was significantly more attractive than the combination containing 1-pyrroline ($t = 3.6$, df = 34, $P < 0.001$). These results indicate that the amount of 1-pyrroline in purified putrescine does not account for the increase in attractiveness that occurs when purified putrescine is added to a mixture of ammonium bicarbonate and methylamine HCl (Experiment 3).

Effect of Observer Bias and pH

Combinations in which water at pH 9 was substituted for a test chemical were not more attractive than ammonium bicarbonate and methylamine HCl alone (Table 3, Pair 4). As in previous experiments, the combination with 1 µg of technical putrescine was significantly more attractive than ammonium bicarbonate and methylamine HCl alone ($t = 5.2$, df = 17, $P < 0.001$). These results indicate that observer bias and pH of test solutions were not significant problems in this work. However, the 4% increase in counts at combinations with water at pH 9 gives an indication that some positive bias may be present in the results.

Relative Attractiveness of Putrescine and 1-Pyrroline in Technical Putrescine

This research indicates that attractiveness of technical putrescine is a function of both putrescine and 1-pyrroline. Both purified putrescine and 1-pyrroline were individually attractive at concentrations equivalent to those in technical putrescine. Despite the finding that each is attractive, 2 lines of evidence indicate that putrescine plays a bigger role than 1-pyrroline in attractiveness of technical putrescine. First, putrescine purified of most 1-pyrroline was more attractive than technical putrescine at some concentrations (Table 1), suggesting that 1-pyrroline may inhibit attractiveness of putrescine in technical putrescine. Second, technical putrescine was more attractive than 1-pyrroline at some concentrations equivalent to those in technical putrescine (Table 2), indicating that 1-pyrroline cannot account for all of the attractiveness of technical putrescine. However, experiments also showed that combinations of ammonia and methylamine with either technical putrescine, purified putrescine or 1-pyrroline were equally attractive (Table 3). Thus, under some conditions such as in the combinations tested here and in the absence of putrescine, 1-pyrroline can substitute for putrescine.

Neural Reception

The evidence that both putrescine and 1-pyrroline are attractive individually, that technical putrescine is less attractive than the putrescine it contains, and that 1-pyrroline can substitute for putrescine in certain combinations with other chemicals, is difficult to reconcile to traditional models of odorant reception. Actually, the results

are not surprising if the 2 chemicals share the same receptor neuron. In this model, the neuron can accept either chemical in the absence of the other, responds better to putrescine, and has a higher threshold response to putrescine when 1-pyrroline also binds. This is a tenable hypothesis based on recent findings that a single insect or mammalian olfactory receptor neuron can accept and respond to numerous similar and sometimes dissimilar odorants (Lemon and Getz 1999, Laurent 1999). The model does not preclude the possibility that additional receptor neuron types that bind one or both chemicals, perhaps at different threshold response levels, also are present on the antenna.

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A NEW SPECIES OF *ANICETUS* (HYMENOPTERA: ENCYRTIDAE) PARASITIZING TERRAPIN SCALE, *MESOLECANIUM NIGROFASCIATUM* (HEMIPTERA: COCCIDAE)

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ABSTRACT

Anicetus carolinensis Meyer (Hymenoptera: Encyrtidae) is proposed as the name of a new species found parasitizing terrapin scale, *Mesolecanium nigrofasciatum* (Pergande) (Hemiptera: Coccidae), in North Carolina. Both sexes are described and illustrated together with notes on the life history, host range, and reproductive behavior of the species.

Key Words: *Anicetus carolinensis*, blueberry, Encyrtidae, terrapin scale, Coccidae, *Mesolecanium nigrofasciatum*

RESUMEN

Proponemos *Anicetus carolinensis* Meyer (Hymenoptera: Encyrtidae) como el nombre de una nueva especie encontrada en Carolina del norte parasitizando la escala terrapin, *Mesolecanium nigrofasciatum* (Pergande) (Hemiptera: Coccidae). Describimos e ilustramos ambos sexos, y damos notas sobre el ciclo de vida, sobre el rango de los insectos hospederos, y sobre el comportamiento reproductivo de la especie.

Terrapin scale, *Mesolecanium nigrofasciatum* (Pergande), is an occasional pest of tree fruits and shrubs throughout much of the southern and eastern United States. It is considered a sporadic pest in commercial blueberry plantings (*Vaccinium* spp.) where it produces copious honeydew that coats the foliage and promotes growth of sooty mold in late summer (Milholland & Meyer 1984). Simanton (1916) provided a comprehensive summary of the terrapin scale's life history. The species is univoltine and overwinters as mated females on host plant stems.

Numerous predators and parasites have been reported attacking the terrapin scale (Simanton 1916; Williams & Kosztarab 1972). These include ladybird beetles, lacewings, a predaceous pyralid, a predatory bug and more than 25 species of parasitic wasps in the families Aphelinidae, Encyrtidae, Eulophidae, and Mymaridae (Simanton 1916; Thompson 1944; Peck 1963). In an effort to assess the potential for biological control of terrapin scale in North Carolina, a survey for endemic parasites was conducted from 1990-1998 in commercial and abandoned blueberry fields in four southeastern counties: Bladen, Duplin, Sampson, and Pender. During the course of the survey we collected a new species of encyrtid wasp, which is here described.

MATERIALS AND METHODS

Each spring, beginning in early March, blueberry branches infested with terrapin scale were collected and confined under laboratory conditions in cardboard emergence cages (Meyer & Nalepa 1991). Collections continued on a biweekly schedule until the overwintered generation of scale could no longer be found in the field (late June). All collected material was held at 21± 2°C for at least 60 days under ambient photoperiod. Parasites were harvested daily as they appeared in emergence cages or from debris at the bottom of the cage after disassembly. Adults were fixed in Kahle's solution and stored in 70% ethanol or mounted on paper points. After stepwise dehydration to toluene through absolute ethanol, some specimens were mounted on glass slides in Kleermount® (Carolina Biological Supply Co., Burlington, NC 27215) for microscopic study.

More than 1200 individual parasites were reared from terrapin scale during the 9-year survey. Representative specimens of unknown species were sent to the North Carolina Department of Agriculture (Kenneth Ahlstrom) or Systematic Entomology Laboratory, PSI, USDA (Michael Schauff or Paul Marsh) for identification. Of these, 62% were identified as *Metaphycus californicus* (Howard), 10% as *Coccophagus lycimnia* Walker, and 8% as other species presumed to be incidentals or hyperparasites (e.g., *Marietta* sp.). The remaining 20% were Encrytidae belonging to an undescribed species in the tribe Cerapterocerini (Noyes 1984).

This new species has a mixture of the features used by Annecke (1967) to separate the genus *Paraceraptrocerus* from *Anicetus*: both the shape

of the antennal scape and length of the antennal club conform to his description for *Paraceraptrocerus*, but all other features including articulation of the pedicel, wing chaetotaxy, surface sculpturing of the head, and segmentation of the antennal club resemble *Anicetus*. Because the name *Anicetus* has priority and Noyes (1984) has already suggested that these genera may be synonymous, the new species is here assigned to the genus *Anicetus*. In Annecke's (1967) key to this genus, females of the new species key out to *A. toumeyellae* (Milliron) but differ notably in shape of the antennal scape, coloration of the legs, and patterning of the forewing. In *A. annulatus*, the only other North American species in this genus, females are paler in color, the antennal scape is triangular, and wings are more uniformly fuscous with a longer marginal vein. No key to the males has been published.

Anicetus carolinensis Meyer, new species

Adult Female

Color generally straw yellow to dark honey brown, metasoma (abdomen) darker than head and thorax. Body length 1.0-1.4 mm (exclusive of ovipositor); width 0.4-0.5 mm at mesosoma (thorax).

Head: Sparsely setaceous and cellulate-reticulate above and between compound eyes, smoother from median ocellus to frontal-facial carina; scrobal basins bare and cellulate (Fig. 1A). Ocellar triangle isoceles, 3:4 base to height ratio. Compound eyes large with ventral and medial margins nearly linear; ommatidia hexagonal, arranged in horizontal rows.

Antennae laterally flattened (Fig. 1B). Scape subrectangular, darkly margined; inner aspect convex, reticulate, and setaceous; outer aspect concave, smoother, and more glabrous except for single row of setae along dorsal margin. Pedicel small, triangular, articulated within subapical cleft on outer dorsal margin of scape. Flagellum composed of funicle with six distinct, articulating units (flagellomeres) and clava with three indistinct, conjoined units. Clava darkly pigmented, matching dorsal margin of funicle and edges of scape, remainder of antenna golden brown. Funicle I more than 1.5× longer than funicle II, scissoring behind scape during antennal flexion; funicles II-VI subequal in length, always exposed. Each funicle unit longer dorsally than ventrally, partially nested, and asymmetrically articulated about below dorsal margin. Setae present on both aspects of entire flagellum, shorter and mixed with peg-like sensilla on ventral margin of clava III.

Mouthparts characteristic of the genus: labrum small and triangular, mandibles tridentate, maxillary palpi 4-segmented, labial palpi 3-segmented.

Mesosoma (Thorax): Pronotum narrow, collarlike. Mesoscutum broadly convex, sparsely setaceous, and dusky brown to fuscous with metallic highlights; notaular lines absent. Axillae and scutellum with fine reticulations; color light yellow to dark honey brown with fuscous setae. Propodeum with lateral posterior corners acute; surface texture smooth; color straw yellow to dark honey brown.

Legs without special modifications, color straw yellow; mesothoracic leg with tibial spur nearly as long as tarsomere I.

Forewing with submarginal vein slender, length equal to greatest width of wing; parastigma slightly thickened. Marginal vein short, length 5-7× its width. Stigmal vein shorter than marginal vein but longer than postmarginal vein. Three circular sensilla present on uncus (Fig. 1E). Costal cell hyaline, glabrous except along leading edge. Basal cell subtriangular, surrounded by single row of setae, truncated apically near base of parastigma by dark, setaceous band (band perpendicular to submarginal vein, fading into linea calva). Remainder of basal triangle hyaline, devoid of setae. Second dark spot, arising from marginal vein, fading apically into a hyaline streak, blending posteriorly into smoky pigmentation. Main blade of wing clothed with short, dark setae; mostly smoky brown in color except for hyaline patches in apical fourth and along trailing edge (Fig. 1D).

Metasoma (Abdomen)**:** Gaster smoky brown in color, dorsal aspect generally heart-shaped, acute apically, longer than wide. Base of gaster produced anterioventrally, fitting into propodeum between metathoracic coxae. Cercal plates retracted to anterior third of abdomen; each plate with three bristles. Ovipositor long, 0.50-0.65 mm in length, arising near base of gaster, extending beyond apex by about half length of mesothoracic tibial spur.

Adult Male

Head and body color predominantly black with weak metallic reflections of green or blue; length 0.9-1.2 mm (exclusive of aedeagus), width 0.3-0.4 mm at mesosoma.

Head: Cellulate-reticulate, lightly setaceous above median ocellus and below antennae. Scrobal basins subcircular, separated by a median ridge. Ocellar triangle equilateral. Compound eyes smaller than in female, separated by more than radius of eye, rounded on ventral and medial margins. Ommatidia hexagonal, arranged in oblique rows.

Antennae light brown in color, with darker setae and sensilla. Scape clavate with globose radicle; inner aspect lightly reticulate, and sparsely setaceous; outer aspect deeply grooved and glabrous. Pedicel globose, articulating within socket on outer apex of scape, sparsely setaceous. Flagellum composed of funicle with six distinct, articulating units (flagellomeres) and clava with three

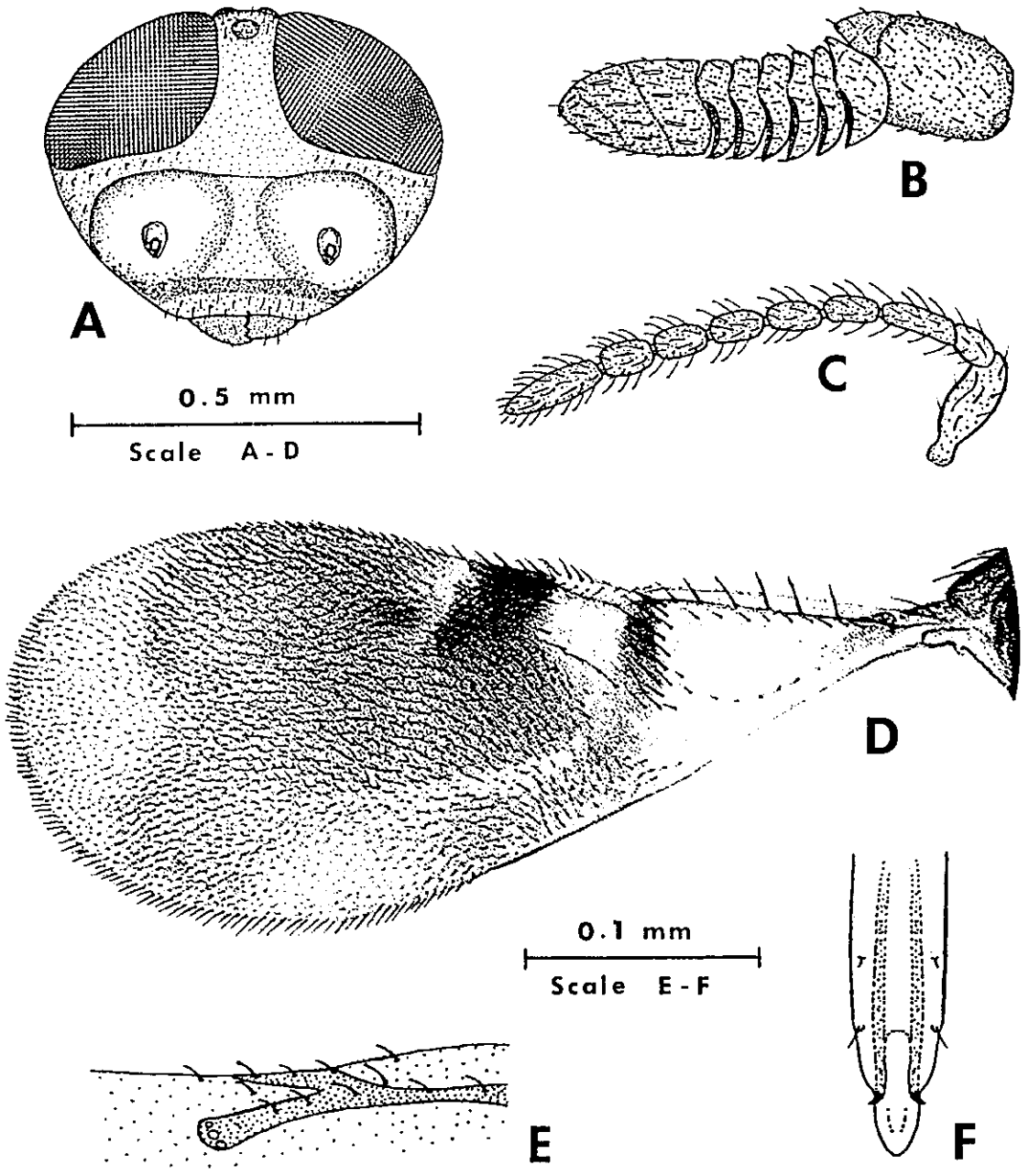

Fig. 1. Distinctive morphological features of *Anicetus carolinensis*. A, Head of adult female, frontal view with antennae removed to expose scrobal basins; B, Right antenna, adult female, inner aspect; C, Right antenna, adult male, inner aspect; D, Left forewing of female, digitally rendered from a photograph; E, Detail of stigmal vein in female's forewing, showing location of circular sensilla; F, Male genitalia, dorsal view.

indistinct, conjoined units (Fig. 1C). Funicle I cylindrical, subequal to scape in length and diameter, more than 1.5× longer than funicle II. Funicles II-VI subequal in length and diameter. Clava barely longer than scape or funicle I, subequal in diameter, pointed at apex. Funicles I-VI and clava densely clothed with long trichoform sensilla.

Mouthparts similar to female: mandibles tridentate, maxillary palpi 4-segmented, labial palpi 3-segmented.

Mesosoma (Thorax): Dark brown to black with metallic highlights. Pronotum narrow, collar-like. Mesoscutellum broadly convex, lightly reticulate, sparsely setaceous; notaular lines absent. Axillae

and scutellum cellulate-reticulate, sparsely setaceous. Propodeum with lateral posterior corners acute, surface texture smooth, color cinnamon to dark smoky brown.

Legs without special modifications; mostly creamy yellow to ivory except for black pulvilli; femur, tibia, and apical tarsomere of metathoracic legs fuscous except around joints; mesothoracic leg with tibial spur nearly as long as tarsomere I.

Forewing hyaline, venation similar to female. Costal cell and basal triangle bare except for setae around perimeter, linea calva distinct, main blade uniformly clothed with short, dark setae.

Metasoma (Abdomen): Gaster generally heart-shaped, rounded at apex, length subequal to width; dark brown to smoky black in color, lighter and more translucent between segments when distended to expose membranes. Cercal plates retracted to middle of abdomen; each plate with three bristles. Genitalia as in Fig. 1F, with digital hooklets small and bent outward.

Type Material

All type specimens were reared from terrapin scale, fixed in Kahle's solution, and preserved in 70% ethanol. Holotype: female emerged 21 V 1991 from terrapin scale collected 2 V 1991 on highbush blueberry (*Vaccinium corymbosum* L.), near town of Ammon, Bladen Co., North Carolina, J. R. Meyer. Allotype: male emerged 20 V 1991 from above scale collection and observed courting holotype. Paratypes: 7 females, 6 males, emerged 18-31 V 1991, same scale collection as Holotype. Holotype, allotype, and 7 paratypes (4 females and 3 males) have been deposited in the NC State University Insect Collection. Six paratypes (3 females and 3 males) have been deposited in the National Museum of Natural History, Washington, DC. Additional specimens, reared from terrapin scale collected 1993-1998 in Bladen, Duplin, Pender, and Sampson Counties, have also been deposited in the NC State University Insect Collection.

Etymology

The name of this species commemorates the state of North Carolina where it was first collected.

Life History

Based on the timing of adult emergence, at least two generations of *A. carolinensis* occur each year (Devorshak 1994). Adults of the overwintering generation emerge in April and early May, while adults of the second generation begin emerging in June and continue until all overwintered scale have dropped from the plant in early July.

Host Range

Despite extensive collections of scale insects on blueberry and other indigenous plants in the southeastern coastal plain of North Carolina, *A. carolinensis* has only been reared from terrapin scale. In the laboratory, however, it has been tested against eight species of soft scale (Devorshak 1994) and found to oviposit in three of them (Table 1). Despite oviposition, no development was detected

TABLE 1. OVIPOSITION RESPONSE OF *ANICETUS CAROLINENSIS* TO COMMON SPECIES OF SOFT SCALE (HEMIPTERA: COCCIDAE).

Scale species	Oviposition
Terrapin scale, *Mesolecanium nigrofasciatum* (Pergande)	
Adult female	Yes
Second instar	No
Indian wax scale, *Ceroplastes ceriferus* (Fabricius)	
Adult female	Yes
Second instar	Yes
Florida wax scale, *Ceroplastes floridensis* Comstock	
Adult female	Yes
First and second instars	Yes
Brown soft scale, *Coccus hesperidum* Linnaeus	
All stages	No
Green scale, *Coccus viridis* (Green)	
All stages	No
Hemispherical scale, *Saissetia coffeae* (Walker)	
All stages	No
Caribbean black scale, *Saissetia neglecta* De Lotto	
All stages	No
Pyriform scale, *Protopulvinaria pyriformis* (Cockerell)	
All stages	No

in either species of *Ceroplastes* and evidence of egg encapsulation was found in Florida wax scale, *C. floridensis* Comstock (Devorshak 1994).

Oviposition Behavior

When presented with a potential host, a gravid female criss-crosses the scale, holding her antennae very close together while tapping and brushing the entire surface of the scale with the ventral surface of her antennal clava. After one or more of these transits, she probes the lateral edge of the scale with her antennae and then, moving to one side, backs up to the scale and inserts her ovipositor beneath the lateral edge of the scale's derm. This behavior is consistently observed with overwintered terrapin scale (adult females), but never with younger stages. By contrast, oviposition behavior has been observed with first and second instars (and adults) of the Florida wax scale and with second instars (and adults) of the Indian wax scale, *C. ceriferus* (Fabricius). In both species of wax scale, female *A. carolinensis* oviposit directly through the dorsal cuticle, not under the edge of the derm.

DISCUSSION

Asynchrony between the bivoltine life cycle of *A. carolinensis* and the univoltine life cycle of its host raises several unanswered questions about the parasite's biology and behavior. When parasites emerge from overwintering scale in April or early May, terrapin scale hosts are large, full of developing embryos, and readily accepted by *A. carolinensis* for oviposition. Crawler emergence usually occurs in late May and early June. By mid-June crawlers have departed and most of the remaining scales are parasitized. When adults of this second generation emerge in late June, a suitable host is no longer present—crawlers and second-stage nymphs are not accepted for oviposition. What is the fate of these individuals? Do they survive the summer and lay eggs on mature scale in the fall? Do they have an alternate host? Or do they simply die without reproducing? Over the past 10 years, we have been unsuccessful in locating an alternative host or collecting adults in the fall. Clearly, we have much more to learn about this insect!

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ILLUSTRATED KEY TO *PSEUDACTEON* DECAPITATING FLIES (DIPTERA: PHORIDAE) THAT ATTACK *SOLENOPSIS SAEVISSIMA* COMPLEX FIRE ANTS IN SOUTH AMERICA

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ABSTRACT

This paper provides an illustrated key in English and Portuguese to 18 South American species of *Pseudacteon* decapitating flies that attack *Solenopsis* fire ants in the *saevissima* complex. The taxonomic history and current status of species in the genus *Pseudacteon* are discussed. *Pseudacteon* flies are of interest because of their unusual life history and potential value as classical fire ant biocontrol agents.

Key Words: biocontrol, taxonomy, ovipositor, parasitoid, Brazil, Argentina

RESUMO

Este trabalho fornece uma chave ilustrada em inglês e português para 18 espécies sul āmericanas de *Pseudacteon* que atacam formigas lava-pés *Solenopsis* do complexo *saevissima*. A história taxonômica e a posição atual das espécies no gênero *Pseudacteon* são discutidas. As pequenas moscas *Pseudacteon* são de interesse devido a sua ciclo de vida incomum e potencial valor como agentes de biocontrole clássico das formigas lava-pés.

Phorid flies in the genus *Pseudacteon* are of particular interest because of: 1) their potential use as classical biocontrol agents for imported fire ants in the United States and other parts of the world (Porter 1998) and 2) their unusual life history (Porter et al. 1995a). *Pseudacteon* flies appear to be promising biocontrol agents because fire ants utilize a suite of highly specific defenses against attacking flies (Orr et al. 1995; Porter et al. 1995b; Morrison 1999). These defenses could only have evolved and be maintained if *Pseudacteon* flies were having evolutionary impacts on fire ant populations or the production of sexuals.

Pseudacteon flies are the kind of parasitoids that give science fiction writers fodder for their stories. Adult females dive in and inject their torpedo-shaped eggs into the bodies of ant workers in only a fraction of a second. Their highly sclerotized external ovipositors (Figs. 1-19) appear to function in a lock-and-key fashion, allowing an egg to be rapidly and precisely inserted into specific locations of the ant thorax. The newly hatched maggot moves into the head of its host where it develops for 2-3 weeks (Pesquero et al. 1995; Porter et al. 1995a). Just prior to pupation, the maggot apparently releases a chemical that causes the intersegmental membranes of its host to dissolve. Within hours, the host worker is decapitated leaving the body still twitching. The maggot consumes everything in the head and pupates inside the empty head capsule, using it as a pupal case (Porter et al. 1995a). Surprisingly, the sex of developing flies appears to be determined by the size of their host rather than by their genes (Morrison et al. 1999).

The genus *Pseudacteon* was described by Coquillett (1907). Female *Pseudacteon* flies are characterized by having fully developed wings, large eyes with hundreds of ommatidia, a subquadrate frons with a median furrow, more than 4 bristles on the frons, unforked wing veins, hind tibia with a dorsal hair palisade, and a symmetrical highly sclerotized ovipositor (Coquillett 1907; Disney 1994). See Borgmeier (1963) for a more complete diagnosis of the genus. Like other phorids, *Pseudacteon* flies have shortened costal and radial veins and a ball-and-socket articulation between the greatly enlarged third antennal segment and the conus of the second antennal segment (Disney 1994).

Twenty-seven species of *Pseudacteon* flies are known to attack fire ants in the genus *Solenopsis* (Porter 1998). About a dozen additional species are known to attack ants in other genera including: *Dorymyrmex, Linepithema, Crematogaster, Lasius, Liometopum, Myrmica,* and *Pseudolasius* (Disney 1994; Brown & Feener 1998). *Pseudacteon* flies have been collected from the following regions: South America, North America, Europe, Asia, Australia, and Indonesia (Borgmeier 1963;

Disney 1994; Brown & Feener 1998; Disney & Michailovskaya 2000).

This paper provides an illustrated key to the 18 described species of *Pseudacteon* flies that are known to attack *Solenopsis saevissima* complex fire ants. Previous keys to these species are impractical to use because they do not include all known species and rely on characters that are either difficult to see or too variable to be effective (Borgmeier 1925, 1969). Fire ants in the *saevissima* complex inhabit regions of South America from the Amazon Basin of Brazil, west to the Andes and south through the Province of Buenos Aires in Argentina (Trager 1991). Most of the *Pseudacteon* species in South America were described by Borgmeier (1925, 1926, 1938, 1962, Borgmeier & Prado 1975). Additional South American species were named by Schmitz (1914, 1923), and Pesquero (2000). The host species of *Pseudacteon conicornis* Borgmeier was previously unknown (Borgmeier 1962), but it is included in this key because it was recently collected attacking *Solenopsis saevissima* ants near Rio de Janeiro (Brown 2000). We also included *P. convexicauda* in this key because it has occasionally been collected over *Solenopsis* fire ants (Borgmeier 1962; Porter 1998); nevertheless, this is very rare and recent collections indicate that it is probably a parasitoid of *Paratrechina* ants (M. A. P., unpubl. data).

Materials and Methods

Photographs of fly ovipositors (Figs. 1-20) were obtained using scanning electron microscopes in the University of Florida Departments of Entomology and Zoology and the Universidade de São Paulo, Intsituto de Fisica in São Carlos. Flies were prepared using standard dehydration techniques and their abdomens were mounted on stubs for gold coating. We used NIH Image (1.62) public domain software (http://rsb.info.nih.gov/nih-image/) to improve the contrast and orientation of the photos. CorelDRAW 6 was used to assemble the plates.

Material Examined

This paper is based primarily on collections made by the authors and inspection of type material from T. Borgmeier in the Muzeu de Zoologia da USP, São Paulo, Brazil. C. R. F. Brandão (Muzeu de Zoologia da USP), B.V. Brown (Los Angeles Co. Museum), L. E. Gilbert (Univ. of Texas at Austin), and P. J. Folgarait (Universidad Nacional de Quilmes, Buenos Aires, Argentina) supplied additional specimens for use with the electron microscope.

Location data for flies illustrated in Figs. 1-19 are as follows: Fig. 1, near Desengano, RJ, Brazil; Fig 2, Rio Claro, SP, Brazil; Fig. 3, Pindamonhangaba, SP, Brazil; Fig. 4, Rio Claro, SP, Brazil; Fig. 5a, Buenos Aires Province, Argentina; Fig. 5b, Rio Claro, SP, Brazil; Fig. 6a, Jundiai, SP, Brazil; Fig. 6b, Goiânia, GO, Brazil; Fig. 7, São Carlos, SP, Brazil; Fig. 8a, Hurlingham, BA, Argentina; Fig. 8b, Goiânia, GO, Brazil; Fig. 9, Rio Claro, SP, Brazil, Fig. 10, São Carlos, SP, Brazil; Fig. 11, Goiânia, GO, Brazil; Fig. 12, Rio Claro, SP, Brazil; Fig. 13, San Ignacio, MS, Argentina; Fig. 14, Rio de Janeiro, RJ, Brazil; Fig. 15, Goiânia, GO, Brazil; Fig. 16, Rio Claro, SP, Brazil; Fig. 17a, Viçosa, MG, Brazil; Fig. 17b, Goiânia, GO, Brazil; Fig. 18, Goiânia, GO, Brazil; Fig. 19a, São Paulo State, Brazil; Fig. 19b, Buenos Aires Province, Argentina.

Results and Discussion

Variation

Several species illustrated in our key exhibit regional variability. Some cases may be intraspecific clinal variation while other cases may be true sibling species isolated by geography or host preferences.

In the case of *Pseudacteon curvatus* Borgmeier, individuals from around São Paulo, Brazil have a more sharply curved ovipositor (Fig. 5b) than those from near Buenos Aires, Argentina (Fig. 5a). The ventral tooth is also sharper in specimens from Brazil (Fig. 5b) and this tooth lacks the medial reinforcement ridge seen in Fig. 5a.

The ovipositor of *Pseudacteon nudicornis* Borgmeier from Jundiai (Fig. 6a) is proportionally wider than that of the specimen from Goiânia (Fig. 6b). Also, the inner margin of the upper plate of the lateral lobes is convex compared to concave for the specimen from Goiânia.

For *Pseudacteon cultellatus* Borgmeier, the terminus of central extension of the ovipositor has a strong lateral extension for specimens collected near Buenos Aires (Fig. 8a), but only a slight extension for specimens collected from Goiânia (Fig. 8b).

The ovipositor of *Pseudacteon affinis* Borgmeier collected from Goiânia (Fig. 17b) is much narrower than it is for flies collected near Viçosa (Fig. 17a).

Pseudacteon obtusus Borgmeier flies from the region around the city of São Paulo are generally small flies (Morrison & Gilbert 1999) that lack aristae on the antennae, but *P. obtusus* collected in western and southern parts of their range are commonly large flies with aristae on the antennae. The absence of aristae is typically a male trait. Male *Pseudacteon* flies are usually smaller than female flies so the absence of aristae in small females may be an allometric trait associated with small size. Large- and small-sized *P. obtusus* have been collected at the same site in northern Argentina, but it is unknown whether large individuals are from a genetically distinct population or merely the facultative result of development in larger hosts.

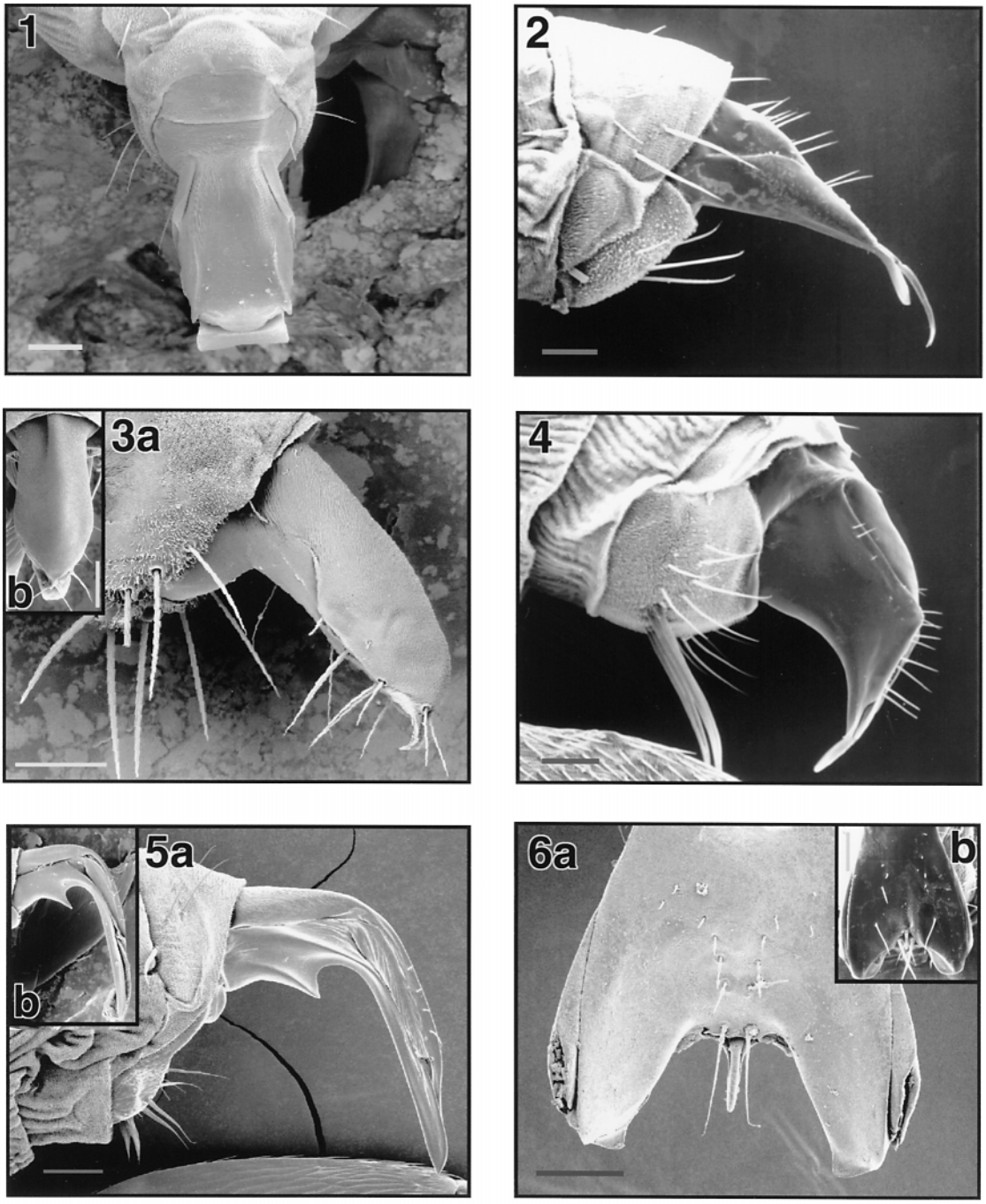


Fig. 1. Dorsal posterior view of *P. conicornis* external ovipositor. Fig. 2. Lateral view of *P. solenopsidis* ovipositor. Fig. 3. *P. convexicauda*; a) lateral view; b) dorsal posterior view. Fig. 4. *P. borgmeieri,* lateral view. Fig. 5. *P. curvatus,* lateral view; a) from Buenos Aires Province, Argentina; b) from São Paulo State, Brazil. Fig. 6. Dorsal-posterior view of *P. nudicornis*; a) from São Paulo State, Brazil, b) from Goiás, Brazil. Bars in figures indicate 50 μm.

Female *Pseudacteon tricuspis* Borgmeier flies collected from São Paulo, Brazil west to Mato Grosso do Sul and south to Santa Fe, Argentina look like Fig. 19a. South and east of Santa Fe through the province of Buenos Aires they look like Fig. 19b. The major differences are that the

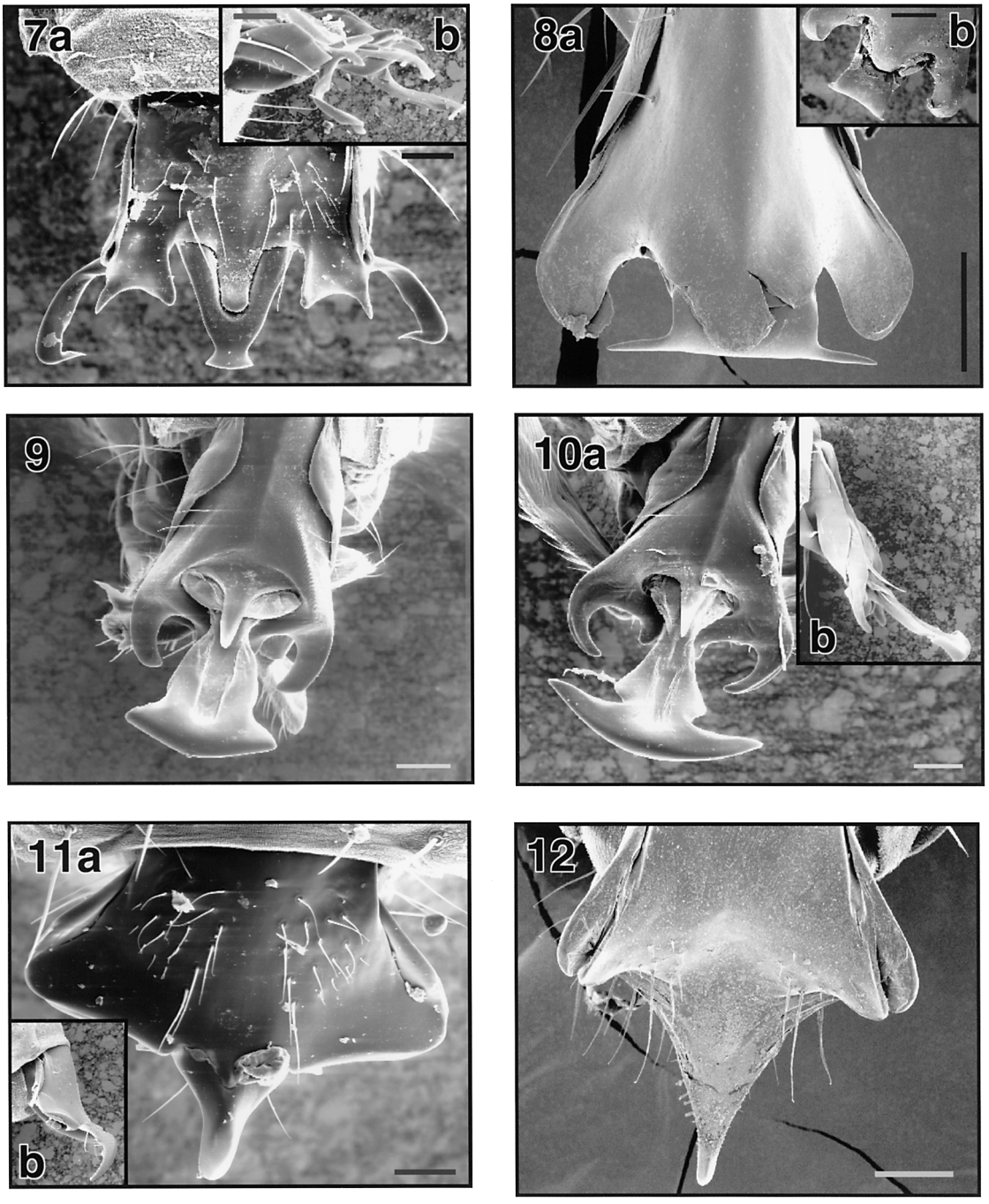


Fig. 7. Ovipositor of *P. fowleri*, b) lateral view. Fig. 8. *P. cultellatus*, a) from Buenos Aires Province, Argentina, b) from Goiás, Brazil. Fig. 9. *P. pradei*. Fig. 10. *P. disneyi*, b) lateral view. Fig. 11. *P. lenkoi*, b) lateral view. Fig. 12. *P. litoralis*. Figures show ovipositors in dorsal-posterior view unless specified otherwise. Bars in figures indicate 50 μm.

central extension of the ovipositor of flies collected south of Santa Fe is broader (about as long as wide) and the membranous filaments are parallel with the central extension and hooked downward at their terminus (Fig. 19b) rather than gently curved and congruent with the lateral lobes (Fig. 19a). These differences correspond to a switch in hosts from *Solenopsis invicta* Buren/ *Solenopsis saevissima* F. Smith to *Solenopsis richteri* Forel. A third variety of *P. tricuspis* from

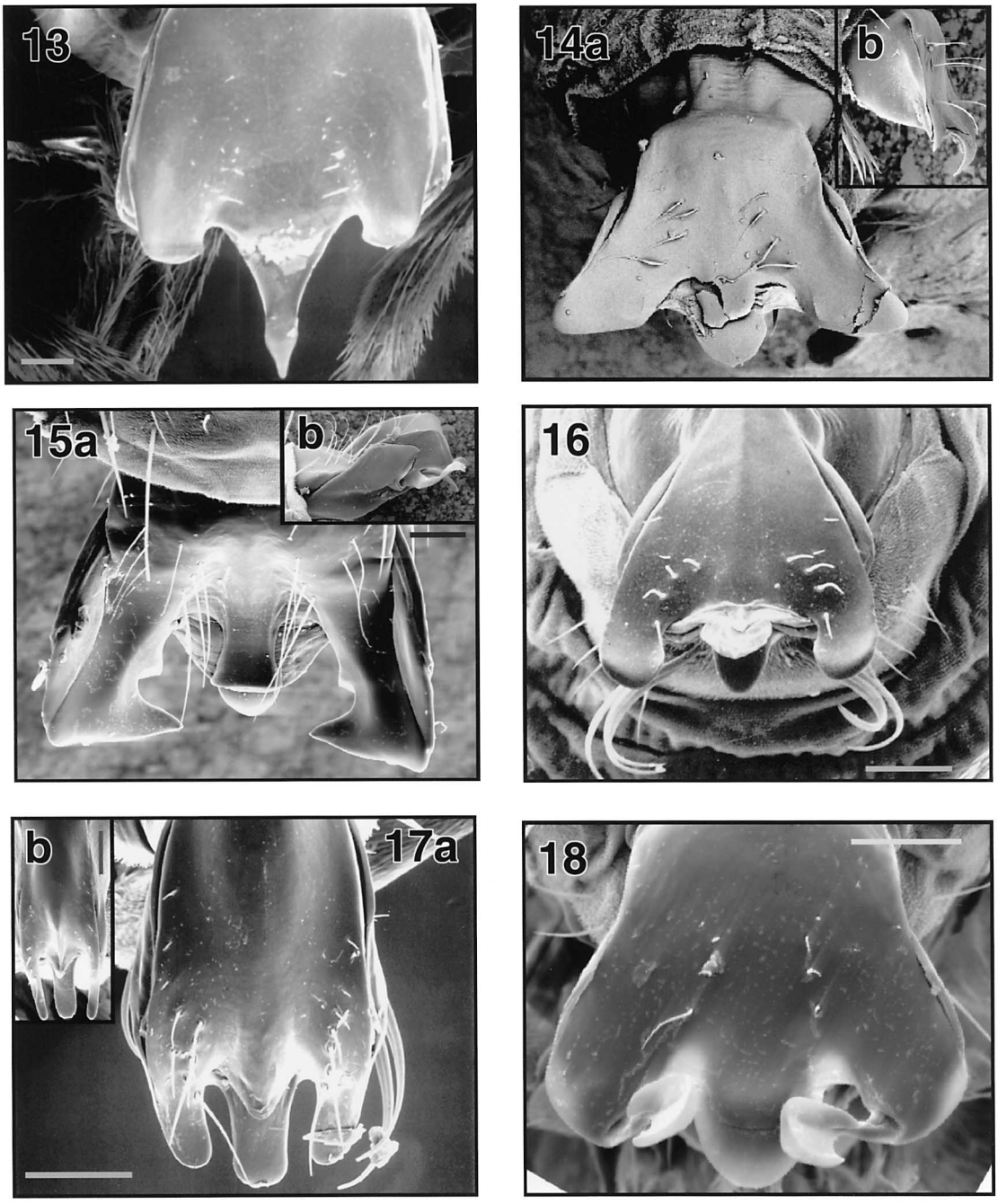
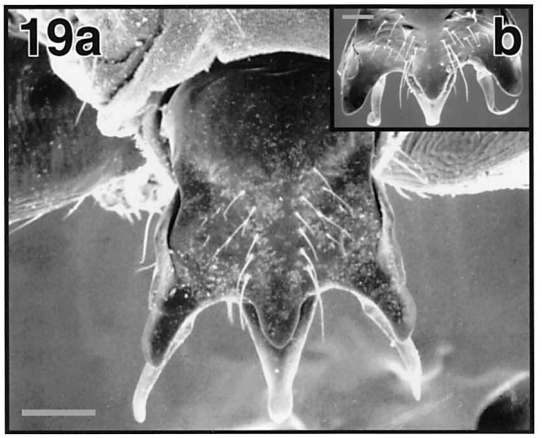


Fig. 13. *P. nocens* ovipositor. Fig. 14a. *P. comatus*, b) lateral view. Fig. 15a. *P. dentiger*, b) lateral view. Fig. 16. *P. wasmanni*. Fig. 17. *P. affinis*, a) from Minas Gerais, Brazil, b) from Goiás, Brazil. Fig. 18. *P. obtusus*. Figures show ovipositors in dorsal-posterior view unless specified otherwise. Bars in figures indicate 50 μm.

Goiânia (not illustrated) is much smaller and has the membranous filaments extending off the lateral lobes at a joint part way up the lobe.

The significance of regional variation is largely unknown; however, different biotypes of the same species or sibling species can be specialized to attack different fire ant hosts. For example, *P. curvatus* from Argentina clearly prefers the native black fire ant (*S. richteri*) over the red fire ant (*S. invicta*) found further to the north (Porter & Briano 2000). Similarly, *P. tricuspis* females from around Buenos Aires strongly prefer *S. rich-*



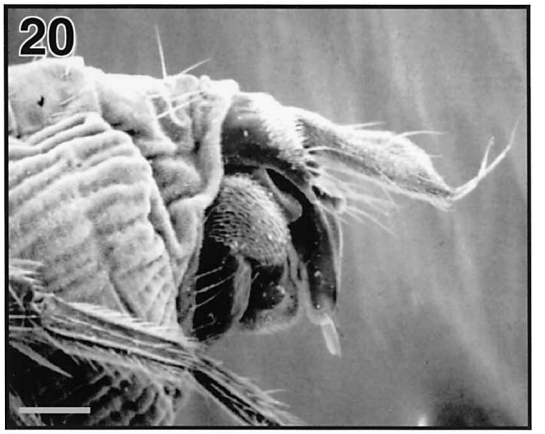


Fig. 19. *P. tricuspis* ovipositor in dorsal posterior view, a) from São Paulo State, Brazil, b) from Buenos Aires Province, Argentina. Fig. 20. Lateral view of *P. tricuspis* male hypopygium, from Brazil. The anal tube extends out prominently with two stout hairs at its terminus. The penis and hypandrium are tucked in below. Males of other known *Pseudacteon* species are very similar in general appearance (Disney 1991) and much more difficult to distinguish than females. Bars in figures indicate 50 μm.

teri fire ants while *P. tricuspis* females from near São Paulo prefer *S. invicta* fire ants (S. D. P., unpubl. data). Matching appropriate *Pseudacteon* biotypes to imported fire ants in the United States is likely to be important in their success as biocontrol agents.

Illustrated Key [Chave Ilustrada]

This illustrated key is for females of *Pseudacteon* species that parasitize *Solenopsis saevissima* complex fire ants in South America. It is based primarily on characteristics of the external ovipositor. [Esta chave ilustrada é para fêmeas de espécies de *Pseudacteon* parasitóides de formigas do complexo *Solenopsis saevissima* na América do Sul. Chave baseada em características dos últimos segmentos esclerotizados do abdome (ovipositor).]

1 Ovipositor simple, without lateral lobes; [Ovipositor simples, sem lobos laterais]; Figs. 1-5 . . . . . **2**

— Ovipositor with lateral lobes in dorsal-posterior view; [Ovipositor com lobos laterais em vista dorsoposterior]; Figs. 6-19 . . . . . **6**

2 (1) Antennae with aristae, ovipositor not flattened dorsoventrally; [Antena com arista, ovipositor não achatado dorsoventralmente] **3**

— Antennae without aristae, ovipositor somewhat flattened dorsoventrally with a small spatulate extension on the end; [Antena sem arista, ovipositor algo achatado dorsoventralmente com um pequeno prolongamento em forma de espátula no final]; Fig. 1 . . . . . ***P. conicornis* Borgmeier**

3 (2) Ovipositor approximately linear in lateral view; [Ovipositor aproximadamente retilineo em vista lateral]; Figs. 2-3 . . . . . **4**

— Ovipositor angled or curved in lateral view; [Ovipositor angulado ou curvado em vista lateral]; Figs. 4-5. . **5**

4 (3) Ovipositor lanceolate with a small membranous extension near terminus; four medium hairs or setae under abdomen just before ovipositor; [Ovipositor lanceolado com pequena peça membranosa no fim; quatro pelos médios sob o abdome pouco antes do ovipositor]; Fig. 2. . . . . ***P. solenopsidis* Schmitz**

— Ovipositor blunt, broadly rounded on dorsum; flat or somewhat concave on ventral surface; eight stout socketed hairs under abdomen before ovipositor, about ½ the length of the ovipositor (probably accidental over *Solenopsis* ants); [Ovipositor em forma de bastão com a superfície ventral plana e dorsal convexa; oito pelos robustos encaixados sob o abdome pouco antes do ovipositor, com aproximadamente metade do comprimento do ovipositor]; Fig. 3 . . . . . ***P. convexicauda* Borgmeier**

5 (3) Ovipositor short with the dorsal surface truncated and directed downward; with several stout hairs extending out under ovipositor, almost as long as the ovipositor; [Ovipositor curto com o dorso da região terminal truncado e ápice direcionado para baixo; vários pelos robustos quase tão longos quanto o ovipositor extendendo sob o ovipositor]; Fig. 4 . . . . . ***P. borgmeieri* Schmitz**

— Ovipositor long, curved downward, with a large ventral tooth near base; hairs on last abdominal segment not unusually long; [Ovipositor longo, curvado para baixo e com um dente grande na região ventral da base; pelos sob o último segmento abdominal não longos]; Fig. 5 . . . . . ***P. curvatus* Borgmeier**

6 (1) Ovipositor bilobed with a small central projection; [Ovipositor bilobado com uma pequena projeção central]; Fig. 6. . . . . ***P. nudicornis* Borgmeier**

— Ovipositor trilobed or not bilobed; [Ovipositor trilobado ou não bilobado]; Figs. 7-19. . . . . **7**

7(6) Two teeth on each lateral lobe separated by a shallow concavity; under each lobe, there is a long sclerotized ice tong-like appendix, curved and pointed at the end; the central piece of the ovipositor is in the form of a "Y"; [Lobos laterais com dois dentes separados por superfície levemente côncava; sob cada lobo há um longo apêndice esclerotizado com ápice curvado e pontiagudo; peça central em forma de "Y"]; Fig. 7. . . . . ***P. fowleri* Pesquero**

— Not as above; [Não como acima] **8**

8 (7) Central extension of ovipositor expanded laterally at end; antenna without arista; [Peça central expandida lateralmente no fim; antena sem arista]; Figs. 8-10 . . . . . **9**

— Central extension not expanded laterally at terminus; antenna with or without an arista; [Peça central não expandida lateralmente no fim; antena com ou sem arista]; Figs. 11-19 . . . . . **11**

9 (8) Central extension of ovipositor broadly rounded at end; [Peça central amplamente arredondada no fim]; Fig. 9-10 . . . . . **10**

— Central extension truncated at end; [Peça central truncada no fim]; Fig. 8. . . . ***P. cultellatus* Borgmeier**

10 (9) Central extension of ovipositor in the form of a bell; [Peça central em forma de sino]; Fig. 9. . . . . ***P. pradei* Borgmeier**

— Central extension in the form of an anchor; [Peça central em forma de âncora]; Fig. 10 ***P. disneyi* Pesquero**

11 (8) Central extension of ovipositor much longer (posteriorly) than the lateral lobes; [Peça central muito mais longa posteriormente do que os lobos laterais]; Figs. 11-13 . . . . . **12**

— Central extension of ovipositor, at maximum, a little longer than the lateral lobes; [Peça central, no máximo, pouco mais longa do que os lobos laterais]; Figs. 14-19. . . . . **14**

12 (11) Central extension hooked downward (Fig. 11b); lateral lobes broadly joined with central extension; the angle formed between a lateral lobe and the central extension is >90°; [Peça central curvada para baixo no ápice (Fig. 11b); lobos laterais fundidos com a peça central; ângulo formado entre um lobo lateral e a peça central é >90°]; Fig. 11. . . . . ***P. lenkoi* Borgmeier & Prado**

— Central extension not hooked downward; angle formed between a lateral lobe and the central lobe is <90°; [Peça central não curvada para baixo; ângulo formado entre um lobo lateral e a peça central é <90°]; Figs. 12-13. . . . . **13**

13 (12) Lateral lobes rounded and extend out diagonally; central extension cylindrical; [Lobos laterais arredondados e direcionados diagonalmente; peça central cilíndrica]; Fig. 12 . . . ***P. litoralis* Borgmeier**

— Lateral lobes truncate and directed posteriorly; central extension flattened; [Lobos laterais truncados e direcionados posteriormente; peça central achatada]; Fig. 13 . . . . . ***P. nocens* Borgmeier**

14 (11) Lateral lobes truncated at ends; [Lobos laterais truncados posteriormente]; Figs. 14-15 . . . . . **15**

— Lateral lobes rounded or pointed at ends; [Lobos laterais arredondados ou ponteagudos]; Figs. 16-19 . **16**

15 (14) Lateral lobes and central lobe of similar length, separated by a small oblique incision; [Lobos laterais simples, separados da peça central por uma pequena incisão oblíqua; lobos laterais e peça central de comprimentos semelhantes]; Fig. 14 . . . . . ***P. comatus* Borgmeier**

— lateral lobes complex, each with a tooth directed medially (Fig. 15); a membranous filament also extends off internal border (Fig. 15b); [Lobos laterais complexos com um dente dirigido para a linha mediana (Fig. 15); na borda interna há um filamento membranoso (Fig. 15b)]. . . . . ***P. dentiger* Borgmeier**

16 (14) Abdomen with several stout hairs extending out under ovipositor, hairs are almost as long as the ovipositor; lateral lobes without membranous appendages; [Último segmento do abdome com vários pelos robustos direcionados sob o ovipositor, esses pelos são quase tão longos quanto o ovipositor; lobos laterais sem apêndices membranosos]; Figs. 16-17 . . . . . **17**

— Without long stout hairs under ovipositor; lateral lobes with membranous extensions; [Sem pelos longos e robustos; lobos laterais com apêndices membranosos]; Figs. 18-19 . . . . . **18**

17 (16) Lateral lobes of ovipositor diverge diagonally; ovipositor about as long as wide; [Placa dorsal do ovipositor com bordas que divergem anteroposteriormente; ovipositor quase tão longo quanto largo]; Fig. 16 . . . . . ***P. wasmanni* Schmitz**

— Lateral lobes of ovipositor subparallel; ovipositor much longer than wide; [Placa dorsal do ovipositor com bordas sub-paralelas; ovipositor muito mais longo do que largo]; Fig. 17 . . . . . ***P. affinis* Borgmeier**

18 (16) Lateral lobes broadly rounded, each with a membranous extension off their inner borders directed medially; membranous extension in the shape of a stocking; [Lobos laterais amplamente arredondados; apêndice membranoso em forma de botina saindo da borda interna dos lobos laterais]; Fig. 18 . . . . . ***P. obtusus* Borgmeier**

— Lateral and central lobes pointed, in form of a trident; membranous filament under each lateral lobe; [Ovipositor em forma de tridente; filamento membranoso vermiforme saindo sob os lobos laterais]; Fig. 19 . . . . . ***P. tricuspis* Borgmeier**

A key to male *Pseudacteon* flies is not provided because most males are undescribed and unknown to science because they are not attracted to fire ant workers. Unlike most South American species, large numbers of *P. tricuspis* males (Fig. 20) are commonly collected in the field because they are attracted to fire ants and attempt to mate with ovipositing females (Porter 1998). *P. curvatus* flies mate away from fire ant mounds shortly after emerging from the pupae (Wuellner & Porter, unpubl. data). The mating behavior of the other 16 species of *Pseudacteon* flies that attack *saevissima* complex fire ants is unknown.

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GRYLLUS CAYENSIS N. SP. (ORTHOPTERA: GRYLLIDAE), A TACITURN WOOD CRICKET EXTIRPATED FROM THE FLORIDA KEYS: SONGS, ECOLOGY AND HYBRIDS

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ABSTRACT

Gryllus cayensis, new species, formerly occurred in tropical hammocks in the Florida Keys but has not been found there since 1972, the initial year of aerial spraying of north Key Largo hammocks for mosquito control. It is now known only from pineland in Everglades National Park. Males of *G. cayensis* make no ordinary calling songs, but some caged males occasionally produce soft 3-4 pulse chirps with a principal frequency of nearly 11 kHz. Males of its sister species, *G. fultoni* (Alexander), which occurs in north Florida, call with loud 2-4 pulse chirps with a principal frequency of about 4.5 kHz.

Key Words: *Gryllus cayensis*, *Gryllus fultoni*, calling song, hybridization, phylogeny

RESUMEN

Se describe una nueva especie, *Gryllus cayensis*, la cual solía existir en los "hammocks" tropicales de los Cayos de la Florida, pero que no se ha encontrado allí desde 1972, año en que se inicio la aspersión aérea en el norte de Cayo Largo para el control de mosquitos. Hoy en día solamente en los bosques de pinos del Parque Nacional de los Everglades. Los machos de *G. cayensis* no hacen llamados normales de canciones, pero algunos machos enjaulados ocasionalmente producen chirridos suaves de 3-4 pulsos con una frecuencia principal cercana a los 11kHz. Los machos de una especie hermana, *G. fultoni* (Alexander), la cual ocurre al norte de la Florida, hacen llamados con un fuerte chirrido de 2-4 pulsos con una frecuencia principal de aproximadamente 4.5 kHz.

Most crickets of the genus *Gryllus* are known as field crickets because they occur in fields and other open habitats. However, three of the nine species known from eastern United States live in woods: *G. vernalis* Blatchley, the northern wood cricket; *G. fultoni* (Alexander), the southern wood cricket; and *G. ovisopis* Walker, the taciturn wood cricket. In this paper, I describe a species that occurs in woods in Florida south of Miami. It differs from *G. fultoni*, its closest relative, in morphology, life cycle, song, and mitochondrial DNA. *Gryllus cayensis* and *G. fultoni* produce fertile hybrids in laboratory crosses.

Gryllus cayensis Walker, **New Species**
Keys Wood Cricket, Fig. 1

HOLOTYPE.—Male, Florida: Monroe Co., north Key Largo, Sec. 26, T59S, R40E, 23-VIII-Aug. 1958, T. J. Walker, leaf litter in tropical hammock, deposited in Florida State Collection of Arthropods (FSCA). Body black; legs and cerci reddish brown; dorsal field of tegmina brownish black; lateral field paler except at rear. Length of body, 20 mm; pronotal length × width, 4.2 × 5.8; length of tegmen, 7.6; length of hind femur, 13.1. Hind wings about half as long as tegmina.

ALLOTYPE.—Female, same data as holotype. Coloration like holotype but slightly paler. Length of body, 21 mm; pronotal length × width, 5.0 × 6.5; length of tegmen, 8.5; length of hind femur, 14.3; length of ovipositor, 14.8.

PARATYPES.—122 males [M], 120 females [F]. FSCA: Florida, Monroe Co., Florida Keys, Key Largo, 3 M (1 reared from juvenile), 1 F, same data as holotype; 1 M reared from juvenile, tropical hammock, 9-VIII-1972, T. J. Walker [TJW]; 10 M, 4 F, progeny of previous male and a female with same data; Sugarloaf Key, 1 F reared from juvenile, hammock litter, 24-VI-1964, TJW and R. E. Love; Big Pine Key, 1 F, 9-IV-1948, collector unknown. Dade Co., Everglades National Park, Long Pine Key, pineland, 1 M, 1 F, 19-VIII-1978, TJW; 1 M, 3 F (reared progeny of 1 F coll. 19-VIII-1978); 2 M reared from juveniles, 6 F, 22-23-IX-1980, Robert Sullivan; 31 M, 47 F (reared progeny from 5 F coll. 22-23-IX-1980); 1 M, 2 F, 13-VII-1988, TJW; 72 M, 52 F (reared progeny of 2 F coll. 13-VII-1988). University Michigan Museum of Zoology [UMMZ]: Florida, Dade Co., 6 mi e. Paradise Key [now Royal Palm Hammock], 2 F, pineland, 19-X-1929, T. H. Hubbell.

Six male and six female reared paratypes from those listed above were sent to UMMZ, U. S. National Museum, Philadelphia Academy of Natural Science, and California Academy of Science.

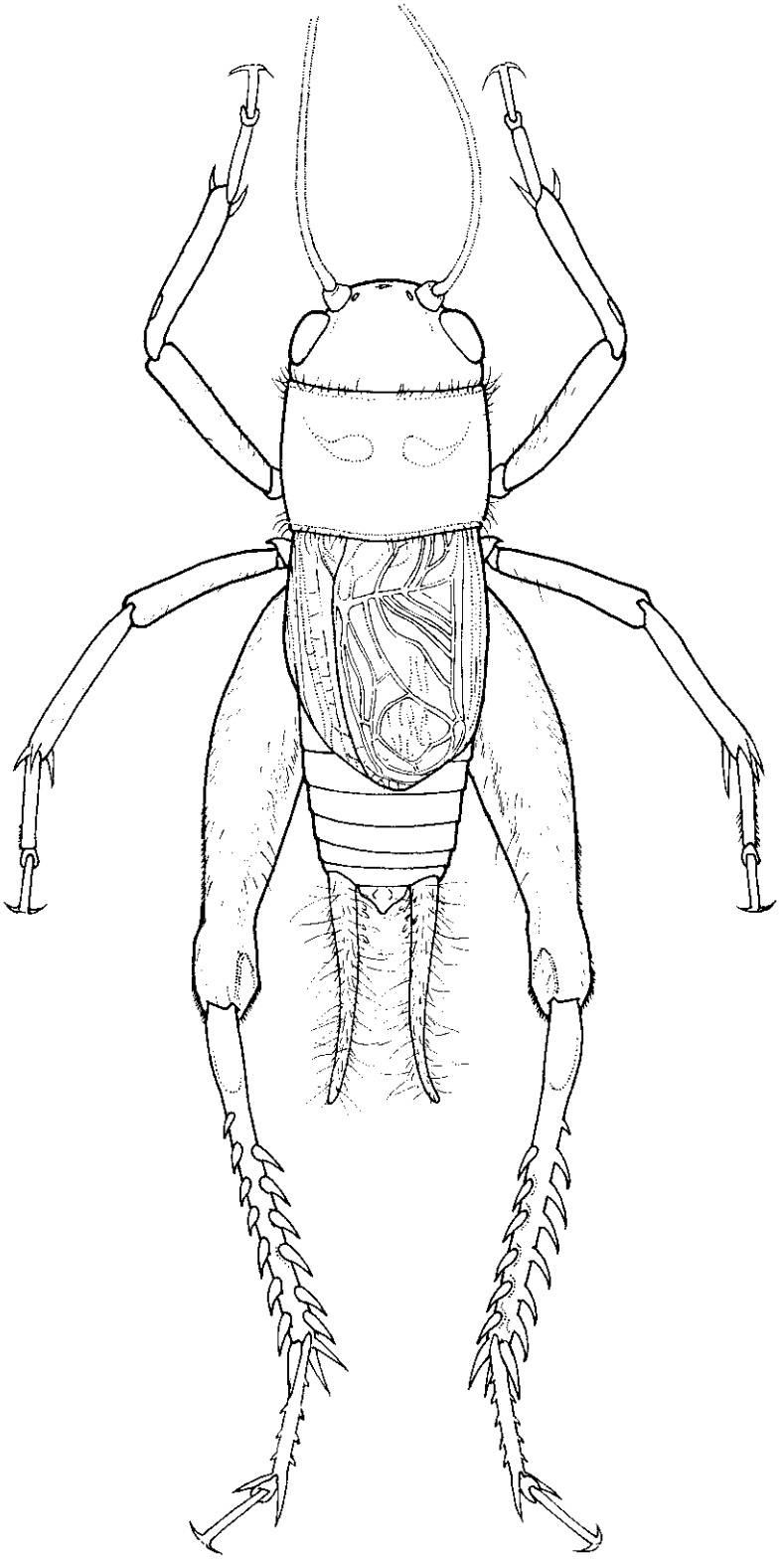

Fig. 1. Drawing of holotype male of *Gryllus cayensis*. Color photographs of living paratypes are accessible from the online version of this article at http://www.fcla.edu/FlaEnt/.

Identification

Four species of *Gryllus* occur in extreme south Florida: *G. assimilis* (Fabricius), *G. cayensis*, *G. firmus* Scudder, and *G. rubens* Scudder. *G. cayensis* is the only one of the four that has any of the following features: reddish brown hind femora, tegmina (measured in situ) shorter than two pronotal lengths, inhabits woods. It is always micropterous, whereas the others are either dimorphic in wing length (*G. firmus* and *G. rubens*) or always macropterous (*G. assimilis*). *G. fultoni*, a wood cricket occurring north of the range of *G. cayensis* and similar to it in many respects, has tegmina that are at least twice the length of the pronotum. The stridulatory files of two males from Key Largo had 110 and 100 teeth and were 2.74 and 2.26 mm long respectively. This makes them indistinguishable from the files of *G. fultoni* (Nickle and Walker 1974).

Song

In the field, males of most *Gryllus* species are easy to identify and to locate by their loud, persistent, species-specific calling songs. However, *G. cayensis* has never been heard to call in the field. Most males in captivity make no sounds when alone, although a few make soft chirps rarely. Only one of five males collected on Key Largo in 1958 was ever heard to stridulate while alone. The soft chirps were tape recorded but the tape was loaned and lost. A male reared from a Key Largo juvenile collected in 1972 was kept for 16 days where it could be monitored for calling during the night and at dawn (my bedroom). It was never heard to stridulate. That male and his consort (also reared) produced eight males that were likewise kept in individual cages in my bedroom. Of four males monitored for 2 weeks, two were never heard, one was heard twice but was too wary to tape, and one produced soft chirps regularly at dawn and was tape recorded. Three of the other males were monitored for 1 week and one was monitored for 4 weeks. None of these was ever heard.

I used CoolEdit 2000 (Syntrillium Software) to analyze the one extant recording of solitary stridulation by *G. cayensis* (Walker Tape Library [WTL] tape 475-2; 22.0°C). Three- and 4-pulsed chirps were produced at a rate of ca. 2.4/s. The pulse rate within the chirps was ca. 33 pulses/s. The principal frequency of the pulses was 10.8 kHz with secondary strong frequencies between 6 and 9 kHz. The chief difference between the rare, soft song of *G. cayensis* and the common, loud song of *G. fultoni* is that the song of the latter species has a principal frequency of ca. 4.5 kHz.

Males of *G. cayensis* from Long Pine Key were also taciturn. Of 24 males reared from females collected 22-23 Sept 1980 and monitored for a week or more in my bedroom, only one was heard. It occasionally produced soft chirps, but not for a tape recorder.

The only other *Gryllus* known to lack a conventional calling song is *G. ovisopis* (Walker 1974). Like *G. cayensis*, it is flightless and occurs in permanent, woodland habitats. In keeping with their lack of calling, both species have reduced tegmina (tegminal length less than twice that of the pronotum). However, males of *Gryllus insularis* Scudder have tegmina that are approximately as short (ca. 1.9 times the length of the pronotum), yet they produce a typical *Gryllus* calling song (D. B. Weissman, pers. comm.).

An aspect of calling that is not generally appreciated is that songs carry poorly between sender and receiver if both are at ground level. Michelsen (1985) calculated that [field] crickets might be able to hear each other on the ground only at distances less than 1 to 2 m. On the other hand, if sender or receiver (or both) is above ground level, transmission is much improved. Thus a cricket flying above a calling male can hear its call at a much greater distance than can a ground-level cricket. That flying crickets hear and respond to songs coming from the ground can be demonstrated with sound-baited traps that catch only flying crickets. For example, thousands of *Gryllus rubens* Scudder and hundreds of *Gryllus firmus* Scudder flew into 1.4 m diameter funnels baited with broadcasts of synthetic calls (Walker 1986). The only way that a male can broadcast to distant, *ground-level* females is to call from a perch. Males of the two large, ground-living, woods-inhabiting, non-taciturn crickets in north Florida often do just that. *Gryllus fultoni* and *Anurogryllus arboreus* Walker males often call from 0.5 to 2 m above ground level by ascending tree trunks (Paul and Walker 1979). Females of these two species are always flightless. A disadvantage of calling from tree trunks is greater exposure to acoustically orienting predators (Walker 1964). In fact a disadvantage of calling from anywhere is that some predators and parasitoids find prey by homing on their calling songs (Burk 1982; Walker 1993). Loss or reduction of calling should be most likely in crickets that are flightless, live in permanent, dense populations, and are plagued by acoustically orienting predators and parasitoids. *G. cayensis* probably met at least the first two of these criteria when it lost its long-range calling song and reduced its solitary stridulations.

Although males of *G. cayensis* seldom stridulate while alone, they readily produce courtship songs when they encounter a female. The reared 1972 Key Largo male that remained silent for 16 days in my bedroom, almost immediately used song to court an introduced female. This was recorded (WTL 475-1; 26.2°C) and found to consist of groups of 3 to 10 pulses often followed by a tick.

The pulse rate within the groups was ca. 57 pulses/s, and the group rate was ca. 5/s. The strongest frequency of the pulses was 5.6 kHz and of the ticks, 15.8 kHz.

Ten-second samples of the courtship and calling songs (WTL 475-1 and 2) were digitized and saved as .wav files. These are accessible from the online version of this article at http://www.fcla.edu/FlaEnt/.

Distribution, Ecology, and Seasonal Life Cycle

G. cayensis is known only from tropical hammocks in the Florida Keys and from pinelands south of N lat 25.4° in Dade Co., Florida. The southernmost Florida records for *G. fultoni* are Marion and Volusia Counties; for *G. ovisopis*, Lake Placid and Punta Gorda. Thus *G. cayensis* is geographically isolated by more than 350 km from *G. fultoni* and by more than 200 km from *G. ovisopis*.

The seasonal life cycle of *G. cayensis* has not been studied in the field, but laboratory rearing, weather records, and collecting records provide clues. In the laboratory at 25°C and 16L:8D photoperiod, development from egg to adult requires about 6 months. Eggs of field-collected adults hatched in about 4 weeks under these conditions. There was never delayed hatch as with the eggs of *Gryllus* species that produce all diapause eggs or mixtures of diapause and nondiapause eggs (Walker 1980). Average temperatures at Key West and Miami are above 25°C from May through October and below 25°C from November through April (USDC 1933, 1960). Adults of *G. cayensis* have been collected in April, July, August, and September; late juveniles in June, July, August, and September; and one early juvenile was collected in August. (Juveniles were reared to adults prior to identification.)

These temperatures and collecting records do not preclude *G. cayensis* from breeding continuously, with all stages occurring at all times. However, the Keys and adjacent mainland Florida have a winter and spring dry season that lasts from November through April. On average, less than 25% of the yearly rainfall occurs during this six-month period (Homestead, Flamingo, and Long Key stations; USDC 1960). During the hot days of April and early May, before the rains start, drought often becomes severe and *Gryllus* hatchlings would probably not survive. If the dry season prevents continuous breeding, large nymphs or diapausing adults would be the expected late dry-season stages, because they have the most favorable surface-to-volume ratios. These could become reproductively active adults in anticipation of, or in response to, the start of summer rains. The progeny of these adults would become adults in late summer, which, in turn, would lay eggs that would produce the large nymphs or diapausing adults required to survive the dry season. Eggs laid in the dry season would either not hatch or produce nymphs that would desiccate.

Rearing and Experimental Crosses

Because the Keys were distant and specimens of *G. cayensis* were difficult to collect, I brought live specimens to Gainesville for further study and for increase through rearing.

Some 85% of the paratypes of *G. cayensis* are reared progeny of females collected as they fed at trails of oatmeal laid in the pineland of Long Pine Key. In 1978, 1980, and 1988, I obtained a total of 206 adults from eight field-collected females.

On 9 Aug 1972, I captured two mid-sized juveniles at oatmeal trails in hammocks on Key Largo. I reared the two under an open shelter in Gainesville and obtained an adult male and female by 26 September. The pair mated by 1 October and the first eggs hatched 5 Nov 1972. The female was deprived of her consort on 29 Oct (for pinning) but continued to lay fertile eggs until she died in mid-December. Throughout her oviposition, I attempted to rear cohorts of her progeny in the field and in the laboratory at 25°C and 16L:8D photoperiod. Under field conditions, none of 200 juveniles survived beyond the first few stadia. Juveniles that hatched in the field in early or mid-November died in about one month; early juveniles transferred to the field from the laboratory in mid-December and mid-January lasted longer but none reached the middle stadia and none survived as long as three months. When many juveniles died at once in the jars in the field, they appeared to succumb to a white mold. Under laboratory conditions, about 400 early juveniles survived to the middle stadia with low mortality, but then their numbers declined week after week. At the same time a few of the juveniles became much larger than their sibs as they reached the final juvenile stadia. This suggested cannibalism, as did finding partially eaten crickets. I therefore divided each laboratory cohort among two or three rearing containers and succeeded in rearing 30 adults. Most of the adults were used in experimental crosses with *G. fultoni* and *G. ovisopis*, the two wood crickets that occur in Florida north of the range of *G. cayensis*.

All *G. fultoni* and *G. ovisopis* used in experimental crosses were second laboratory generation crickets from stock collected in Alachua County, Florida. Five replicates of these four crosses were set up in the spring of 1973 as appropriate crickets matured: *cayensis* × *cayensis*, *cayensis* × *fultoni*, *fultoni* × *cayensis,* and *ovisopis* × *cayensis* (male parent listed first). Because of a shortage of crickets, only four replicates of *cayensis* × *ovisopis* and one replicate each of *fultoni* × *fultoni*, and *ovisopis* × *ovisopis* were established. Neither the C × O nor O × C crosses produced progeny. All other

types of crosses produced progeny: C × C (4 of 5 replicates), C × F (4 of 5), F × C (3 of 5), F × F (1 of 1), O × O (1 of 1).

Two F_1 males of the C × F cross were monitored for calling for one month in my bedroom. Neither was ever heard.

No further crosses were set up, but the progeny from one of the C × F crosses produced numerous F_2 hatchlings from which seven males and a female were reared. The males were monitored for calling and the songs of four were tape recorded (WTL 475 × 484-1, 2, 4, 5; 20.0-22.2°C). The chirp rate was ca. 2.0/s and the principal frequency was ca. 5.0 kHz. The songs were reminiscent of *G. fultoni* though weaker.

Phylogeny and Species Status

Results of the laboratory crosses indicated that *G. cayensis* was more closely related to *G. fultoni* than to *G. ovisopis*. They did not prove that *G. cayensis* and *G. fultoni* were conspecific, because species of *Gryllus* that fail to hybridize where they occur together in the field often produce fertile hybrids in the laboratory. For example, in no-choice, laboratory crosses *G. rubens* will hybridize with *G. assimilis* and with *G. texensis* Cade and Otte, species with which *G. rubens* lives in south Florida and west Florida respectively (Bigelow 1960; Walker 2000).

North American *Gryllus* have been used for numerous comparative studies of physiology, behavior, and ecology. Such studies have been hampered by the lack of a consensus phylogeny of the species. Molecular techniques now promise to provide one. Harrison and Bogdanowicz (1995) studied the mitochondrial DNA restriction site maps for eight *Gryllus* species from eastern North America, including the six that occur in peninsular Florida. They concluded that *G. cayensis* and *G. fultoni* were sister species and that *G. veletis* (Alexander and Bigelow) and one or more unidentified *Gryllus* species from western U.S. were a sister group to the *G. fultoni*/*G. cayensis* group. *Gryllus ovisopis* (the other taciturn wood cricket), *G. pennsylvanicus* Burmeister, and *G. firmus* formed a distinct group, well separated from the *G. cayensis*/*G. fultoni*/*G. veletis* group. The sequence divergence between *G. cayensis* and *G. fultoni* was much greater than that between *G. ovisopis* and either *G. firmus* or *G. pennsylvanicus* (0.027 vs. 0.002-0.010), which adds to the evidence that *G. cayensis* merits species status. [Note: The two *G. cayensis* used by Harrison and Bogdanowicz were from Long Pine Key (19 Aug 1978) rather than from Key Largo.]

Huang et al. (2000) expanded the mt DNA database for North American *Gryllus* to include three more U.S. species and the complete cytochrome b gene and a portion of the 16S rRNA gene. They did not include *G. cayensis*, but otherwise confirmed the relationships reported above, while adding *G. integer* (from California) to the *G. veletis*/*G.fultoni*[/*G. cayensis*] clade.

The origin of *G. cayensis* and *G. fultoni* from a common ancestral species seems likely to have occurred when Pleistocene fluctuations in sea levels isolated south Florida woods and wood crickets from north Florida ones. Some crickets that occur in tropical south Florida apparently got there by flying or rafting from Cuba; however, *G. cayensis* is flightless, and rafting seems unlikely since the eggs are laid in soil. Zayas (1974) makes no mention of a Cuban counterpart to *G. cayensis*.

Probable Extirpation from the Florida Keys

My first experience with *G. cayensis* was at mid-morning, 23 August 1958, when I observed numerous individuals in the leaf litter of a tropical hammock on north Key Largo. I easily collected five adults and a large nymph. Since then, I've collected only three individuals in the Keys: one nymph from hammock leaf litter on Sugarloaf Key in June 1964 and two nymphs feeding at a trail of oatmeal laid in a hammock on north Key Largo, 9 Aug 1972. (Oatmeal was dribbled as a trail shortly after sunset and the trail was repeatedly searched with a light during the first half of the night.) On 1 and 2 June 1973, I got no specimens from oatmeal trails through the hammock that was successfully searched in 1972. On 5 Aug 1987, I found no specimens along oatmeal trails laid in two hammock areas near where I'd first found *G. cayensis* in 1958. On 6 Aug 1987 and 12 Jul 1988 I unsuccessfully searched three oatmeal trails laid on Big Pine Key. The 1987 trail was in hammock and pineland. The two 1988 trails were in Watson's and Cactus Hammocks.

The failure to collect *G. cayensis* along oatmeal trails in the Florida Keys from 1973 forward contrasts with the success of the same technique on the mainland. Each time oatmeal trails were laid in the pineland of Long Pine Key, three or more individuals were collected: 16 Aug 1978 (n = 3), 22 and 23 Sept 1980 (n = 8), 13 Jul 1988 (n = 5).

The most likely cause of the apparent disappearance of *G. cayensis* from the Florida Keys is aerial and ground application of insecticides by the Monroe County Mosquito Control District. Fogging with truck-mounted units began in 1951 and aerial spraying began in 1962. However, until 1967, all applications were in the well-populated parts of the Keys from mid Key Largo south. In that year the District began malathion fogging of north Key Largo from trucks. In 1972 they switched to ultra low volume application of 93% fenthion (Baytex) from trucks and aerial application of 4% naled (Dibrom) from DC-3 aircraft (Emmel 1995).

The switch to organophosphate insecticides and to aerial spraying thus coincided with the ap-

parent disappearance of *G. cayensis* from north Key Largo. Several lines of evidence suggest, but do not prove, that the spraying caused the disappearance. First, organophosphate insecticides are nonspecific and highly toxic (Matsumura 1985). Second, when I sought *G. cayensis* on Key Largo in 1973, I noted that there were no crickets calling in the hammocks. This was strange because on all previous visits to hammocks in the Keys the tinkling chirps of *Cyrtoxipha gundlachi* Saussure had been heard in abundance. Thirdly, the population history of *Papilio ponceanus* Schaus (Schaus' swallowtail) on north Key Largo supports the contention that mosquito control had lasting effects on nontarget insects. *Papilio ponceanus* once occurred throughout the Keys and adjacent mainland Florida but by 1976 was officially classed as "threatened" and by 1984 as "endangered" (Emmel 1995). Through 1972 it was commonly seen and collected on north Key Largo. From 1973 through the mid 1980s, it was rare or missing (Emmel 1995). Studies of the toxicity of fenthion and naled to *Papilio cresphontes* Cramer (a standin for *P. ponceanus*) showed that the concentrations sprayed on the hammocks of Key Largo were at least 400 times greater than the LC-50 for *P. cresphontes* (Eliazar 1992; Emmel 1994).

When spraying of north Key Largo hammocks ended, in the mid 1980s, *P. ponceanus* began to return, probably by immigration from Old Rhodes, Elliott and smaller keys in Biscayne National Park. On these keys, which were never sprayed, *P. ponceanus* populations were continuously present. The same keys may be home to permanent populations of *G. cayensis*, unless, perhaps, they were eliminated by the saltwater storm surge that temporarily covered them during Hurricane Andrew's assault in August 1992.

Unlike *P. ponceanus*, *G. cayensis* is flightless. If *G. cayensis* has been eliminated from Key Largo, it is unlikely to reestablish soon even if abundant populations exist on Old Rhodes and Elliott Keys.

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Songs and color photographs of the taciturn wood cricket

[a supplement to the article "*Gryllus cayensis* n. sp. (Orthoptera: Gryllidae), a taciturn wood cricket extirpated from the Florida Keys: songs, ecology and hybrids." Florida Entomologist 84(4): 700-705.]

Songs (.wav files)

10 sec sample of the courtship song (Walker Tape Library 475-1)
10 sec sample of the calling song (Walker Tape Library 475-2)

Photographs

Male, Everglades National Park, Dade County, Florida.

Female, Everglades National Park, Dade County, Florida.

For more information on this and related species, see "Singing Insects of North America" at http://buzz.ifas.ufl.edu/.

NATIVE HYMENOPTERAN PARASITOIDS ASSOCIATED WITH *ANASTREPHA* SPP. (DIPTERA: TEPHRITIDAE) IN SEROPEDICA CITY, RIO DE JANEIRO, BRAZIL

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ABSTRACT

Parasitoids associated with five species of *Anastrepha* were recovered from host fruits that belong to 12 species of plants growing in Seropedica city, Rio de Janeiro, Brazil. We recovered six native hymenopteran parasitoid species: *Doryctobracon areolatus* (Szépligeti), *Utetes* (*Bracanastrephae*) *anastrephae* (Viereck), *Opius bellus* Gahan (Braconidae, Opiinae), *Aganaspis pelleranoi* (Brèthes) (Figitidae, Eucoilinae), *Trichopria anastrephae* Lima (Diapriidae, Diapriinae) and an unidentified species of Pteromalidae. The most abundant parasitoid species was *D. areolatus*, representing 61.8% of all parasitoids. The parasitoid species recovered were well established in a wide diversity of fruit and *Anastrepha* fly species, including economically important pests such as *A. fraterculus, A. obliqua* and *A. sororcula*. The analysis of the relative abundance of the recovered parasitoids in different fruit species suggests, at least for the three encountered opiine parasitoids, that the host-parasitoid relationship was influenced by certain physical characteristics such as size and weight of the host fruit. Our results support the original proposal of M. Aluja and J. Sivinski (pers. comm.) that some native host plant species for the *Anastrepha* flies facilitate parasitoid multiplication. They deserve attention as natural enemy reservoirs and may be important to biological control strategies within fruit fly integrated management programs.

Key Words: biological control, fruit flies, tritrophic relationship, Braconidae, Figitidae, Diapriidae

RESUMEN

Parasitoides asociados a cinco especies de *Anastrepha* fueron recuperadas de frutos hospederos pertenecientes a 12 especies de plantas, en el municipio de Seropedica, Rio de Janeiro, Brasil. Se recuperaron seis especies de parasitoides himenópteros: *Doryctobracon areolatus* (Szépligeti), *Utetes* (*Bracanastrephae*) *anastrephae* (Viereck), *Opius bellus* Gahan (Braconidae, Opiinae), *Aganaspis pelleranoi* (Brèthes) (Figitidae, Eucoilinae), *Trichopria anastrephae* Lima (Diapriidae, Diapriinae) y una especie no identificada de Pteromalidae. La especie más abundante fue *D. areolatus*, representando 61,8% de todos los parasitoides. Las especies recuperadas de parasitoides están bien establecidas en una amplia diversidad de especies de frutos y moscas *Anastrepha*, incluyendo especies plagas como *A. fraterculus, A. obliqua* y *A. sororcula*. El análisis de la abundancia relativa de los parasitoides recuperados en las diferentes especies de frutos sugiere que por lo menos para los tres parasitoides Opiinae colectados, la relación parasitoide-hospedero fue influenciada por ciertas características físicas tales como tamaño y peso de los frutos hospederos. Nuestros resultados apoyan la original propuesta de M. Aluja y J. Sivinski (comunicación personal) de que algunas especies de plantas nativas hospederas de moscas *Anastrepha* facilitan notablemente la multiplicación de los parasitoides y así merecen atención como depósito de éstos agentes de mortalidad y como herramientas para las estrategias de control biológico dentro de los programas de manejo integrado de las moscas de las frutas.

Most frugivorous tephritid species in Brazil belong to the genus *Anastrepha* Schiner (Zucchi 1988). Of the 94 reported Brazilian species, four are serious pests: *Anastrepha fraterculus* (Wiedemann), *Anastrepha grandis* (Macquart), *Anastrepha obliqua* (Macquart), and *Anastrepha sororcula* Zucchi (Morgante 1991; Zucchi 2000). Traditionally, insecticidal bait sprays have controlled these species, although some attempts to apply classical or augmentative biological control have been made in Brazil (Carvalho et al. 1999). Braconid parasitoids, mainly Opiinae, have been included in the majority of these biological control programs, and continue to be emphasized in aug-

mentative programs against *Anastrepha* species in the New World because of their relative host specificity and ease of production (Clausen et al. 1965; Wharton 1997; Knipling 1992). *Diachasmimorpha longicaudata* (Ashmead), an exotic Old-world opiine, was recently introduced into Brazil and has been mass-released in a attempt to control *Anastrepha* populations on an area-wide basis in some regions (Nascimento et al. 1998). Information about the native natural enemies of the fruit flies, mainly parasitoids that might overlap in their niches with introduced species, is important to avoid the displacement of valuable biocontrol agents (see Samways 1997; Sivinski et al. 1998).

In this survey we have systematically sampled native and exotic plant species growing in the city of Seropedica, RJ, a region with abundant wild hosts and backyard gardens, aiming to identify larval-pupal fruit fly parasitoids. As far as we are aware, no biological control of *Anastrepha* spp. has been attempted in the sampled area, thus the results should reflect the natural status of fruit fly natural enemies in the area.

Materials and Methods

From November 1997 to April 1999, fruit samples from 12 different plant species of six families, all known to be potential tephritid hosts, were collected in backyard gardens and in areas of wild vegetation throughout the city of Seropedica, Rio de Janeiro state, in the southeast of Brazil (22°45'S latitude, 43°41'W longitude, and 33 m above sea level).

The fruit samples included eight native species: Surinam cherry (*Eugenia uniflora* L.), Brazilian cherry (*Eugenia brasiliensis* Lam.), jaboticaba (*Myrciaria cauliflora* Berg.), guava (*Psidium guajava* L.) (all Myrtaceae), hog-plum (*Spondias mombin* L.), Spanish prune (*Spondias purpurea* L.) (Anacardiaceae), abiu (*Pouteria caimito* Radlk.) (Sapotaceae), and inga (*Inga affinis* de Cand.) (Leguminosae). Four exotic species were also included: mango (*Mangifera indica* L.) (Anacardiaceae), carambola (*Averrhoa carambola* L.) (Oxalidaceae), loquat (*Eriobotrya japonica* Lindl.) (Rosaceae), and tropical almond (*Terminalia catappa* L.) (Combretaceae).

Samples of mature fruits were randomly collected from the ground under host trees, and placed in labelled paper bags. Subsequently, they were taken to the laboratory of the "Centro Integrado de Manejo de Pragas *Cincinnato Rory Gonçalves*" (CIMP CRG) at the "Universidade Federal Rural do Rio de Janeiro" located in the city of Seropedica. In the laboratory, they were removed from the collection bags. Each fruit species was placed separately in plastic sieves, which, in turn were placed on top of plastic containers with sand at the bottom as a pupation substrate. These containers were kept at ambient temperature and humidity. Following this, every second day they were inspected to ascertain if the sand needed to be moistened. At that time, if the pupae were formed, the sand was sifted to remove the pupae, which were then placed in plastic boxes on sand that was moistened, when necessary, and covered with organdy for holding until emergence of flies and parasitoids.

All emerged flies and parasitoids were preserved in vials filled with 70% alcohol until identified. The Tephritidae and some parasitoid species were identified by the authors with the aid of available literature (Zucchi 1978; Steyskal 1977; Leonel Junior 1991). J. A. Guimarães (ESALQ/USP, Piracicaba, SP) made the identification of some parasitoid species. Voucher specimens were placed in the entomological collections of CIMP CRG.

In this study, associations among parasitoids and fruit flies were assumed when only one species of tephritid emerged from one sample of the fruit species.

Results and Discussion

We sampled 2,720 fruits from 12 plant species infested under natural conditions by tephritid larvae. *Anastrepha* and parasitoid specimens were recovered from every plant species. A total of 3,313 *Anastrepha* flies and 1,234 parasitoids was recovered.

Five *Anastrepha* species, *A. fraterculus* (Wiedemann), *A. sororcula* Zucchi, *A. obliqua* (Macquart), *A. distincta* Greene, and *A. serpentina* Wiedemann were recovered. Egg and pupal parasitoids were not found in our collections; because all of the *Anastrepha* were collected as larvae, they would not have been obtained even if present in the area. Most of the parasitoids (97.6%) belonged to the family Braconidae. Specimens of the Figitidae, Diapriidae, and Pteromalidae represented less than 3% of all parasitoids recovered.

Six species of larval-pupal hymenopteran parasitoids were reared in association: *Doryctobracon areolatus* (Szépligeti), *Utetes* (*Bracanastrephae*) *anastrephae* (Viereck), *Opius bellus* Gahan (Braconidae, Opiinae), *Aganaspis pelleranoi* (Brèthes) (Figitidae, Eucoilinae), *Trichopria anastrephae* Lima (Diapriidae, Diapriinae) and an unidentified species of Pteromalidae.

D. areolatus was the most abundant parasitoid species (61.8% of all recovered parasitoids). Its greater relative abundance was previously reported by Aguiar-Menezes & Menezes (1997) collecting in Itaguai city, Rio de Janeiro and by Canal et al. (1995), Leonel Junior et al. (1995) and Matrangolo et al. (1998) collecting in other parts of Brazil. This species is one of the most common and widespread native parasitoids of *Anastrepha* in the New World, ranging from Mexico to Argentina (Wharton & Marsh 1978; Baranowski et al. 1993; Aluja et al. 1990; Katiyar et al. 1995; López

et al. 1999). *Utetes anastrephae* and *O. bellus* comprised 27.2 and 8.7% of all parasitoids recovered, respectively. *A. pelleranoi* and *T. anastrephae* were rarely encountered during this study. The few specimens of these species represented only 1.8 and 0.3% of all parasitoids, respectively.

D. areolatus also exhibited the broadest host range. It attacked larvae of all five *Anastrepha* species recovered and foraged for hosts in all of the plant species sampled (Table 1). The other parasitoid species were also generalists (i.e., attacking multiple fly species often in multiple hosts), with the exception of *T. anastrephae*, which was observed only in association with *A. fraterculus* in hog-plum. Lima (1962) had previously reported *A. fraterculus* as the host of *T. anastrephae*. We found *O. bellus* in association with *A. fraterculus* and *A. sororcula* in Surinam cherry. *Utetes anastrephae* and *A. pelleranoi* were associated with *A. fraterculus*, *A. sororcula* and *A. obliqua* in different host plants. Arrigoni et al. (1987), Leonel Junior (1991), Leonel Junior & Zucchi (1993), and Aguiar-Menezes & Menezes (1997) also identified the same guild of three species of Braconidae as parasitoids of *A. fraterculus, A. sororcula* and *A. obliqua*.

There was little or no host plant preference shown by *A. pelleranoi* and the opiine parasitoids. They attacked larvae in different plant species, as has also been observed by Hernandez-Ortiz et al. (1994), Ovruski (1994), Wharton et al. (1981) and López et al. (1999). However, we also found that the recovered parasitoid species differed in relative abundance among the different fruit species sampled (Table 2). Apparently, they were influenced by fruit characteristics, such as size, pulp depth and rind thickness.

In general, the recovered parasitoid species occurred in greater number in plant species with smaller fruits, such as Surinam cherry, Brazilian cherry and Spanish prune (Table 2). According to Leonel Junior (1991) and Sivinski (1991), smaller fruits with thin pulps and skins have a higher parasitism of fruit flies because the chances of the parasitoid finding and attacking the larva are greater. In larger fruits, the tephritid larvae receive protection against parasitoid attack by being sheltered under a great amount of pulp. Lathrop & Newton (1933), Lawrence (1981) and Glas & Vet (1983) reported that the opiines *Opius mellus*, *Diachasmimorpha longicaudatus,* and *Opius alloeum* find their host by vibrotaxis (larval movement). Per-

TABLE 1. RELATIONSHIP BETWEEN FRUIT FLIES, HOST PLANTS AND PARASITOIDS IN SEROPEDICA CITY, RIO DE JANEIRO, BRAZIL THROUGHOUT 1997-1999.

Parasitoids	Species of *Anastrepha*	Fruit host
Braconidae (Opiinae)		
D. areolatus	*fraterculus*	hog-plum, Spanish prune, guava, jaboticaba, Surinam cherry, Brazilian cherry, carambola, loquat, abiu, tropical almond
	obliqua	mango, hog-plum, Spanish prune, guava, jaboticaba, Brazilian cherry, carambola
	sororcula	mango, guava, jaboticaba, Surinam cherry, Brazilian cherry, carambola
	serpentina	abiu
	distincta	inga
U. anastrephae	*fraterculus*	Spanish prune, guava, jaboticaba, Surinam cherry, Brazilian cherry, carambola
	obliqua	mango, Spanish prune, Brazilian cherry, carambola
	sororcula	mango, Spanish prune, guava, Surinam cherry, Brazilian cherry, carambola
O. bellus	*fraterculus*	Surinam cherry
	sororcula	Surinam cherry
Figitidae (Eucoilinae)		
A. pelleranoi	*fraterculus*	Surinam cherry, Brazilian cherry, carambola
	obliqua	carambola
	sororcula	Brazilian cherry
Diapriidae (Diapriinae)		
T. anastrephae	*fraterculus*	hog-plum
Pteromalidae		
sp. indeterminate	*fraterculus*	hog-plum, carambola

TABLE 2. THE NUMBER AND THE RELATIVE ABUNDANCE OF PARASITOIDS IN THE DIFFERENT TEPHRITID HOST FRUIT SPECIES SAMPLED IN SEROPEDICA CITY, RIO DE JANEIRO, BRAZIL, DURING 1997-1999.

Plant species (fruit no.)	Total of recovered parasites	Parasitoid species[1] and number of specimens (Relative abundance in %) in the fruit samples					
		Da	Ua	Ob	Ap	Ta	P
Exotic:							
M. indica (143)	19	19 (100)	—	—	—	—	—
E. japonica (330)	14	14 (100)	—	—	—	—	—
T. catappa (109)	18	18 (100)	—	—	—	—	—
A. carambola (144)	21	12 (57.1)	6 (28.6)	—	2 (9.5)	—	1 (4.8)
Native:							
I. affinis (179)	41	41 (100)	—	—	—	—	—
P. caimito (188)	49	49 (100)	—	—	—	—	—
M. cauliflora (302)	93	58 (62.4)	35 (37.6)	—	—	—	—
P. guajava (112)	32	19 (59.4)	13 (40.6)	—	—	—	—
E. uniflora (367)	290	19 (100)	62 (21.5)	107 (37.0)	4 (1.0)	—	—
E. braziliensis(390)	377	117 (40.5)	194 (51.5)	—	16 (4.2)	—	—
S. purpurea (330)	237	167 (44.3)	25 (10.5)	—	—	—	—
S. mombim (126)	43	212 (89.5)	—	—	—	4 (9.3)	2 (4.7)
Total (2,720)	1,234	763	335	107	22	4	3

[1]Da = *D. areolatus,* Ua = *U. anastrephae,* Ob = *O. bellus,* Ap = *A. pelleranoi,* Ta = *T. anastrephae*, and P = Pteromalidae.

haps vibrations produced by larvae feeding inside the fruit could be more easily perceived by parasitoid females in smaller fruits than in larger ones. However, the eucoilid *A. pelleranoi* enters previously existing holes in fruits to search for host larvae within the pulp (Ovruski 1994), and may not be as affected by fruit size as the braconids, which remain on the fruit surface and reach the host larvae inside the fruit with their ovipositor.

Of all the parasitoids recovered, *D. areolatus* was the species which occurred most frequently in all fruit species sampled, except in Brazilian cherry (Table 2). In some fruit species, it was the only braconid species recovered. This may be due to a relatively long ovipositor that allows it to reach larvae in both large and small fruits (see Gonçalves 1938, Matrangolo et al. 1998, Sivinski et al. 1997). On the other hand, *O. bellus* with the shortest ovipositor (only 0.68 ± 0.05 times longer than the gaster), and *U. anastrephae*, whose ovipositor is 0.81 ± 0.06 times the length of the gaster (Leonel Junior 1991), were more abundant in a narrow range of smaller fruits. *Doryctobracon areolatus*, which has the longest ovipositor of the species collected (2.04 ± 0.32 times longer than the gaster) (Leonel Junior 1991), became more efficient relative to co-occurring parasitoids as the size of fruits increased. In our study, *U. anastrephae* was relatively more abundant than *D. areolatus* only in Brazilian cherry, the smallest fruit sampled. As discussed by Sivinski et al. (1997), the native parasitoid species have interacted over a long period, and as a result their niches may have diverged. Besides ovipositor length, another factor may contribute to the competitiveness of *D. areolatus.* According to Matrangolo et al. (1998), *D. areolatus* is able to parasitize larvae of both second and third instars, while *U. anastrephae* and *Opius* spp. oviposit only in the last instar. This would allow *D. areolatus* to have access to larvae prior to the other parasitoids.

We also observed that the native parasitoid species from our study areas preferentially attacked *Anastrepha* larvae in native, wild fruit spe-

cies (Table 2). More than 90% of all the parasitoids were recovered from native fruits. According to Lopéz et al. (1999), a switch from a native plant to an exotic one has interesting evolutionary and ecological implications because it probably allows fruit flies to escape parasitism. In their study in Veracruz, Mexico, it was observed that the parasitism in native hog-plum fruits placed at ground level was 80% compared to 18.2% in similarly treated mangos. The latter are both larger (up to 270 times larger than hog-plum) and exotic fruits.

One practical consideration that can be drawn from our study is that the low host specificity showed by the native parasitoid species suggests that their augmentation to control a particular species of pest fruit flies may be less effective than expected because they will forage on non-target species. On the other hand, according to M. Aluja and J. Sivinski (pers. comm.), since they attack hosts in a wide variety of plant species, and certain wild, native plants usually yield significant numbers of parasitoids, these plants serve as parasitoid reservoirs, particularly if they harbor non-pest tephritids. Such plants and associated insects could be managed to naturally augment parasitoid numbers and to sustain parasitoid populations in commercial orchards and in adjacent native vegetation (see also López et al. 1999; Aluja 1999). If so, a major challenge will be to develop vegetational designs that optimize pest regulation. This difficulty will only be overcome by further analyses of the nature and dynamics of the tritrophic relationships. Aluja (1996) has recently provided a detailed discussion on habitat manipulation (e.g., orchard design and trap-cropping scheme) as an alternative fruit fly management strategy. Such an approach was successfully tested by Aluja et al. (1997) with *Toxotrypana curvicauda* in papaya groves.

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KALOTERMES APPROXIMATUS HABITAT IN SOUTH CAROLINA

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ABSTRACT

Kalotermes approximatus (Snyder) habitat was studied in South Carolina. This species was found in live and dead, standing, hardwood trees. Height and girth of infested trees were variable with a mean (±SD) of 11.51 ± 7.41 m and 72.60 ± 41.41 cm, respectively. Moisture content was the only measured parameter that was predictable at 23.74 ± 5.05%. Ten of the 19 (52.6%) trees infested with *K. approximatus* had tree holes. Tree holes were on the southwest, south, southeast, or east side of the tree. *Kalotermes approximatus* is not a common species in South Carolina. Approximately 1200 trees having characteristics similar to the 19 infested trees were inspected without positive results.

Key Words: Drywood termites, Kalotermitidae, Isoptera

RESUMEN

El hábitat de *Kalotermes approximatus* (Snyder) fue estudiado en Carolina del Sur. Esta especie fue encontrada en árboles verticales, de madera dura, vivos y muertos. La altura y circunferencia de árboles infestados fueron variables con un promedio ±DS de 11.51 ± 7.41m y 72.60 ± 41.41 cm, respectivamente. El contenido de humedad fue el único parámetro medido que fue consistente a 23.74 ± 5.05%. Diez de los 19 árboles infestados con *K. approximatus* tenían huecos de árbol. Huecos de árbol estaban al suroeste, sur, sureste, o lado este del árbol. *Kalotermes approximatus* no es una especie común en Carolina del Sur. Aproximadamente 1200 árboles con características similares a los árboles infestados fueron inspeccionados sin obtener resultados positivos.

Little is known about the ecology and behavior of the drywood termite, *Kalotermes approximatus* (Snyder). This species was first described from a soldier found in northern Florida (Banks and Snyder 1920). A dealated adult found in a dead bald cypress tree from Cape Henry, Virginia was described in 1924 (Snyder). Snyder (1925) later provided a complete description of a winged *K. approximatus* adult, also collected in Virginia. This species is now recorded in coastal areas of the southeastern United States from Virginia to Florida, and along the Gulf Coast to New Orleans, Louisiana (Potter 1997).

Ecological studies on *K. approximatus* are limited to reports of types of trees in which they are found (Table 1). Nalepa (1998) reported the distribution of *K. approximatus* in North Carolina based on extension records. From these extension records, this species is known to infest dead or damaged trees, primarily hardwood. It is unknown if termites caused the initial damage or if damage was pre-existing. A record as far inland as Charlotte, NC is also reported. This is significant because all previous records in the U.S. were from coastal areas. This species is not considered a major pest, however it does occasionally infest structures (Potter 1997).

This research was conducted as part of a larger study to catalog the termite fauna and their distribution in South Carolina (Hathorne et al. 2000). Only three *K. approximatus* records for the state were held in the Clemson University Arthropod Collection (CUAC) when this project began. None of the records had accompanying habitat data. The purpose of this research was to describe the habitats in which *K. approximatus* was found. Emphasis was placed on infested tree species, size and condition, and moisture content.

MATERIALS AND METHODS

Kalotermes approximatus was collected from various wooded areas in South Carolina. A systematic grid sampling scheme was originally attempted but proved to be ineffective. Many of the randomly selected grids were located on properties that were inaccessible or impractical to survey. Sites were selected by driving on major highways and stopping periodically to search in accessible wooded areas. These included state parks, frontage roads, campgrounds, and private properties located, in most cases, within five miles of a major highway. Approximately 40 sites were sampled in 27 counties.

Termite presence was indicated by large galleries packed with frass (Snyder 1924) and large worker castes. The workers were similar in size and appearance to pre-alates of *Reticulitermes fla-*

TABLE 1. PUBLISHED RECORDS OF TREE SPECIES INFESTED BY *KALOTERMES APPROXIMATUS* (SNYDER).

Tree species	Location	Reference
Walnut—*Juglans nigra* L.	North Carolina	Nalepa 1998
Red Cedar—*Juniperus virginia* L.	North Carolina	Nalepa 1998
Sweet Gum—*Liquidambar stryaciflua* L.	Florida	Banks and Snyder 1920
	Florida	Miller 1949
Magnolia—*Magnolia spp.*	Florida	Miller 1949
Cherry—*Prunus serotina* Ehrh	Florida	Hetrick 1961
Pear—*Pyrus communis* L.	Florida	Hetrick 1961
White Oak—*Quercus alba* L.	North Carolina	Nalepa 1998
Oak—*Quercus spp.*	Florida	Miller 1949
Bald Cypress—*Taxodium distichum* L.	Virginia	Snyder 1925
Elm—*Ulmus spp.*	North Carolina	Nalepa 1998

vipes (Kollar), the Eastern subterranean termite, but did not have wing pads. Once an infested tree was found, soldiers or alates were collected, and placed in a plastic, 2-dram vial containing 95% ethanol. Date, location, and sample number were recorded and also placed into each vial. Leaves, if available, were collected to determine tree species. Samples were returned to Clemson University for identification. Global Positioning System (GPS) coordinates (longitude/latitude) were recorded using a Garmin® GPS 12 Personal Navigator™ (Garmin International, Inc., Olathe, KS 66062) which has an accuracy of 1-5 M.

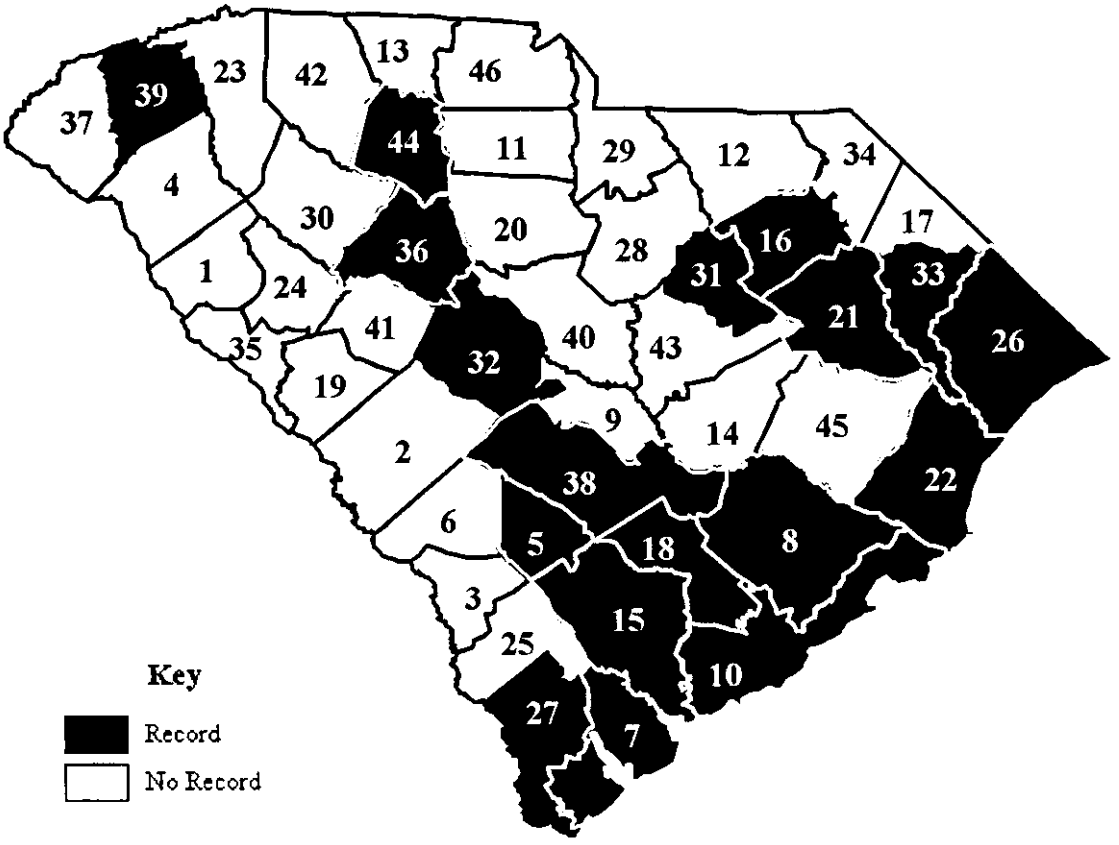
Measurements of infested trees included location, tree species, height, girth, and position of damaged area, if applicable. Tree height was estimated with a tangent height gauge (Kager Inc. Lunenburg, MA). Tree girth and damaged area were measured. A compass was used to determine the ordinal position of the tree hole. A single reading of moisture content of the damaged area was taken using a Protimeter® Minor IV (Marlow, Bucks. SL7 1LX, England). The variability of moisture meter readings is unknown, but may be influenced by wood type, ambient temperature and other unidentified factors. Vegetation surrounding infested trees was evaluated on a scale of 1-3; 1 = little to no surrounding vegetation, sporadic spacing of trees, 2 = some surrounding trees and little underbrush, and 3 = heavy underbrush. Voucher specimens were deposited in the CUAC. GPS data labels were included.

RESULTS AND DISCUSSION

A total of 19 infested trees were found after searching in 27 counties (Hathorne et al. 2000). *Kalotermes approximatus* was found in 16 of those counties (Fig. 1). Counties in which sampling occurred, but *K. approximatus* was not found include Anderson, Beaufort, Cherokee, Greenville, Hampton, Kershaw, Laurens, Oconee, Pickens, Richland, and Spartanburg Counties in South Carolina. We are not implying that *K. approximatus* does not occur in counties in which we did not find it, nor that it does not occur outside the area sampled. Table 2 gives tree species from which *K. approximatus* were collected. Of the trees infested, 13 (68%) were alive and 6 (32%) were dead snags. Snags are defined as standing dead trees with few to no limbs, leaves, or top. Tree height ranged from 1.36 to 22.86 m. Average tree height (±SD) was 11.51 ± 7.41 m. Tree girth ranged from 2.82 to 157.48 cm. Average tree girth (±SD) was 72.60 ± 41.41 cm. Moisture content ranged from 13 to 29%. Average moisture content (±SD) was 23.74 ± 5.06% at damaged area.

Tree holes were present in ten (52.6%) of the infested trees that were still alive. Tree hole height ranged from 6.40 to 39.37 cm. Tree hole width ranged from 15.00 to 188.00 cm. Average tree hole height (±SD) was 17.28 ± 11.50 cm. Average tree hole width (±SD) was 56.60 ± 52.26 cm. The positions of the tree holes were southwest (1), south (2), southeast (4), and east (2). Eleven (58%), six (32%), and two (10%) samples had surrounding vegetation levels of 3, 2, and 1, respectively.

A description of *K. approximatus* habitat becomes more clear when observations from sampled areas that did not produce *K. approximatus* are included. This termite species was not common in the areas sampled. Approximately 330 person-h were spent searching areas in 27 counties in South Carolina. Many potential habitats were explored. Approximately 1200 trees were sampled. Data on location, tree species, height, girth, and position of damaged area were not taken on trees not infested. All samples collected were from hardwood trees, although other tree species (about 30%) such as Pine (*Pinus* spp.), Palm (*Sabal palmetto* (Walt.)), Conifers (*Juniperus* spp.), and Rhododendrons (*Rhododendron* spp.) were sampled. The exact number of each sampled tree species is unknown. Other sampled habitats include large vines and galls. Felled trees also were examined, but all specimens found were from standing, live or dead trees.



Counties

1	Abbeville	9	Calhoun	17	Dillon	25	Hampton	33	Marion	41	Saluda
2	Aiken	10	Charleston	18	Dorchester	26	Horry	34	Marlboro	42	Spartanburg
3	Allendale	11	Chester	19	Edgefield	27	Jasper	35	McCormick	43	Sumter
4	Anderson	12	Chesterfield	20	Fairfield	28	Kershaw	36	Newberry	44	Union
5	Bamberg	13	Cherokee	21	Florence	29	Lancaster	37	Oconee	45	Williamsburg
6	Barnwell	14	Clarendon	22	Georgetown	30	Laurens	38	Orangeburg	46	York
7	Beaufort	15	Colleton	23	Greenville	31	Lee	39	Pickens		
8	Berkeley	16	Darlington	24	Greenwood	32	Lexington	40	Richland		

Fig. 1. Known distribution of *Kalotermes approximatus* (Snyder) in South Carolina by county.

Tree holes of many different sizes were examined; those that contained termites had a height ≥6.0 cm and a width ≥15.0 cm. The range of these measurements was due to the varied habitats from which they were taken. All tree holes were facing southern positions between east and southwest. Perhaps position of the tree hole with regard to amount of sunlight or rainfall from the prevailing southwestern direction affects termite presence, but the true significance is unknown. Some *K. approximatus* specimens were found living in close proximity to subterranean termites (*Reticulitermes* spp.) (2), black carpenter ants (*Camponotus pennsylvanicus* (De Geer)) (2), and an undetermined ant species (1).

SUMMARY

Kalotermes approximatus collected from standing, live or dead hardwood trees occurred most frequently (63%) in Oak (*Quercus* spp.). If tree holes were present, they measured larger than 6.0 cm × 15.0 cm and were facing east, southeast, south, or southwest. Average tree height and

TABLE 2. SPECIES OF TREES INFESTED WITH *K. APPROXIMATUS* IN SOUTH CAROLINA IN 1999.

Tree species	Condition	Number of samples
Dogwood (*Cornus* spp.)	alive	2
Maple (*Acer* spp.)	alive	1
Water Tupelo (*Nyssa aquatica* L.)	alive	1
Sweet Gum (*Liquidamber styraciflua* L.)	alive	1
Water Oak (*Quercus nigra* L.)	alive	1
Laurel Oak (*Quercus laurifolia* Michx.)	alive	1
Virginia Live Oak (*Quercus virginiana* Mill.)	alive	1
Post Oak (*Quercus stellata* Wangenh.)	alive	1
undet. Oak (*Quercus* spp.)	alive	4
undet. Oak (*Quercus* spp.)	dead	4
undetermined	dead	2

girth, and tree hole width and height, were not dependable indicators of *K. approximatus* habitat because of their large standard deviations. The average moisture content was relatively stable and may be an important characteristic in providing *K. approximatus* suitable habitat.

None of the characteristics measured guaranteed termite presence. Many trees were sampled that had these characteristics (approximately 1200), or similar ones, and yet termites were found in only 1.6% of those sampled. Some sampled trees appeared to have damage made by *K. approximatus*, but no termites were found. Also, termites may have been present, but deep in the wood and inaccessible.

A more in-depth study should be conducted to include comparisons of trees having *K. approximatus* and trees that do not. Research into cohabitation with other insect species, flight and dispersal patterns, and substrate preference are all possible areas for investigation.

ENDNOTE

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MASS REARING OF *ANASTREPHA FRATERCULUS* (DIPTERA: TEPHRITIDAE): A PRELIMINARY STRATEGY

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The South American fruit fly, *Anastrepha fraterculus* (Wiedemann), occurs from Mexico to Argentina and attacks some 80 species of host plants, including mango, citrus, guava, apple and coffee (Da Silva et al. 1996). In extensive fruit producing regions of Uruguay, Argentina and Peru, the only two fruit fly species of economic and quarantine importance are *A. fraterculus* and the introduced Mediterranean fruit fly, *Ceratitis capitata* (Wiedemann) (Manso & Lifchitz 1992). Unfortunately, there is as yet no environmentally friendly and effective strategy as Sterile Insect Technique (SIT) to use against *A. fraterculus.* If no reliable and economic methods were found, any possible benefits from *C. capitata* control in areas where it is sympatric with *A. fraterculus,* would be greatly reduced. The ability to mass-rear *A. fraterculus* is the key to development of SIT. At the *A. fraterculus* mass rearing Workshop held in 1996 at Viña del Mar, Chile, various participants from Argentina, Brazil, Colombia and Peru reported on their efforts to rear this fruit fly under laboratory conditions (Ortiz 1999). It was agreed that the main limiting factor to successful mass rearing was the need to develop a technique that would promote effective oviposition, facilitate collection of the eggs, and assure maximum fertility of the eggs (Salles 1992, 1999)

Here we describe a new method to potentially mass-rear *A. fraterculus* that produces high egg fertility and allows eggs to be collected easily with a minimum handling.

REARING ROOM: Rearing conditions were 23 ± 2°C and 60-80% R.H., light intensity ranged from 4,000 to 5,000 lx, with a photoperiod of 12:12 (L:D).

CAGES: The colony was kept in iron-framed cages (0.96 × 0.60 × 0.30 m), with a front and rear panel. The rear panel was covered with a fabric (voile) with 25 holes per linear centimeter. The front panel was made of the same fabric coated with a thin layer of transparent silicon rubber (0.5 mm thickness). This panel is very similar to that used for *A. obliqua* in Mexico (Dominguez, 1998). One or 2 days before emergence, 8,500 pupae were placed in each cage. After 10-14 days adults mated and begun oviposition. Adults were kept in the cages for 40 days.

EGG COLLECTION: Females laid their eggs through the oviposition panels onto foam rubber sheets (0.01 × 0.90 × 0.60 m), which were moistened with a mixture of water and peach juice (3:1) to avoid the dehydration and to attract females to oviposit. After 24 h the foam rubber sheets were taken out and washed in water to collect the eggs. The eggs were placed in a wet chamber (petri dishes with wet filter paper in the bottom) and kept at a temperature of 23-26°C until hatching. After 48 h the eggs began to hatch.

LARVAL DEVELOPMENT: The diet described by Salles (1992) was used with the addition of streptomycin sulfate at rates of 1 g per thousand to avoid bacterial contamination. Two hundred grams of diet was poured over the trays (18 × 12 cm) 2 cm deep. After 48 h the eggs were placed on the larval diet at a density of 8 to 10 eggs per gram of diet. The trays were placed in racks and covered with a fine voile mesh to prevent contamination by *Drosophila* spp. Wet sand was incorporated in the bottom of the racks. The larvae developed in the diet and, 16 days later, they crawled out of the trays and buried in the sand to pupate.

PUPATION: The pupae were collected and maintained, in a small container with sterilized wet sand. Fifteen days later they were introduced in cages to begin a new cycle.

ADULTS: Adults were maintained on a mixture of yeast hydrolyzed enzymatic 10 g; corn protein 10 g; sugar 40 g; water 50 ml; vitamins (Dayamineral, Abbott) 500 mg; aminoacids (Aminocefa 5%, Roux Ocefa) 1 ml. Water was also supplied to the adults.

This rearing has been carried out over 18 generation (F18) without problems.

QUALITY CONTROL: The quality of insects was assessed using some of standard quality control based in IAEA, USDA, FAO Quality Control publication (IAEA, USDA, FAO. 1998) and Orozco et al. (1983).

REARING PARAMETERS: Results of tests mentioned above are shown in Table 1.The main differences between our rearing technique and 3 previously published methods are shown in Table 2. The four rearing techniques used different oviposition devices. Nuñez & Guzman (1999) and Salles (1992, 1999) used colored hemispheres or domes to attract the female fruit flies and to stimulate oviposition, but they had to be placed inside the cage, which made handling difficult. Using

TABLE 1. REARING PARAMETERS OF THREE GENERATION TAKEN IN ACCOUNT TO EVALUATE REARING OF *ANASTREPHA FRATERCULUS*, TEST WITH EXPERIMENTAL DIET MENTIONED IN A TEXT.

Parameters	F3	F8	F12
Fertility (%)	84 ± 5.3*	75 ± 3.8	81 ± 2.4
Egg-pupa recovery (%)	44.9 ± 7.05	48.6 ± 3.0	46 ± 5.2
Weight of 100 pupae (g)	1.8 ± 0.2	1.5 ± 0.2	1.4 ± 0.3
Adult emergence (%)	68.5 ± 19.62	61 ± 15.9	65 ± 12.3
Male:female ratio	1:0.98	1:1.51	1:1.23

*Average ± SD.

oviposition panels (as in Gonzalez et al.1971, and our technique), allowed a much easier egg collection from outside the cages. In our case, collecting the eggs on rubber foam sheet kept the eggs hydrated, and improved egg hatch.

All adult diets used similar ingredients, a protein source plus sugar, but we found that the combination of hydrolyzed protein and corn protein was the best for female fecundity and egg hatch (Table 2).

The pupal weight obtained was slightly lower than the one obtained in Colombia by Nuñez & Guzman (1999).

Survival from pupa to adult was significantly better in Peru (Gonzalez et al. 1971) and Colombia (Nuñez et al. 1999).

The survival rate from egg through to adult obtained in our rearing was 44%. In Colombia survival to the adult stage was only 9.5%. In Peru 50.5% survival was achieved in small scale laboratory rearing but when insect were mass reared, survival dropped to only 5.3%.

This rearing methodology results in a more efficient egg collection with a good survival rate through all life history stages. Future studies will have the focus on refining and improving this new methodology, and larger scale testing, following small-scale test replication.

We gratefully acknowledge the excellent suggestions and review by Dr. Pablo Liedo Fernández from Ecosur, México; Dr. Pablo Cancino and Biol. Emilio Hernández from MOSCAFRUT, CONASAG-DGSV, Mexico.

SUMMARY

A new technique for mass rearing *A. fraterculus* (Wiedemann) was developed. Use of silicon rubber on the cage wall encouraged oviposition and allowed and easy egg collection. When adults were reared on a diet of hydrolyzed enzymatic yeast and corn protein, females laid eggs with 83% successful development, which resulted in a feasible mass rearing process.

TABLE 2. COMPARISON BETWEEN OUR REARING TECHNIQUE AND THREE PREVIOUSLY PUBLISHED METHODS FOR *A. FRATERCULUS*.

	Salles (1992)	Gonzalez et al. (1971)	Nuñez and Guzman (1999)	Jaldo et al.
Oviposition devices	Fruit juices + agar covered with Parafilm	Red nylon cloth	Colored paraffin dome	Silicon white cloth
Adult diet	Hydrolyzed corn protein + brown sugar	Hydrolyzed brewers yeast + sugar	Hydrolyzed brewers yeast + Sugar	Hydrolyzed corn protein + sugar + hydrolyzed brewers yeast
Egg hatch %	20-70%	45%	66%	84%
Egg/Female	394	415	—	625
Larval diet basic ingredients	Brewers yeast wheat germ	Torula yeast carrot powder	Torula yeast wheat germ	Brewers yeast wheat germ
Pupal weight (100 pupae)	—	1.3 g	2.0 g	1.8 g
Pupal survival %	—	99.15%	76%	68.5%
Egg-Pupae Recovery %	—	5.3%	9.5%	44%

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DISCOVERY OF MACROPTERY IN *PSEUDOMETAPTERUS UMBROSUS* (HETEROPTERA: REDUVIIDAE)

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Pseudometapterus umbrosus (Blatchley) was described (as *Metapterus umbrosus*) in 1926 from Florida, apparently based on a single nonmacropterous male adult. It subsequently was transferred to the new genus *Pseudometapterus* by Wygodzinsky (1966) in his landmark revision of the emesine reduviids. He reported he had obtained information from R. Hussey who had examined the type and several additional specimens, apparently all from Florida [Wygodzinsky listed the species' distribution as "Southern United States (Florida)]." Hussey expanded Blatchley's description but apparently did not mention wing form. Although Wygodzinsky did not mention wing form specifically in his discussion of the species, he used "micropterous or apterous" as a diagnostic character in his key to separate four species, including *P. umbrosus*, from *P. obtusus* (Piza), which he called "winged."

McPherson (1991) reported the presence of *P. umbrosus* in southern Illinois based on two male adults collected on 27 July 1972 from the LaRue-Pine Hills Ecological Area (now LaRue-Pine Hills Natural Research Area) and housed in the Southern Illinois University Entomology Collection (SIUEC); both specimens are micropterous. Subsequently, Hagerty and McPherson (1999) reported that this species apparently is univoltine in southern Illinois and overwinters as adults. Further, it occurs on spider webs and plants (*Heuchera parviflora* Bartling) on sandstone bluffs and on spider webs on limestone bluffs. This information was based on 43 adults collected in Jackson and Union counties from April to November, 1996-1998, all of which are micropterous and also housed in the SIUEC.

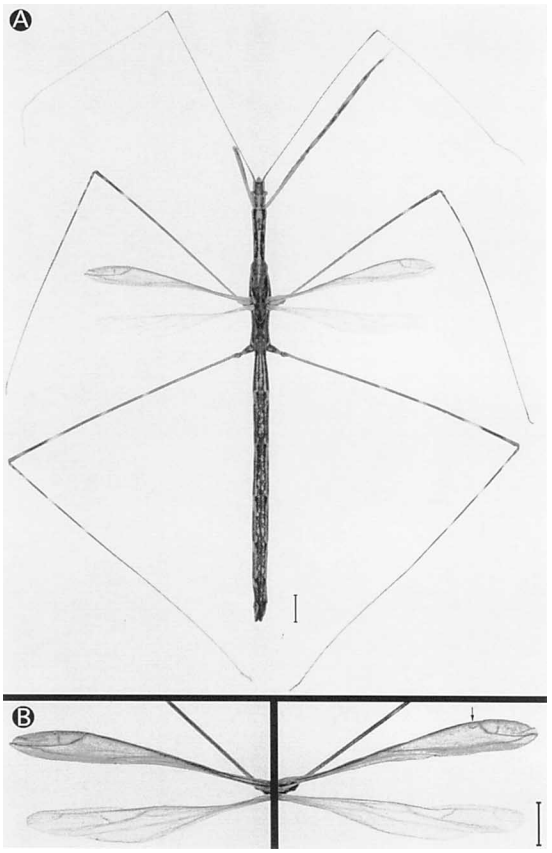

Fig. 1. *Pseudometapterus umbrosus.* A, Macropterous female. B, Closeup of wings (note extra vein [arrow] in right hemelytron). Scale bar equals 1.0 mm.

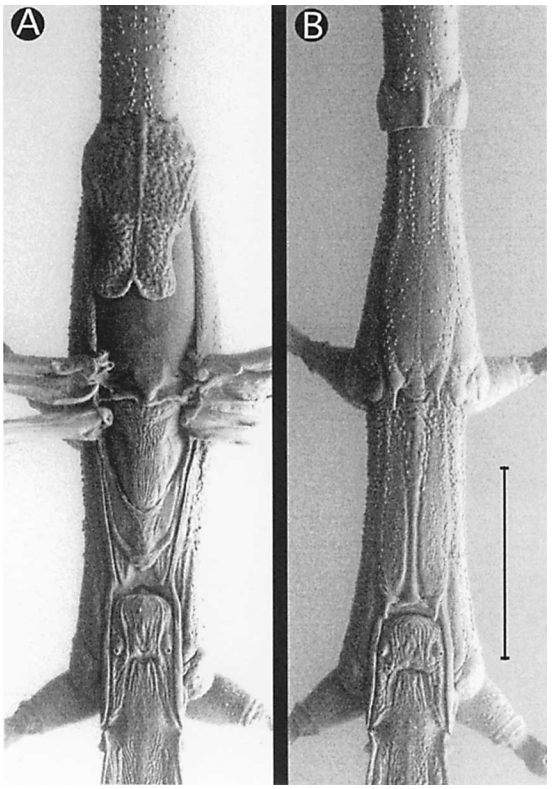

Fig. 2. *Pseudometapterus umbrosus*, pterothorax. A, Macropterous female. B, Micropterous female. Scale bar equals 1.0 mm.

From February 1999 to November 2000, a more detailed study of the biology of this emesine was conducted at Little Grand Canyon, Jackson County, including life history, laboratory rearing, and descriptions of the immature stages. The study site involved two small areas (14 × 2.4 m, 20 × 2.4 m) separated by approximately 140 m. Thirty-nine adults were collected, all of which are micropterous. An additional 790 observations were made on adults that were not collected. Even though some of these observations undoubtedly involved the same individuals because the study site is small, it is significant that, with only one exception, none of the adults is macropterous.

The exception, a macropterous female, was collected on 12 August 2000 (Fig. 1A and B). It was perched on the rock face amidst several other specimens. Interestingly, its pterothorax (Fig. 2A) shows more development than that of the typical micropterous specimen (Fig. 2B). In addition, there is a slight difference in the venation between the forewings; the right hemelytron has what appears to be an extra vein (Fig. 1B). The specimen is housed in the SIUEC.

SUMMARY

Macroptery in *Pseudometapterus umbrosus* is reported for the first time, based on a female specimen collected in southern Illinois.

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LANDSCAPE FABRIC AS A PHYSICAL BARRIER TO NEONATE *DIAPREPES ABBREVIATUS* (COLEOPTERA: CURCULIONIDAE)

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There are few options available to Florida producers of citrus and ornamentals for control of root-feeding weevils such as the Diaprepes root weevil, *Diaprepes abbreviatus* (L.). Currently, there is no recommended method for control of the soil-borne larvae of *D. abbreviatus* (Futch et al. 2001). Foliar sprays for control of adults have not been shown to be effective in reducing larval damage. While entomopathogenic nematodes may be effective in reducing larval populations (Bullock et al. 1999), their use is problematic due to complications of formulation, delivery, and application. Increasing damage from *D. abbreviatus* and recent recalls of a defective commercial nematode product underline the precarious situation for growers and the need for new control options.

Adult *D. abbreviatus* and other weevils such as species of *Artipus* and *Pachnaeus*, oviposit by cementing eggs in a layer between leaves or other surfaces. Neonate larvae fall to the ground, burrow into the soil and feed on progressively larger roots as they grow. A physical barrier to prevent neonate larvae from reaching tree roots could be an effective, nontoxic control of root weevils as well as potentially providing a number of collateral benefits to citriculture. If technically viable in groves, a properly designed barrier could offer multiple returns on initial investment over several years including effective, long-term, nonchemical control of root-feeding weevils; reduced use of irrigation water and pump energy; nonchemical weed control; and reduction of soil erosion. In this study we determined the ability of neonate *D. abbreviatus* larvae to penetrate a range of commercially available weed cloth fabrics in controlled laboratory experiments.

Weed cloth was purchased from local retailers and included Weed-X and Weed Proof (Dalen Products Inc., Knoxville, TN), and Weed Block and Commercial Landscape Fabric (Easy Gardener Inc. Waco, TX). Further fabric samples were obtained from Dalen Products Inc. and Synthetic Industries, Gainesville, GA. During the course of the experiment, the Weed-X product name was discontinued by the manufacturer and replaced by the similar Weed Shield and Professional Weed-X products. Organdy cloth (1 mm mesh openings) was used as a control for all trials. Neonate *D. abbreviatus* were obtained from a laboratory colony maintained at the U.S. Horticultural Research Laboratory, Ft. Pierce, FL (Lapointe and Shapiro 1999; Lapointe 2000). All experiments were conducted at a constant temperature of 26 ± 1°C in growth chambers with a photoperiod of 14:10 L:D.

The test apparatus consisted of two plastic containers joined by a plastic collar (Magenta GA-7-3 vessel, Magenta Corp., Chicago, IL). The fabrics to be tested (Table 1) were placed between the chambers and sealed at the edges by the collar. The upper surface of the fabric was covered with 10 mm of sterilized sandy soil. Forty neonates (12-36 h old) were released in the upper chamber and observed at 24 h intervals. Neonates that penetrated the barrier were collected in the lower chamber.

The spun polyester/polyolefin bi-layer products were very effective barriers to neonate penetration (Table 2). These products are continuous films designed to be water permeable but without large pores that would allow neonate passage. The plastic films have varying densities of perforations (0.5 mm diam) equal to or slightly larger than the width of the head capsule of neonates (Quintela et al. 1998) that permitted penetration of 50 to 75% of neonate *D. abbreviatus*. Two prod-

TABLE 1. DESCRIPTION AND SOURCE OF WEED CLOTH PRODUCTS TESTED.

Product Name	Description	Source
Weed-X	Spun polyester/polyolefin film bi-layer	Dalen Products Inc., Knoxville, TN
Weed Proof	Perforated film	Dalen Products, Inc.
Weed Shield	Spun polyester/polyolefin film bi-layer	Dalen Products Inc.
Professional Weed-X	Spun polyester/polyolefin film bi-layer	Dalen Products Inc.
Weed Block	Perforated polyolefin film	Easy Gardener Inc., Waco TX
Commercial Landscape Fabric	Spun-bonded polyester	Easy Gardener Inc.
Lumite 994GC	Woven polyester	Synthetic Industries, Gainesville, GA

TABLE 2. MEAN NUMBER (±SE) AND % PENETRATION BY NEONATE *D. ABBREVIATUS* LARVAE THROUGH 7 COMMERCIALLY AVAILABLE WEED CLOTH FABRICS.

Product	No. of neonates (% penetration)	
	24 h	48 h
Trial 1		
Weed-X	0.1 ± 0.1 (0.3) a	0.1 ± 0.1 (0.3) a
Commercial Landscape Fabric	3.7 ± 1.9 (9.2) a	4.2 ± 2.3 (10.6) a
Weed Proof	17.6 ± 1.3 (43.9) b	21.7 ± 1.7 (54.2) b
Weed Block	29.6 ± 2.9 (73.9) c	30.8 ± 3.1 (76.9) c
Control	26.3 ± 2.2 (65.8) c	32.6 ± 2.0 (81.4) c
Trial 2		
Weed Shield	0.0 ± 0.0 (0.0) a	0.0 ± 0.0 (0.0) a
Professional Weed-X	0.0 ± 0.0 (0.0) a	0.1 ± 0.1 (0.4) a
Lumite 994GC	0.6 ± 0.3 (1.5) a	1.1 ± 0.5 (2.9) a
Control	29.0 ± 2.5 (72.5) b	27.0 ± 2.1 (67.5) b

Means followed by the same letter within trials do not differ significantly at $\alpha = 0.05$ (Ryan-Einot-Gabriel-Welsch Multiple Range Test).

ucts were intermediate in that they reduced penetration compared with the organdy cloth control of the perforated plastic films, but allowed some neonates to pass through them. One of these (Commercial Landscape Fabric) consisted solely of spun-bonded polyester. This product is a mesh of polyester fibers that allowed neonates to burrow through. The second (Lumite 994GC) was a surprisingly efficient barrier compared with the continuous film products even though Lumite 994GC is woven with openings of varying size between the plastic strands.

Issues of cost and methods of field deployment remain to be addressed. These will determine whether landscape fabrics are economically viable alternatives for control of root weevils.

SUMMARY

The spun polyester/polyolefin bi-layer products acted as a physical barrier to *Diaprepes* by preventing downward penetration by neonate larvae in laboratory experiments. If issues of cost and field deployment can be resolved, landscape fabric has potential as a component of an integrated approach to control of root weevils. Mention of a trademark or proprietary product does not constitute a guarantee or warranty of the product by the U.S. Department of Agriculture and does not imply its approval to the exclusion of other products that may also be suitable.

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ADDITIONAL FLORIDA RECORDS OF THE SELDOM-COLLECTED *LASIOMERUS ANDABATA* (HEMIPTERA: NABIDAE)

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Information on the distribution and biology of North American nabids is most extensive for species associated with agroecosystems (Henry & Lattin 1988; Lattin 1989; Braman 2000). For example, *Nabis alternatus* Parshley, *N. americoferus* (Carayon), *N. roseipennis* Reuter, and *N. rufusculus* Reuter are well-studied generalist predators that help suppress pests of alfalfa, cotton, soybean, and other crops (e.g., Werner & Butler 1957; Braman 2000). In contrast, relatively little is known about the bionomics of nabids found outside managed systems. An obscure North American species is *Lasiomerus andabata* Kerzhner, known in the United States only from Florida. Torre-Bueno's (1912) record from Brownsville, Tex. (as *N. signatus* Uhler), as the first for North America, apparently refers to the nearly cosmopolitan *N. capsiformis* Germar (Harris 1928).

Kerzhner (1992) described *L. andabata* from Guatemala, Mexico, and the United States (Marion Co., FL), noting that this slender-bodied, usually brachypterous species has been confused with *L. signatus*, known from Central America, South America, and the West Indies, and with *L. spinicrus* Reuter, a Brazilian species. Thus, Blatchley (1926) reported *L. andabata* from Dunedin, FL, as the brachypterous form of *L. spinicrus*; seven adults were sifted from plant debris along the bay front and the border of a pond from 27 November to 17 April. The only other published U.S. record of this seldom-collected nabid is a female (paratype), taken on 5 June 1969, in the Ocala National Forest near Halfmoon Lake (Kerzhner 1992).

Here I provide new Floridian records of *L. andabata* based on specimens in the Florida State Collection of Arthropods, Gainesville (FSCA), and my recent collecting. Specimens that I collected are deposited in the National Museum of Natural History, Smithsonian Institution, Washington, D.C.

Material Examined. USA: Florida: Highlands Co., Rt. 70 near entrance to Hufty Tract, Archbold Biological Station, 9.3 km S of Lake Placid, 17-IV-1998, A. G. Wheeler, 2 ♀♀, 1 ♂; 17-III-1999, A. G. Wheeler, 3 ♀♀, 1 ♂, 1 nymph; Orange Co., Winter Park, 21-VII-1944, H. T. Fernald, 1 ♀ (FSCA); Polk Co., Bartow, Kissengen Springs, 15-II-1949, R. F. Hussey, 1 ♀ (FSCA); Rt. 27, 3.2 km S of Waverly, 18-IV-1998, A. G. Wheeler, 1 adult, sex unknown; St. Lucie Co., White City, 14-VII-1983, K. Hibbard, 1 ♀ (FSCA).

Material in the FSCA was determined as *Nabis spinicrus* Reuter by R. F. Hussey (1944 and 1949 specimens) and F. W. Mead (1983 specimen). The specimens I collected were beaten from the crowns of bushy beardgrass or bushy bluestem, *Andropogon glomeratus* (Walter, Britton, Sterns & Poggenburg; Poaceae). The plants in Highlands County grew along the road in dry, disturbed habitat; those in Polk County were in a wet ditch.

I thank Thomas J. Henry, Systematic Entomology Laboratory, USDA, Washington, D.C., for identifying *L. andabata*; Tom and Tomohide Yasunaga, Hokkaido University of Education, Ainosato, Sapporo, Japan, for companionship in the field; Rebecca Yahr, Department of Botany, Duke University, Durham, NC (formerly with the Archbold Biological Station, Lake Placid, FL), for identifying the grass *Andropogon glomeratus*; and Peter H. Adler, Department of Entomology, Clemson University, for reviewing a draft of the manuscript.

SUMMARY

The mostly neotropical nabid *Lasiomerus andabata* Kerzhner (Hemiptera: Nabidae), known previously in the United States from two localities in Florida, is recorded from five additional Floridian localities. In Highlands and Polk counties, brachypterous adults and a nymph were beaten from the crowns of *Andropogon glomeratus* (Walter) Britton, Sterns & Poggenburg (Poaceae).

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PERIGENES SIMILIS (HEMIPTERA: LYGAEOIDEA: RHYPAROCHROMIDAE) IN FLORIDA: NOTES ON HABITS AND HABITATS

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The myodochine rhyparochromid *Perigenes similis* Barber was described from a female collected at Brownsville, Tex. (Barber 1906). This relatively heavy-bodied myodochine (ca. 5.5-7.0 mm long) ranges in the eastern United States from central Virginia to Florida; west of the Mississippi River it is known from Iowa and Missouri west to New Mexico and Texas (Ashlock & Slater 1988; Slater & Baranowski 1990; Hoffman 1996). Slater and Baranowski (1990) analyzed the distribution of Floridian Lygaeoidea and categorized *P. similis* as a "southern U.S. species, including the Southwest," an element comprising only 6% of the state's lygaeoid fauna.

Perigenes similis can be distinguished from the more northern and morphologically similar *P. constrictus* (Say) by the second antennomere being subequal in length to the fourth antennomere (in *P. constrictus* antennomere II is 1.5 times longer than antennomere IV) (Slater & Baranowski 1990). Hoffman (1996), however, pointed out that the second antennomere can be as much as 1.2 times the length of the fourth in *P. similis* and that relative lengths of the antennal segments are not always reliable in distinguishing the two species. Males of *P. similis* have uniformly yellow femora, whereas males of *P. constrictus* have the profemora and apical fourth of the metafemora black (Froeschner 1944; Slater & Baranowski 1990; Hoffman 1996). The dorsal habitus of *P. similis* is illustrated by Slater and Baranowski (1990: Fig. 90).

Little biological information is available for *P. similis*. Adults are attracted to lights, and most of the numerous Floridian records are of adults collected "at light" or at blacklight traps (Hussey 1952; Slater & Baranowski 1990). Blatchley (1926) collected adults (as *P. constrictus*) in Florida by beating dead leaves of cabbage palmetto (*Sabal palmetto* [Walter] Schult. & Schult.) and by sifting weed debris. Adults have been taken in Missouri by sweeping weedy fields (Froeschner 1944) and in Virginia by sweeping grasses and sedges (Hoffman 1996). Habitats typically are ruderal exposed sites—fields, roadsides, and vacant lots—with an apparent preference for more mesic conditions than *P. constrictus* (Slater & Baranowski 1990). In Virginia, *P. similis* has been found in marshy areas and near standing water (Hoffman 1996). Collection dates range from early June to early October in Missouri (Froeschner 1944) and early June to late August in Virginia (Hoffman 1996). Adults can be collected in southern Florida nearly year round, with most records during May to September (Slater & Baranowski 1990). The literature on this species does not mention the nymphs.

Here I record the habitats in which nymphs and adults of *P. similis* were collected in Florida from March 2000 to April 2001 and provide notes on the habits and seasonality of this lygaeoid. Voucher material has been deposited in the National Museum of Natural History, Smithsonian Institution, Washington, D.C.

Material examined (all collections by the author; Roman numerals = nymphal instars): FLORIDA: Columbia Co., Sprite Loop, 0.1 km E. of Rt. 41, 3.2 km S. of Mikesville, 30°08.3'N, 82°57.1'W, 22 Mar. 2000, 1 II, 1 III, 3 IV, 1 V, ex crowns of *Muhlenbergia capillaris var. filipes* + 1 V ex crown of *Andropogon* sp. Hamilton Co., jct. Rt. 129 & SW 79 Terrace, 0.3 km N. of Suwannee River, 2 km NE. of Suwannee, 30°23.8'N, 82°56.0'W, 1 III, ex crown of *Andropogon* sp., 23 Mar. 2000; 1 ♂, 1 ♀, 2 III, 1 IV, 1 V, ex crowns of *Andropogon* sp., 27 May 2000; 2 ♂, 1 II, 1 III, 1 IV, 5 V, ex crowns of *Andropogon* sp. + 1 ♀, 1 V, sweeping *Coreopsis* sp. and *Gaillardia* sp., 2 June 2000; 1 ♂, ex crown of *Andropogon* sp., 29 Nov. 2000. Lake Co., Rt. 27, 11 km N of Groveland, 28°39.4'N, 81°51.2'W, 1 ♂, ex crown of *Andropogon* sp., 3 Mar. 2001. Suwannee Co., Rt. 129, McAlpin, 30°08.3'N, 82°57.1'W, 2 ♂, 3 ♀, 8 III, 5 IV, 5 V, ex crowns of *Andropogon* sp., 3-4 Mar. 2000; 3 ♂, 3 ♀, ca. 20 III-V, ex crowns of *Andropogon* sp., 23 Mar. 2000; 1 ♂, ex crown of *Andropogon* sp., 27 May 2000; 1 III, ex crown of *Andropogon* sp., 29 Nov. 2000; 1 I, 4 II, 4 III, 2 IV, 2 V, ex crowns of *Andropogon* sp., 2 Mar. 2001; 2 III, ex crowns of *Andropogon* sp., 21 Apr. 2001; Rt. 129, 1.2 km S. of O'Brien, 30°01.7'N, 82°56.6'W, 1 IV, ex crown of *Andropogon* sp., 4 Mar. 2000.

The field-type habitats from which *P. similis* was collected were ruderal sites along highways. Both sites that were sampled most frequently—one in the eastern Panhandle (Hamilton Co.) and the other in northern peninsular Florida (Suwannee Co., McAlpin)—have a rather sparse litter layer with only a few small (<0.25 m^2) patches of open sand. The site in Hamilton County, in an area of mesic flatwoods, has saw palmetto (*Serenoa repens* [W. Bartram] Small) within 25 m of the road, rank forbs scattered among broomsedge (bluestem) (*Andropogon* sp.) and other grasses, and a roadside planting of composites (blanketflower [*Gaillardia* sp.] and tickseed [*Coreopsis* sp.]). Vegetation near the highway, including some of the *Andropogon* plants that were sam-

pled, has now been eliminated by road construction. The site in Suwannee County can be described as disturbed sandhills. Plants at this site, in addition to *Andropogon*, include prickly-pear (*Opuntia humifusa* [Raf.] Raf.); bracken fern (*Pteridium aquilinum* [L.] Kühn); black medic (*Medicago lupulina* L.); forbs such as goldenrod (*Solidago* sp.), dog-fennel (*Eupatorium capillifolium* [Lam.] Small), and other composites; and blackberry or dewberry (*Rubus* sp.).

Except for an adult and a nymph of *P. similis* that were swept from the roadside planting of *Coreopsis* and *Gaillardia* in Suwannee County, all other individuals were beaten from the crowns of grasses. One collection was made from gulf hairawn (*Muhlenbergia capillaris* [Lam.] Trin. var. *filipes* [M. A. Curtis]), a grass that is sometimes given specific status, whereas all other collections were from bluestem or broomsedge (*Andropogon* spp.). The plant at the main sites in Hamilton and Suwannee counties probably is *A. tenuispatheus* (Nash) Nash, a species often listed as *A. glomeratus* (Walter) Britton et al. var. *pumilus* (Vasey) Vasey ex Dewey (e.g., Wunderlin 1998).

Perigenes constrictus inhabits the litter layer of exposed, ruderal sites in Connecticut (Sweet 1964); in Florida, *P. similis* also might be mainly geophilous. Nymphs of all instars and occasional (ca. 10) exuviae (cast skins were recognizable as *P. similis* by being setose) were beaten from crowns of *Andropogon*, suggesting that this lygaeoid's presence on grasses is more than accidental. The crowns of bunchgrasses would provide more moist conditions than the sandy substrate and might be typical of the mesic habitats from which this species has been recorded (Slater & Baranowski 1990; Hoffman 1996). Although rhyparochromids are characteristic of open, hot, xeric environments, some species show behaviors for minimizing their exposure to high temperatures of the substrate (Sweet 1964). The habitats occupied by *P. similis* in northern Florida do not qualify as open xeric sites in Sweet's (1964) classification; even so, the use of the basal stems and crowns of bunchgrasses might allow *P. similis* to avoid a substrate that is hot by day and to forage in the litter layer at night for seeds of grasses and forbs. The crowns of grasses also might offer some protection from predators.

Nymphs and adults of another myodochine rhyparochromid, *Paromius longulus* (Dallas), were beaten from *Andropogon* grasses at all sites from which *P. similis* was collected. The former lygaeoid is found on grasses rather than in the litter layer (Slater & Baranowski 1990; A. G. W., pers. obs.) and apparently feeds on such grasses. Whether the presumed seed-feeding *P. similis* feeds on the basal stems and new growth of grasses is not known. Nymphs and adults were beaten in March mainly from *Andropogon* plants with and without new growth at the base; they also were beaten from dead plants, both erect and sprawling on the ground, such plants apparently being used only for shelter.

Perigenes constrictus is bivoltine in Connecticut, the second-generation adults persisting until late autumn and the overwintering eggs hatching the following spring (Sweet 1964). Although my irregular collecting of *P. similis* does not allow the number of generations to be determined with confidence, this rhyparochromid appears to be at least bivoltine in northern Florida. The adults observed in early March are considered to represent those of a spring (first) generation; three fifth instars collected in early March 2000 eclosed within 24 hours. A prolonged period of egg hatch is suggested by the presence in early March of first through fourth instars along with fifth instars and adults. In the case of *P. constrictus*, Sweet's (1964) studies of egg diapause suggested a staggered hatch and "a protective spreading out of the spring eclosion." My collection of early instars of *P. similis* during March and in late May to early June suggests the production of a second generation. Whether another generation is produced during summer was not determined. Only a third instar and an adult were observed at the two principal collecting sites in late November.

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Summary

Adults and nymphs of all instars of *Perigenes similis*, a rhyparochromid lygaeoid, were beaten from the crowns of bunchgrasses, mainly *Andropogon* spp. (Poaceae), in Florida. Populations in the eastern Panhandle and the northern peninsula developed in ruderal sites (roadsides) of disturbed sandhills and mesic flatwoods and appeared to be at least bivoltine.

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EARLY ABSCISSION IN HACKBERRY LEAVES BEARING *PACHYPSYLLA* GALLS (HOMOPTERA: PSYLLIDAE)

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Early leaf abscission has been reported in several species of plants attacked by insects, e.g., leaf miners (Faeth et al. 1981), gall aphids (Williams & Whitham 1986), and psyllids that do not form galls (Clarke 1962, 1963). In northern Florida, the leaves of hackberry (*Celtis leavigata* Willd.) are commonly exploited by the glabrous nipple gall *Pachypsylla* sp. (possibly *Pachypsylla celtidiscucurbita* Riley, Yang & Mitter 1994). Observations of very early leaf fall from hackberry trees on the University of Florida campus in Gainesville, Florida, in late August revealed that most fallen leaves bore galls of this psyllid.

Accordingly, we sampled leaf fall from hackberry trees throughout the autumn of 1995 to determine whether galled leaves represented a greater proportion in early than in late leaf falls. We chose 3 widely separated sites on the University of Florida campus. Site 1 was a large, solitary hackberry tree near Keys Residential Complex, site 2 was a small patch of hackberry trees of various sizes on the northwest edge of campus, and site 3 was a large, solitary hackberry tree near the Psychology Building. At each site on 8-IX-95, we delineated a sample area (1.5 m by 1.0 m) where we cleared all leaves. On 29-IX-95, 6-XI-95, 21-XI-95, 29-XI-95, and 6-XII-95, we collected all leaves in each sample area. We later inspected the leaves for galls and calculated the percent of leaves bearing galls. We analyzed the changes in percent galled leaves over time at each site with an ANCOVA model after arcsine transforming percent data.

Our analysis of the data presented in Table 1 revealed that as autumn progressed, leaves bearing galls represented a significantly decreasing percent of fallen leaves ($P = 0.0009$). The percent of fallen, galled leaves averaged over all 3 sites showed the expected trend: 50.55% (29-IX-95), 44.90% (6-XI-95), 40.97% (21-XI-95), 31.27% (29-XI-95), and 30.60% (6-XII-95).

Early abscission of exploited leaves may be an induced plant defense because it can kill exploiters by preventing them from completing development (Williams & Whitham 1986; Prezler & Price 1993). However, leaf abscission may more often be viewed as a plant response to leaf damage, especially if the attacker emerges before leaf abscission or completes development even in abscised leaves (Stiling & Simberloff 1989). Whether adults of *P.* sp. emerge before leaf abscission or nymphs complete development in abscised leaves is not known. But, adults of the closely related *Pachypsylla celtidismamma* (Fletcher) do emerge from galls in *Celtis occidentalis* L. before leaf fall (Lill 1998). Thus, early leaf abscission in trees attacked by gall-making psyllids could be simply a response to leaf damage.

We thank Susan Halbert of the Florida Division of Plant Industry for taxonomic information on *Pachypsylla* species.

SUMMARY

We sampled leaf fall from hackberry trees at 3 sites on the University of Florida campus in Gainesville, Florida, during the autumn of 1995 to determine whether leaves bearing galls represented a greater proportion of total leaves in early than in late leaf falls. The proportion of fallen, galled leaves decreased significantly from 29-IX-95 to 6-XII-95. Early leaf abscission in trees attacked by gall-making psyllids could be simply a response to leaf damage.

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TABLE 1. PERCENT LEAVES BEARING *PACHYPSYLLA* SP. GALLS (SAMPLE SIZES IN PARENTHESES) FOR EACH DATE AND SITE.

	Site 1	Site 2	Site 3
29-IX-95	53.82% (275)	42.29% (253)	56.50% (200)
6-XI-95	48.67% (226)	46.18% (262)	39.45% (218)
21-XI-95	45.15% (268)	35.02% (317)	43.97% (257)
29-XI-95	38.10% (189)	31.37% (204)	26.25% (259)
6-XII-95	37.89% (293)	23.70% (173)	28.17% (387)

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LEKKING BEHAVIOR OF THE BLACK SOLDIER FLY (DIPTERA: STRATIOMYIDAE)

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The black soldier fly, *Hermetia illucens* (L.), (Diptera: Stratiomyidae), is a large (13 to 20 mm), wasp-like fly (May 1961). It has three generations per year in the southeastern United States and can be collected from late spring through early fall (Sheppard et al. 1994). Breeding occurs all year in the tropics. Larvae occur in assorted decomposing materials, such as fruits, animals, and manure (James 1935).

The black soldier fly is interesting because its presence can be used to solve many of the problems associated with large manure accumulations at confined animal feeding operations (CAFO). Problems, such as pest insects, water pollution and odors, are a product of excess nutrients (manure) at the CAFO. Soldier fly larvae concentrate excess manure nutrients into valuable feedstuff and other products (ca. $200 per ton), which can be economically transported (unlike manure at ca. $10-20 per ton). This would relieve local nutrient overload (Sheppard & Newton 2000)

House fly, *Musca domestica* L., control due to manure being colonized by the black soldier fly has been reported by Furman et al. (1959), Tingle et al. (1975), Sheppard (1983), and Axtell and Arends (1990). Additionally, Tingle et al. (1975) documented that black soldier fly larvae reduce waste within poultry facilities. Sheppard (1983) followed up their work and determined that the black soldier fly can reduce manure accumulation by 42-56%. Concentrations of nitrogen, and other nutrients are also significantly lower in this reduced manure, thus further reducing the potential for pollution.

Soldier fly prepupae can be easily self-harvested by directing their search for pupation sites into collection bins (Sheppard et al. 1994). Approximately 58 tons of prepupae can be collected in five months from the manure of a single layer facility, housing approximately 100,000 hens (Sheppard et al. 1994). The prepupae can be used as feed (42% protein, 35% fat) for a variety of livestock (Newton et al. 1977; Sheppard et al. 1994). This feedstuff, when dried, has an estimated value comparable to soybean or meat and bone meal. If used live, as specialty feed, or marketed to exploit its other unique qualities (essential fatty acids and chitin), the value of the product may be higher (Sheppard et al. 1994).

This manure management system depends on a robust soldier fly population for dependable inoculation of the manure with larvae. Presently, little is known about the biology of *H. illucens*.

Tingle et al. (1975) described the black soldier fly mating behavior. Males were attracted to "calling" females in the same "resting" area and mating occurred on the ground with the male and female facing opposite directions. However, Copello (1926) noted that mating occurred during flight. We provide a description of the mating, which differs from that provided by Tingle et al. (1975), and lekking behaviors of the black soldier fly, which may be important to maintaining this natural waste management system.

The study site was a poultry farm (three California style open-sided layer houses side-by-side) located in Bacon County, in the coastal plain region of Georgia. Observations were made during the mid-day (1100-1400 h) on 21 and 30 July 1998. Various weeds and grasses grew around the poultry facilities with a hardwood forest located approximately 100 m to the north. The forest edge was covered with a mixture of kudzu, *Pueraria lobata* (Wild), and morning glory, *Ipomoea* species. A pond, approximately 15 m in diameter, was located on the eastern side of the forest.

Large numbers of soldier flies were observed at two sites: within the chicken houses (a known larval habitat) and along the edge of the woods, especially a 10 to 15 m stretch of kudzu and morning glory facing the poultry facilities. We used an aerial net to sample these areas. We judged that there were several hundred soldier flies present during our collection periods. Adults collected from the forest edge were 91.9% (n = 109) male, while those collected from the poultry facilities were primarily female (91.3%, n = 123) apparently seeking oviposition sites. Furman et al. (1959) and Sheppard et al. (1994) suggest that adults live in a wild environment and that those observed in livestock facilities are newly emerged or ovipositing females.

Hermetia illucens males present at the forest edge generally rested individually on the surface of morning glory and kudzu leaves. Male movement was observed when members of the same species were present within its vicinity (i.e., flying above the resting male or landing on the same leaf). Arrival of another male would prompt the resting male to close and grapple with the invader. This would result in the two vertically spiraling approximately 0.5 to 1.5 m above the resting male's leaf. Once within this elevation range, the two would part with one returning to the leaf and the other leaving the vicinity. Females were similarly greeted, however males would grasp passing females during this aerial encounter and descend *in copula*. No chasing or mating activities were observed at the layer house where ovipositing females predominated.

Similar behaviors have been observed for another stratiomyid species (Alcock 1990). *Hermetia comstocki* Williston males have been observed aggregating at agava trees and resting individually on the upper leaf surfaces. Resting males were observed repelling other approaching males. The "victor" of the engagement would return to the leaf while the "loser" would leave the vicinity. This scenario was defined as a territorial or lekking behavior (Alcock 1990). Additionally, these sites of high male density may serve as attractants to females ready for mating (Alcock 1990). Similar patterns of lekking behavior have been reported for hymenopteran species, and other dipterans (Toft 1989 & O'Neill 1983).

SUMMARY

We describe the lekking behavior of the black soldier fly. If this lekking behavior at specific habitats is needed for *H. illucens* mating to occur, the identification and conservation of these sites near CAFOs would be important. Without these sites, we hypothesize that mating may be reduced or not occur at all, resulting in a reduction in the soldier fly population and associated benefits. We would like to thank J. Ruberson and J. Greene for their helpful comments on this manuscript.

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IMPROVED TRAP CAPTURE OF *EUSCHISTUS SERVUS* AND *EUSCHISTUS TRISTIGMUS* (HEMIPTERA: PENTATOMIDAE) IN PECAN ORCHARDS

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Some phytophagous stink bugs (Hemiptera: Pentatomidae) are economically important pests of pecan, *Carya illinoensis* (Wang.) K. Koch, throughout the Southeastern U.S. Feeding damage to fruit before shell-hardening usually causes fruit abscission whereas after shell-hardening, feeding punctures induce localized, black lesions on the kernel (Demaree 1922; Osburn et al. 1966). Ellis & Dutcher (1999) estimated that during 1997, losses and cost of control of kernel-feeding hemipterans in Georgia, alone, were $1.8 million. Also, because these lesions are bitter, affected kernels must be removed during postharvest processing.

Predominant pentatomid species attacking pecan are *Acrosternum hilare* (Say), *Euschistus servus* (Say), *E. tristigmus* (Say), and *Nezara viridula* (L.). Sampling for these species on pecan typically is done using visual searches of terminals or knockdown insecticide sprays (Ellis et al. 2000). However, a pentatomid trap developed by Mizell & Tedders (1995) and coupled with a *Euschistus* spp. aggregation pheromone identified by Aldrich et al. (1991) has been used to monitor *E. servus* and *E. tristigmus* in pecan (Mizell et al. 1997; Yonce & Mizell 1997; Cottrell et al. 2000). In fact, Yonce & Mizell (1997) reported that 93% of pentatomids captured from pecan orchards in these pheromone-baited traps were *E. servus* and *E. tristigmus*.

Although *Euschistus* spp. are attracted to, and enter, these traps, some are not prevented from escaping over time (T. E. Cottrell, pers. obs.). This leads to the need for frequent sampling intervals. Cottrell et al. (2000) reported that traps were sampled 3× per wk (except during winter months when traps were sampled 1× per wk). By preventing pentatomids from escaping, the need for frequent sampling could be decreased. But adding physical constraints to prevent escape might deter or prevent pentatomids from entering the trap. However, placing a selected insecticide inside the trap would not require modifications.

The objective of this study was to determine prevalence of escape by pentatomids from traps and to compare numbers of adult *E. servus* and *E. tristigmus* captured in pheromone-baited traps, with and without addition of an insecticide.

All studies were done at the Southeastern Fruit and Tree Nut Research Laboratory in Byron, GA. *Euschistus tristigmus* adults were collected during August 2000 from a mature pecan orchard in pheromone-baited yellow pyramidal traps. Traps consisted of 2.8-liter clear plastic PET jars (United States Plastic Corp., Lima, OH) on top of 1.22-m-tall yellow pyramidal traps (Mizell & Tedders 1995; Cottrell et al. 2000). All baits were made by loading rubber septa with 40 μl of the *Euschistus* spp. aggregation pheromone, methyl 2,4-decadienoate (Bedoukian Research, Inc., Danbury, CT). Collected *E. tristigmus* were held in the laboratory in 19 × 14 × 10 cm (l × w × h) vented plastic containers (Tristate Plastic, Henderson, KY) at a photoperiod of 14:10 (L:D) and room temperature. Snap beans (*Phaseolus vulgaris* L.) were provided as a food source. Specimens were held for ≤72 h in the laboratory. Males and females were marked on the pronotum with yellow and pink nontoxic acrylic Liquitex® (Binney & Smith, Easton, PA), respectively. Three males and one female were placed in each of eight unbaited traps in a mature pecan orchard (separate from where *E. tristigmus* were initially collected). After 24 h, traps were checked; numbers of *E. tristigmus* remaining and mortality were recorded. Percentage escape by *E. tristigmus* was calculated.

Testing the effect of using an insecticide in traps was done from June 30 through August 11, 2000 in a mature pecan orchard. Traps were arranged in a randomized complete block design using five replications and three treatments. Traps within blocks were separated by 90 m and blocks were separated by 90 m. All traps were baited and baits changed weekly. The three treatments used included traps with and without the addition of an insecticidal ear tag (Saber™ Extra, Coopers Animal Health, Inc., Kansas City, KS) sampled 1× per wk and traps without ear tags that were sampled 3× per wk. Active ingredients in the ear tag were lambda-cyhalothrin (10%) and piperonyl butoxide (13%). Collected pentatomids were returned to the laboratory for identification. *Euschistus servus* and *E. tristigmus* data were analyzed separately using analysis of variance (ANOVA) (SAS Institute Inc. 1996). Least significant difference (LSD) was used to separate means when a significant difference was found ($P \leq 0.05$).

A high percentage of *Euschistus tristigmus* escaped from traps during this study. After 24 h, percentage escape (±SE) was 90 ± 7%. Both sexes demonstrated a high rate of escape (96 and 88% by males and females, respectively). Four males, from three traps, died during the evaluation and were excluded from analysis. No females died during the study. The high percentage escape after only 24 h may have occurred because these traps did not contain the aggregation pheromone that might arrest or decrease local movement by

Euschistus spp. Additionally, confining these field-collected individuals in the laboratory could have created an agitated state whereby the stink bugs were compelled to disperse. Nonetheless, these results clearly demonstrate that this stink bug trap did not retain the pentatomids.

Significantly higher numbers of *E. servus* were captured in traps that were sampled 1× per wk and contained the insecticidal ear tag compared with traps that were sampled 1× or 3× per wk and did not contain the ear tag ($F = 6.60$; df = 2, 14; $P < 0.05$) (Fig. 1A). A similar trend was observed with trap captures of *E. tristigmus* across treatments. However, the difference only was significant between traps sampled 1x per wk with and without ear tags ($F = 6.17$; df = 2,14; $P < 0.05$) (Fig. 1B). A concern with using an insecticide in conjunction with the baited trap could be that *E. servus* and *E. tristigmus* are repelled from entering the trap. Results from this study demonstrate that the ear tag insecticide did not repel *Euschistus* spp. In fact, use of the ear tag improved trap captures of *E. servus* and *E. tristigmus*, by preventing escape, thus allowing sampling intervals to be increased. Another noted benefit of using the insecticide with the trap in this study was that captured specimens were not removed by foraging red imported fire ants, *Solenopsis invicta* Buren (Hymenoptera: Formicidae), plus various spider species were prevented from blocking the trap entrance with their webbing (T. E. Cottrell, per. obs.).

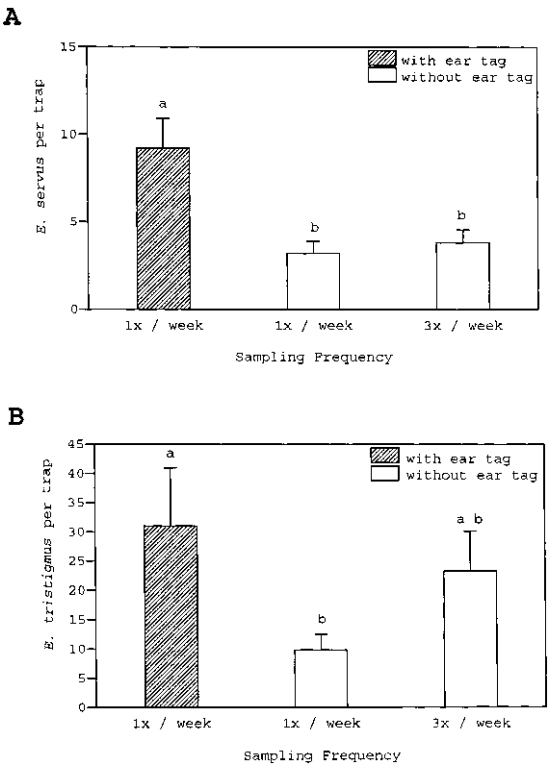

Fig. 1. (A) Capture of *E. servus* and (B) *E. tristigmus* in pheromone-baited traps that were sampled 1× per wk (with or without addition of an insecticidal ear tag) and 3× per wk. Unlike letters above columns indicate significant difference ($P < 0.05$).

SUMMARY

Yellow pyramidal stink bug traps baited with the *Euschistus* spp. aggregation pheromone offer a more convenient method of sampling these pests than visual searches or knockdown insecticidal sprays. However, a high incidence of stink bugs that enter these traps may also escape. Addition of an insecticidal ear tag to the trap significantly improves capture by preventing escape.

J. A. Payne critically reviewed and improved an earlier draft of this manuscript. Mention of trade names or commercial products in this publication is solely for the purpose of providing specific information and does not imply recommendation or endorsement by the U.S. Department of Agriculture.

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DISTRIBUTION OF THE CICADAS (HOMOPTERA: CICADIDAE) OF THE BAHAMAS

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While identifying material in the Florida State Collection of Arthropods (FCSA), I found specimens of cicadas that represent new distribution records for the cicadas that inhabit the Bahamas.

The Bahamas are an archipelago of approximately 700 islands and islets and 2400 cays north of the Greater Antilles (Cohen 1998). These islands were almost completely inundated around seventy thousand years ago during the last interglacial thaw after the Sangamon Ice Age (Cranton & Saunders 1992). Thus, the terrestrial fauna and flora are of relatively recent origin.

The first cicada to be described from the Bahamas was *Diceroprocta bonhotei* (Distant 1901). It has been attributed to New Providence and Andros Islands (Davis 1928). Specimens in the FCSA were collected in Nassau, New Providence, Bahamas which substantiates the distribution previously reported (Davis 1928). In addition, one specimen from the FCSA was collected on Eleuthera which extends the distribution of *D. bonhotei* approximately 80 km east-northeast of New Providence Island. I have also identified a single specimen of *D. bonhotei* in the K. C. Emerson Entomology Museum at Oklahoma State University from Norman's Cay which is one of the northern Exuma Cays approximately 75 km southeast of Nassau. These new records extend the known distribution of *D. bonhotei* to the eastern and central cays of the northern island group.

The distribution of *D. bonhotei* is restricted to the Bahamas. *Diceroprocta bonhotei* is morphologically related to *D. cleavesi* Davis (1930) and *D. caymanensis* Davis (1939a) from the Cayman Islands, *D. biconica* (Walker) (Davis 1932; Davis 1935) and its variety from the Florida Keys, Cuba, the Isle of Pines, and Mexico (Metcalf 1963), and *D. bicosta* (Walker) (Davis 1928) reported from Cuba and Central America (Metcalf 1963). The morphological similarities suggest a common ancestry for the *Diceroprocta* species of the West Indies.

A second cicada species found in the Bahamas, *Ollanta caicosensis* Davis, was originally described from South Caicos Island (type location), Acklin's Island, East Caicos Island, West Caicos Island, and Great Inagua Island (Davis 1939b). All but Acklin's Island are part of the Turks and Caicos Island group which forms the southeastern end of the Bahama Island chain. I have identified specimens in the FSCA that extend the known range of *O. caicosensis* in the Commonwealth of the Bahamas. The newly identified specimens were collected on Mayaguana and Long Island. The Mayaguana specimens fill the gap in the distribution for the Turks and Caicos group to Acklin's Island. The Long Island specimen extends the known range of *O. caicosensis* some 170 km northwest of Acklin's Island across the Crooked Island Passage. This places *O. caicosensis* on islands of the Bahamas Platform proper.

The genus *Ollanta* has a broad, discontinuous distribution. *Ollanta* species are found in the Bahamas (Davis 1939b), Central America (Metcalf 1963), and Hispaniola (Ramos 1983). The ancestor of *O. caicosensis* may have migrated from the west onto the large island that would become the Bahamas during the last glacial period. Bahamian organisms that do not migrate easily show more affinities to the fauna of Cuba and Hispaniola than to that of the mainland United States (Cranton & Saunders 1992). This would support the hypothesis of an eastward migration of the ancestors of *O. caicosensis* across Cuba or a northward migration from Hispaniola.

The two Bahamian cicada species differ in size. *Diceroprocta bonhotei* is a relatively large species (body length 29-35 mm, wing span 89-110 mm) that inhabits the northwestern islands. *Ollanta caicosensis* is a much smaller species (body length 18-22 mm, wing span 52-65 mm) that inhabits the southeastern half of the Bahamas and the Turks and Caicos.

I wish to thank Julieta Brambila of the Florida State Collection of Arthropods and Donald Arnold of the K. C. Emerson Entomology Museum for their assistance during my visits.

SUMMARY

This paper reports on the distribution of the two cicada species of the Bahamas. *Diceroprocta bonhotei* inhabits the islands of the northwest while *Ollanta caicosensis* is found on the central and southeastern islands into the Turks and Caicos. New distribution records are given for both species.

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RED IMPORTED FIRE ANTS EXPAND THEIR RANGE ACROSS THE WEST INDIES

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The islands of the West Indies have long been home to fire ants (Mann 1920, Wheeler 1905, Wilson 1971), but until the last two decades, this meant only the tropical fire ant, *Solenopsis geminata* (Fabricius). A potentially more serious pest, the red imported fire ant, *Solenopsis invicta* Buren, is now expanding its range in this region. The expansion of *S. invicta*'s range outside the United States has received relatively little attention. Buren (1982) first reported it in Puerto Rico from three mounds in El Tuque, a seaside park near Ponce. It is now very common and widely distributed in Puerto Rico. We collected *S. invicta* at the following locations: Guayama (April 1992, SDP [Porter et al. 1997]), Mayaguez (October 1995, LRD), and Ponce (September 1997, LRD). Mounds were observed and disturbed but no specimens were taken from San Juan (November 1997, LRD), Luquillo Beach (November 1997, LRD), and the Caribbean National Forest (November 1997, LRD).

The red imported fire ant has been reported from several islands in the Bahamas (Fig. 1). In a recent review of Bahamian ant biogeography, Morrison (1998) found records of *S. invicta* from San Salvador (Deyrup 1994). This species has since been discovered on New Providence and North Andros Islands (Deyrup et al. 1998). The following collections provide new records for *S. invicta* on other Bahamian islands (Fig. 1). Zach Prusak collected foraging *S. invicta* workers on Gorda Cay (= Castaway Cay, October 1997) as stray workers near a large resort construction site but he did not find nests. John Mangold collected *S. invicta* (May 2000) on Abaco Island (Marsh Harbor, Island Breeze) and Grand Bahama Island (Redwood Inn and Freeport airport).

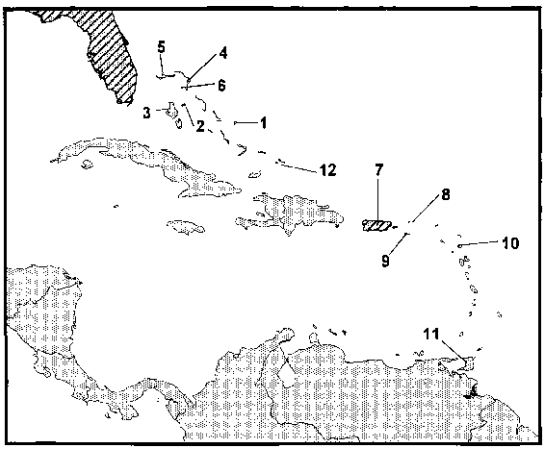

Fig. 1. Known distribution of the red imported fire ant, *Solenopsis invicta*, in the West Indies. The Bahama Islands: 1) San Salvador, 2) New Providence, 3) North Andros, 4) Abaco, 5) Grand Bahama, 6) Gorda Cay). Other Caribbean locations: 7) Puerto Rico, 8) British Virgin Islands, 9) U.S. Virgin Islands, 10) Antigua, 11) Trinidad, 12) The Turks and Caicos Islands; Providenciales Island. Puerto Rico and Florida are marked with bold hash marks because they are generally infested by *S. invicta*.

The following are new records from other parts of the West Indies (Fig. 1). Barbara L. Thorne sent fire ants to us from the British Virgin Islands (Guana Island, October 1996) that we identified as *S. invicta*. The presence of this species on Guana Island is, apparently, a recent occurrence. Snelling (1993) spent the month of October 1992 collecting ants there and did not find *S. invicta*. Rudy G. O'Reilly, Jr. collected additional specimens containing alate males and females from four large colonies on the National Guard facility at Estate Fredensborg about 9 km west of Christiansted on the island of St. Croix, US Virgin Islands (November 1997). John Mangold collected specimens of *S. invicta* from a mound along highway 66, about 0.8 km east of highway 663, St. Croix, US Virgin Islands (November 2000).

John Mangold also collected specimens of *S. invicta* from 7 sites on the island of Providenciales, Turks & Caicos (May and June 2001).

Ron Barrow provided 4 samples of *S. invicta* from Antigua, collected at the following locations (January 2000): All Saints; Gambles Terrace, St. Johns; Paynter's Paradise, St. George; Buckley's Village. These constitute the first records from the eastern edge of the Lesser Antilles.

In June 2000, two large colonies containing alates were found in Trinidad near Caroni Swamp on the western coast of the island. Classical morphological identifications of these samples were supplemented with gas chromatographic analysis of cuticular hydrocarbons and venom alkaloids. (Vander Meer 1986; Vander Meer & Lofgren 1988). Because the western edge of Trinidad is only approximately 10 km from the Venezuela coast an invasion of northern South America by *S. invicta* might be expected. Established populations of *S. invicta* are also very likely on other islands in the Lesser Antilles. Improved quarantine efforts may slow the spread of this ant (Lockley & Collins 1990), but mated queens are known to disperse 20-32 km over the ocean (Banks et al. 1973; Wojcik

1983) so they may be able to jump between some of the islands. *Solenopsis invicta* is likely to invade Jamaica, Hispaniola, and Cuba, if indeed it is not already present on one or more of these islands.

Clearly, the red imported fire ant is spreading and becoming a threat throughout the West Indies and may require intensified local quarantine efforts. Resources committed to early detection and eradication of incipient infestations could also greatly delay ecological and economic problems caused by this highly aggressive invasive ant species (Lofgren 1986).

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Summary

We present new records for *Solenopsis invicta* from the Bahama Islands (Abaco Island, Grand Bahama Island, and Gorda Cay) and the first records from the British Virgin Islands (Guana Island); the United States Virgin Islands (St. Croix, 2 sites); the Turks and Caicos Islands (Providenciales, 7 sites), Antigua (4 sites); and the island of Trinidad. These records indicate that this potentially damaging species is becoming widely distributed across the West Indies.

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SEASONAL WING POLYMORPHISM IN SOUTHERN CHINCH BUGS (HEMIPTERA: LYGAEIDAE)

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St. Augustinegrass, *Stenotaphrum secundatum* (Walt.) Kuntze lawns are used throughout the southern United States for their climatic adaptation and their ability to tolerate full sun to moderate shade. The southern chinch bug, *Blissus insularis* Barber is the plant's most damaging pest (Crocker 1993). The adaptability of this insect is shown by its developing resistance to insecticides (Reinert & Portier 1983) and overcoming host plant resistance (Busey & Center 1987; Cherry & Nagata 1997).

Southern chinch bugs (SCB) can occur as either macropterous or brachypterous adults. However, other than anecdotal reports, there are little field data on the occurrence of these wing forms in SCB. Also, reasons for the occurrence of brachypterous versus macropterous adults in SCB are poorly understood. Wilson (1929) reported that both macropterous and brachypterous SCB adults occur in Florida and these vary in relative numbers during the year, but no data were given. Komblas (1962) reported that population density was a factor in SCB wing form, noting that a larger percentage of nymphs raised under crowded conditions developed into macropterous adults than did uncrowded nymphs. Leonard (1966) discussed migration as an important factor in SCB wing formation. Lastly, Reinert and Kerr (1973) noted that although macropterous and brachypterous adults may be found in SCB, the latter predominates. However, reasons for the occurrence of the two wing forms were not discussed. The objectives of this study were to determine the seasonal occurrence of wing polymorphism in SCB in southern Florida and to determine if wing polymorphism is correlated with field population density.

Chinch bugs were collected from infested St. Augustinegrass lawns in Palm Beach County, Florida from December 1999, to December 2000. Five new SCB infestations were located each month by looking for damaged yellow grass and then visually confirming the presence of SCB. Insects were collected by suctioning for 5 minutes a 1×1 m area at each infestation. Nymphs and adults were collected by suction into a gasoline powered modified WeedEater® Barracuda blower/vacuum (Poulan/WeedEater, Shreveport, LA). The use of a suction technique for sampling SCB was described by Crocker (1993). After collection, samples were frozen for later counting in a laboratory. Samples were passed through as U.S.A. Standard Testing Sieve #10 (2 mm opening) to remove large debris. Microscopic examination was used to determine the sex and wing form of each adult and count nymphs.

In order to determine possible seasonal differences in wing polymorphism, samples from 3 month periods were pooled. For the purposes of this paper, winter is defined as December, January, and February, spring is March, April, and May, summer is June, July, and August, and fall is September, October, and November. These definitions correspond to seasonal definitions for the North Temperate Zone (Guralnik 1982). Mean differences in population density (nymphs + adults per sample) between seasons were determined using Tukey's test. Mean differences in percentage macropterous adults (macropterous adults/total adults per sample) between seasons were also determined using Tukey's test (SAS 1996). Pearson's correlation (SAS 1996) of percentage macropterous adults versus SCB density (adults, nymphs, or total = adults + nymphs) in all samples (N = 60) was conducted to examine possible relationships between wing form and field population density. Pearson's correlation for percentage macropterous males (macropterous males/total adults) versus percentage macropterous females in all samples (N = 60) was also conducted to determine if both sexes were responding similarly to the factor or factors causing macroptery in the field.

There was no significant difference in population density between the four seasons (Table 1). However, means during the winter-spring were lower than the summer-fall. Hence, data from winter and spring were pooled and compared against pooled data from summer and fall. The summer-fall population density (mean = 1746, SD = 3447) was significantly greater (alpha = 0.05) than winter-spring population density (mean = 431, SD = 682) by t-test analysis (t = 2.1, 58 DF). These data are in general agreement with Komblas (1962) and Reinert and Kerr (1973). Komblas (1962) reported that SCB populations decreased during winter in Louisiana. Reinert and Kerr (1973) also reported that field populations of SCB decrease drastically in cooler weather.

There was no significant difference in percentage of macropterous adults between the four seasons (Table 1). However, as with population density, means during the winter-spring were again lower than the summer-fall. Hence, data from the winter and spring were again pooled and compared against pooled data from the summer-fall. The summer-fall macroptery (mean = 22.3, SD = 18.1) was significantly greater (alpha = 0.05)

TABLE 1. SEASONAL POPULATION DENSITY AND PERCENTAGE OF MACROPTEROUS ADULTS OF SOUTHERN CHINCH BUGS.

	Population density		
Season	Mean[1]	SD	Range
Winter	457.8	982.4	11-3953
Spring	404.8	549.9	2-1737
Summer	1207.1	1038.8	24-3501
Fall	2285.1	5085.5	61-20019
	Macropterous adults		
Season	Mean[2]	SD	Range
Winter	13.5	12.7	0-33.3
Spring	11.2	15.3	0-46.4
Summer	21.0	16.9	0-48.9
Fall	23.6	19.7	0-69.2

[1]Mean bugs (nymphs + adults) per one m^2 sample. There was no significant difference (alpha = 0.05) in means between the four seasons using Tukey's test (SAS 1996). However, there was a significant difference (alpha = 0.05) in mean chinch bugs in pooled data of the winter-spring versus summer-fall periods using t-test analysis (t = 2.1, 58 DF).

[2]Mean percentage macropterous adults (macropterous adults/total adults) per one m^2 sample. There was no significant difference (alpha = 0.05) in means between the four seasons using Tukey's test (SAS 1996). However, there was a significant difference (alpha = 0.05) in mean percentage of macropterous adults in pooled data of the winter-spring versus summer-fall periods using t-test analysis (t = 2.4, 58 DF).

than winter-spring macroptery (mean = 12.3, SD = 13.9) by t-test analysis (t = 2.4, 58 DF). These latter data are consistent with Komblas (1962) report that macropterous adults predominated during the fall in Louisiana. The association of increased macroptery at higher field densities is corroborated by correlation analysis. Pearson's correlation analysis for percent macroptery versus population density in samples throughout the year (N = 60) gave significant (alpha = 0.05) positive correlation coefficients of 0.32, 0.53, and 0.33 for nymphs, adults, and total SCB. Pearson's correlation for percentage macropterous males (macropterous males/total adults) versus percentage macropterous females in samples throughout the year also gave a significant (alpha = 0.05) positive correlation coefficient of 0.63. These latter data indicate that both sexes were responding similarly to the factor or factors causing macroptery in the field.

In summary, the percentage of macropterous adults was higher during the summer-fall when population densities were also higher. Similarly, percentage macropterous adults was positively correlated with population densities in samples taken throughout the year. However, these data report field occurrence and correlation, but do not explain direct causation for macroptery in SCB which is probably more complex. For example, various factors such as heritability, population density, and host plant condition may affect wing dimorphism in insects (Denno & Peterson 2000). Moreover, factors may interact in causing macroptery. For example, the incidence of macroptery in the oriental chinch bug, *Cavelerius saccharivorus* Okajima is density dependent, but also strongly increased by seasonal factors such as long daylength and high temperature (Fujisaki 2000). My data fit the general model of increased macroptery at higher densities for population dispersal (see Denno & Peterson 1995 for discussion). However, controlled laboratory studies are needed to determine more precisely what factor or factors are causing changes in macroptery in SCB.

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SUMMARY

The population density of southern chinch bugs was greater during the summer-fall than the winter-spring. Analogously, macroptery was also greater during the summer-fall than the winter-spring. Macroptery was positively correlated with population densities from samples taken throughout the year.

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USE OF DIATOMACEOUS EARTH AND ENTOMOPATHOGEN COMBINATIONS AGAINST THE RED IMPORTED FIRE ANT (HYMENOPTERA: FORMICIDAE)

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Thelohania solenopsae Knell, Allen, & Hazard is a common intracellular pathogen of fire ants, *Solenopsis* spp., in South America and was recently discovered in the USA (Williams et al. 1998). Williams & Oi (1998) found that infected *S. invicta* Buren colonies produced smaller worker populations and decreased queen weights compared to uninfected colonies. This protozoan alone will not solve the *S. invicta* problem in the USA but could be used with other biological agents, natural products, or insecticides in a fire ant IPM program.

The LC_{50} for *Beauveria bassiana* (Balsamo) Vuillemin was 4.5× higher for workers from healthy colonies than for workers from *T. solenopsae*-infected colonies (Brinkman & Gardner 2000). Stimac et al. (1993) combined diatomaceous earth (DE) with *B. bassiana* in tests against *S. invicta*, but further studies are needed. The objective of the research reported herein was to determine the interaction of DE with either *T. solenopsae* or *B. bassiana* against fire ant workers.

Solenopsis invicta colonies infected with *T. solenopsae* were originally obtained from USDA ARS CMAVE, Gainesville, FL. Healthy colonies were collected from a pasture located 8 km northwest of Griffin, GA. These colonies were tested to confirm presence or absence of *T. solenopsae* by using procedures of Williams et al. (1998). Sixty-two percent of workers from the *T. solenopsae*-infected colonies possessed octet stage spores. *Thelohania solenopsae* was not detected in workers from local colonies. Test arenas were 35-ml clear plastic cups containing dental plaster (¼ volume of cup) and Fluon® (Northern Products Inc., Woonsocket, RI 02898) coated on the inside walls. The treatments tested on workers from healthy colonies were untreated controls, DE alone, *B. bassiana*, and *B. bassiana* + DE. Workers from *T. solenopsae*-infected colonies were treated with DE. Untreated workers were kept as controls. BotaniGard® ES (Mycotech Corp., Butte, MT 59701) was pipetted in cups on the surface of the dental plaster at a rate of 2.4×10^6 *B. bassiana* CFUs per cm^2. Cups that were treated with DE each received 0.1 g of Celite 545® (Fisher Scientific, Pittsburgh, PA 15275).

Ten ants were placed in each cup. Honey was provided as a food source, and cups were placed on wet foam. A hole in the bottom of each cup allowed the dental plaster to maintain moisture. Mortality was checked daily for 10 d. Treatments were replicated 10 times in a randomized complete block design with repeated measures. Analysis of data was with the PROC MIXED procedure (Littell et al. 1996); means were separated by LSD ($\alpha = 0.05$).

At 10 d after exposure, mortality of healthy workers exposed to DE alone was 29% (Fig. 1). Arthur (2000) reported that insect mortality is directly related to DE exposure interval and Stimac et al. (1993) observed almost twice this level of mortality of fire ants after 22-30 d of exposure to DE.

The mortality of ants from *T. solenopsae*-infected colonies that were exposed to DE was significantly ($F = 46.44$; df = 5,9; $P = 0.0001$) higher than observed with other treatments with 89% dead by 10 d after exposure. Although this mortality was subadditive (Cossentine & Lewis 1984), it was relatively high. According to Cossentine & Lewis (1984), mortality is subadditive

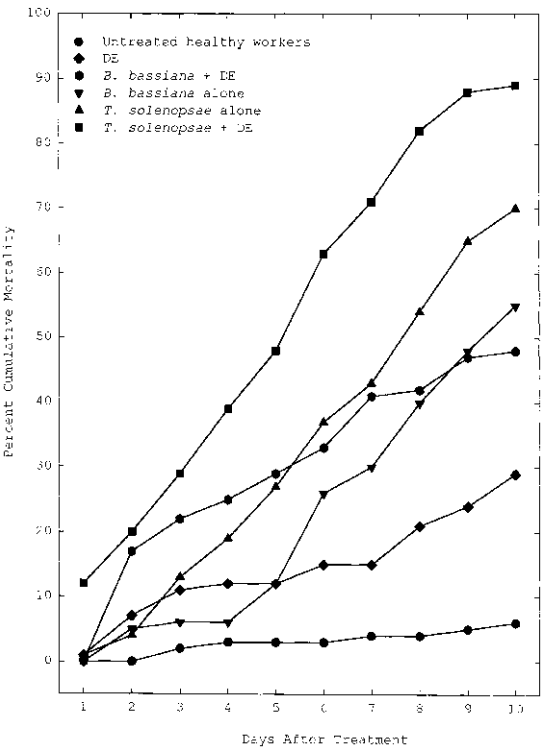

Fig. 1. Cumulative percentage mortality of *Solenopsis invicta* workers from healthy and *Thelohania solenopsae*-infected colonies exposed to diatomaceous earth (DE), *Beauveria bassiana*, or nothing.

when it is less than the sum of the effects of the two pathogens, but greater than the effect of either component alone. *Thelohania solenopsae* and DE affect fire ants in different modes; yet, DE exposure increases the level and rate of death of workers from infected colonies. This suggests that the two are compatible for use against fire ants.

Mortality of fire ants from healthy colonies treated with *B. bassiana* alone was lower than that caused by *B. bassiana* + DE for 8 d after exposure. After that time, mortality resulting from exposure to *B. bassiana* alone increased to 55% by 10 d after exposure (Fig. 1). Also, there was no significant difference in mortality between untreated ants from *T. solenopsae*-infected colonies and healthy ants following exposure to *B. bassiana* + DE. Results of this study indicate that combining DE with *B. bassiana* does not increase fire ant mortality above that caused by exposure to *B. bassiana* alone. The abrasive action of DE appears not to enhance the mode of action of the fungal conidia in breaching the fire ant exoskeleton.

Summary

Pathogen and diatomaceous earth (DE) combinations were tested on *Solenopsis invicta* in laboratory studies. Mortality for healthy fire ants treated with *Beauveria bassiana* was not greatly increased by exposure to DE. Mortality of fire ants infected with *Thelohania solenopsae* and exposed to DE was relatively high. Results suggest that *T. solenopsae* and DE are compatible for use against fire ants.

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In 1989 the New York Entomological Society published The Torre Bueno Glossary of Entomology [TBGE], compiled by Stephen Nichols with the help of 50 editorial contributors. That book is a thorough reworking and great expansion of J. R. de la Torre Bueno (1937) A Glossary of Entomology. It is a scholarly work with high editorial standards, and is now out of print.

CABI has filled the void with a new dictionary [GHDE]. GHDE is larger, with page size 6.5 × 9.5 inches (cf. 6 × 9 inches), with smaller font, 2 columns of text per page (cf. one), and 1032 pages (cf. 840). To calculate the difference in content, I counted the number of words on p. 478 of TBGE (418), and that in the left column of p. 478 of GHDE (360), this page chosen at random. Thus, I estimate that GHDE contains 212% of the words in TBGE. Unfortunately, I noticed 2 typographical errors in that left column of p. 478 of GHDE ("Myrmeleonidae" [should be Myrmeleontidae] and "conjuction"), whereas I noticed none in TBGE. This seems to me to typify the difference between the two: GHDE contains roughly twice the amount of information, but TBGE is much more carefully edited.

GHDE came about through three decades of note-taking by Gordon Gordh, greatly expanding Torre Bueno (1937). It is no way a "rip-off" of TBGE, indeed it omits some of the terms defined in TBGE, and some of the omissions are unfortunate. GHDE also has several other features that are not included in TBGE. First, it includes references to biographies and/or bibliographies of prominent deceased entomologists, for which the most complete source is a work by Pamela Gilbert (1977), endearingly known to entomologists as the "dictionary of dead buggists" or words to that effect. Second, it tries to include all family-level names of insects, which is a tall order given the recent spate of name changes (many the result of cladistic studies). Third, it includes very many "common" names of insects (see below). Fourth, it includes (p. 1011-1023) a list of the unabbreviated names of scientific periodicals consulted.

The list of scientific periodicals was given to aid readers in finding the references cited in the text, which there are given in abbreviated form. It would have been a more useful feature if a few more hours had been given to its editing—to eliminate typographical errors, to ensure that all names really are spelled in full (without any words omitted), and with insertion of all diacritical marks (accents) needed for correct orthography of Czech, French, Portuguese, Spanish, and other European languages. If those things had been done, it could have been used as a good partial source of unabbreviated names of entomological (and some other) journals.

Because more and more journals are requiring authors to cite unabbreviated periodical titles in references cited in submitted manuscripts, a convenient and accurate source would be useful. The World List of Scientific Periodicals was last published in 1964. No other list is even close to its adequacy. No more recent list includes all of the newer periodicals that include works in entomology. The lists that include current "standard abbreviations" (that is, standards used in the USA) are no better than third-rate because they ignore periodicals that have ceased publication and, in general, they ride roughshod over orthography of any language but English.

Inclusion of English-language "common" names also is a tall order. In my view a "common" name is one that has arisen in the language of ordinary people, and is widely used (such as butterfly or dragonfly or ladybird). In general, insect orders have such common names, most insect families lack them, and extremely few insect genera or species have them. Most of those that exist are used in most English-speaking countries. I think that such "folk" names should be given precedence over later, invented names—and, if they have arisen in one English-speaking country, should be used in others to label the same insect species (assuming there is no similar "folk" name in the other countries). However, entomologists in some countries (USA, Canada) have established committees to decree what should be the "common" name in that country of an insect group (order, family, genus) or species. Among other actions, these committees have decreed names that, in my view, are not "common"—they are wholly invented and thus are "vernacular" (not Latin, but English) but are not "common" names because they are not commonly used (by most of the people). Here are just four examples:

Spodoptera frugiperda (Smith) (Lep., Noctuidae) is called "fall armyworm" in the USA. Perhaps this "common" name was decreed, or perhaps it arose as a folk name. However, *S. frugiperda* also occurs outside the USA in the Caribbean. Are Jamaicans forced to use the expression "fall armyworm" in their tropical country which has no autumn season (called "fall" in the USA), or are they free to use their own names "trashworm", and "ratoonworm" for this insect?

Elasmopalpus lignosellus (Zeller) (Lep., Pyralidae) is called "lesser cornstalk borer" in the USA, presumably by decree of some entomologist or entomological committee. In Jamaica, it is called "jumping borer" because the larva jumps when disturbed.

Saccharosydne saccharivora (Westwood) (Hem., Delphacidae) has been called "canefly" for hundreds of years in Jamaica. In the US litera-

ture, it has been labelled "West Indian sugarcane delphacid." Are Jamaicans supposed to give up their true common name and adopt the cumbersome (and much later) name decreed by some committee in the USA? Should it not be the other way around?

Pieris rapae (L.) (Lep., Pieridae) has for a very long time been called "the small white butterfly" ("small white" for short) in England, part of its native range. However, after it arrived in the USA, its larva was labelled "the imported cabbageworm" by some entomologist. Which name should take precedence?

The senior author, Gordon Gordh, is sensitive to the issue of variant common names in various parts of the English-speaking world. There are about 50 countries outside the USA where English is an official language, and their combined population is much greater than that of the USA. This book might have fared less well in the hands of an author without substantial experience outside the USA.

Is this book worth its price? Absolutely. The authors quote a 19th century statement: "Terms are the tools of the teacher; and only an inferior hand persists in toiling with a clumsy instrument when a better one lies within one's reach." That statement is very appropriate—entomologists need this book no matter that they already own a copy of "The Torre Bueno Glossary of Entomology." A CD-ROM version would be useful and should sell for a small fraction of the book price.

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HARDIE, J., AND A. K. MINKS (eds.). 1999. Pheromones of Non-Lepidopteran Insects Associated with Agricultural Plants. CABI Publishing, Wallingford, Oxon, UK. Hardback, ISBN 0-85199-345-1. $140.

A compilation of pheromone work on insects other than Lepidoptera has been overdue, and this book, edited by Hardie and Minks, is an excellent and needed addition to pheromone literature. There are 17 chapters on pests and beneficial insects. The 13 chapters on pest insects tend to be organized along taxonomic lines, although the beetles get 5 of the 13 chapters. Included are chapters on tephritid fruit flies, gall midges, scarab beetles, sap beetles, weevils, forest beetles, stored-product beetles, sawflies and seed wasps, aphids, scale insects, phytophagous bugs, grasshoppers and locusts, and termites. There follow 4 chapters on beneficial insects organized along ecological lines, including a chapter each on predators, parasitoids, parasitoid hosts, and bees. Species and subjects are indexed separately. In addition to the obvious use of the subject index, it is useful if one wants to know which insects produce a particular semiochemical, or which insects respond behaviorally to a chemical. For example, one can easily determine that α-pinene is a semiochemical responded to, or produced by, numerous insects, as detailed from page 10 to page 342. Numerous trap types are described and indexed. In the subject index, a chemical compound is indexed by the first letter of its chemical name, but preceded by designations of chirality or numbers indicating positions of double bonds. For example, (*Z*)-7,15-hexadecadien-4-olide is indexed with other topics beginning with "h". There are many illustrations of chemical structures, and numerous black and white photos of insects, tables, and graphic figures.

The specialists who have written the chapters in this book have provided a valuable service, not only in summarizing and interpreting the chemical, ecological, and behavioral information on a particular group of insects, but also in collating an extraordinarily vast pheromone literature. Thus, a wide audience is likely to find the book useful. Each chapter ends with an extensive bibliography, providing the student or specialist an easy way to get into the literature. Students and young scientists will find the book invaluable as an introduction to chemical ecology or a potential research problem. There are brief discussions of the practical applications of pheromones in most chapters, but it is not a "how to use pheromones" book. Nevertheless, it should help crop and plant protection consultants to integrate selected use of pheromones into their management strategies. Teachers of insect chemical ecology and pheromone physiology will find a wealth of information to illustrate both the diversity of insect chemical ecology, and the evolutionary theme that pervades all of biology. The book is indispensable for pheromone research.

The book comprises 466 pages printed on high quality paper with easily read print, and the heavy hard cover has interesting photos of pentatomid bugs that are 3-dimensionally layered in different sizes and at different depths. This is a beautiful book that provides much valuable information.

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