while the latter has been reduced to an empty, shrivelled skin. The Aleochara rests for a few days and then pupates. Two weeks later the mature adult is ready to emerge.

The adult beetle chews a hole in the wall of the still-tough puparium and comes out. Now it will find a mate, take up the work of enlarging and maintaining the ancestral galleries and chambers, and continue the decimation of the cabbage maggots. In a season as many as 80 percent of the cabbage maggots in a field may fall victim to the aggressive beetles.

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**Parasites and Predators**

*C. P. Clausen*

The cottony-cushion scale, a small, inactive insect that feeds on the sap of the leaves and twigs of citrus trees, was first found in California in 1872. Within 15 years it had spread over the entire citrus-producing area of the State and threatened to destroy the industry. In many orchards the fruit crop was a complete loss, and in some the trees themselves were killed. The situation was desperate, as no method of control was known, and many growers gave up hope of relief and pulled out their trees.

It was known that the scale occurred in Australia. It probably originated there and had reached California by unknown means, possibly on nursery stock. That knowledge yielded one ray of hope—a parasite was known to attack it and appeared to hold it in check in its native home.

C. V. Riley, entomologist of the United States Department of Agriculture, became keenly interested in the problem and laid plans to send a qualified entomologist to Australia to obtain the parasite. He selected Albert Koebele, at that time engaged in studying other insect problems in California. Koebele had studied the cottony-cushion scale, attempting to control it by various means, and it was he who first concluded that the pest must have come from Australia. Difficulties arose, however. At that time it was almost impossible to obtain funds for foreign travel. Finally Koebele went to Australia, but as a representative of the State Department to the Melbourne Exposition.

Koebele arrived in Sydney late in September 1888 and immediately with the aid of an Australian entomologist was able to find the parasite, a tiny fly,
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Cryptochaetum iceryae. Many thousands were dispatched to California. Fortune favored him still more, however, when, a few weeks later, he discovered the previously unknown but now famous vedalia. Both the beetles themselves and their larvae were found to feed greedily upon the eggs and the larvae of the scale, and on them only.

The first shipment of vedalia by Koebele reached California November 30, 1888. It comprised 28 beetles. Additional shipments followed. By the end of the following March a total of 514 had been received.

The beetles thrived. In less than 2 years after the arrival of the first shipment, the scale was under complete control throughout the citrus-growing sections of the State. It has remained so ever since. This highly successful outcome was due to the beetle rather than to the parasitic fly, the original object of the search, though it likewise became established and abundant. Koebele’s trip cost less than $5,000; it has saved the citrus industry millions.

Koebele’s later investigations in New Zealand and Australia in 1891–92 and to other Pacific regions were financed by the Department of Agriculture and the California State Board of Horticulture. He found and forwarded several valuable mealybug and scale insect predators, four of which adapted themselves to California. Among them was the well-known Australian lady beetle which during the 1920's was reared and distributed to the number of 40 million or more each year for the control of the citrophilus mealybug, another citrus pest in California closely related to the cottony-cushion scale.

Koebele was the pioneer among entomological explorers who search the far places of the world for parasites and predators to be used in controlling insect pests in this country. This method is now termed “biological control” to distinguish it from chemical control, which involves the use of insecticides. All available natural enemies, including parasitic and predaceous insects and disease-producing organisms as well, whether native or of foreign origin, are used in this program. In biological control the first cost is usually the only cost; the application of chemicals, on the contrary, must be repeated year after year and often several times each season.

Most of our destructive insect pests are not native to this country. They have gained entry in various ways, some as long ago as Colonial days. Nearly every injurious insect is attacked in its native environment by one or more parasites and predators which hold it in check. When a pest gains entry into a new country, its natural enemies are usually left behind. The pest therefore can increase unhampered by their attack. That is why many insects of foreign origin are more destructive in the United States (or any new habitat) than in their home country.

One precedent for Koebele’s work was not entirely successful. In 1883–84 and following years, C. V. Riley imported a small wasp, Apanteles glomeratus, from England to combat the imported cabbageworm, a European pest that appeared first in Canada about 100 years ago. The parasite became established and abundant in all sections, but failed to control it.

So spectacular was Koebele’s success with the cottony-cushion scale that the Bureau of Entomology began a large-scale search in 1905 in Europe for natural enemies of the gypsy moth and brown-tail moth. Those two destroyed or damaged forest and ornamental trees over a wide area in New England. The explorations from 1905 to 1914 covered all Europe and Japan, and were renewed and completed in 1922–27. Thirteen species of parasites and predators were successfully established in New England as a result of this work. The frequency and destructiveness of the gypsy moth outbreaks have been appreciably reduced as a result of these importations. The brown-tail moth has subsided to a position of little importance.
Other forest- and shade-tree pests that have been dealt with in the same way are the satin moth, oriental moth, birch leaf miner, and larch casebearer. The satin moth was a serious pest of poplar and willow in New England and the Pacific Northwest before 1930. *Compsilura concinnata*, *Eupteromalus nidulans*, and *Apanteles solitarius* (which had been imported for use against the gypsy moth and the brown-tail moth) reduced greatly the infestations in New England. *Apanteles* and *Meteorus versicolor* gave satisfactory control in the Pacific Northwest.

The oriental moth occurs in a few places in Massachusetts. Its parasite, *Chaetexorista javana*, obtained from Japan in 1929–30, in most years has effectively controlled the pest, but it apparently cannot withstand the occasional severe winters in Massachusetts; consequently the pest increases during the seasons following such winters.

Among the pests of cereal and forage crops, the alfalfa weevil, which had become established in Utah, was the first on which investigations were undertaken. Importations from Italy in 1911–13 resulted in the establishment of a parasite, *Bathyplectes curculionis*, which destroys a high proportion of the larvae. The real value of this parasite in controlling the pest is difficult to determine, but parasite attack, in conjunction with a change in cutting practices, has given fairly satisfactory control.

The project for biological control of the European corn borer is the largest yet undertaken. It covered the years from 1920 to 1935, with activities centered mainly in the European countries but extending also to Japan, Korea, and Manchuria. Six species of parasites are known to be well established as a result of shipments during the period. Unfortunately four of them are severely restricted by climatic conditions and are established only in limited areas. The two most valuable are *Lydella stabulans grisescens* and *Macrocentrus gifuensis*. *Lydella* is widely distributed in the Eastern, Middle Atlantic, and North Central States. In some localities it may parasitize 50 percent or more of the borers. *Macrocentrus* is common only in southern New England.

Several attempts have been made to find effective natural enemies of the sugarcane borer. A considerable number of parasites were found in Cuba and several South American countries and introductions have been made intermittently since 1915. Two large importations were from Argentina and Peru in 1929–32. Not a single species of the many that have been released in Louisiana has become established, because of climatic conditions, mainly winter temperatures too low for the parasites to survive, and because of the practice of cutting the cane annually, which eliminates most of the parasite population and provides unfavorable conditions for increase in the spring.

Two parasites, *Lixophaga diatraeae* from Cuba and *Bassus stigmaterus* from Peru, have become established in Florida. These, especially *Lixophaga*, have been responsible for a considerable degree of control in the Felsmere area.

The oriental fruit moth, which came to this country from Japan, is a destructive pest of peaches in the eastern half of the United States. A large-scale program was undertaken in the 1930's to import its natural enemies from Japan and Korea. More than 20 species of parasites were imported and colonized throughout the infested area. Several showed promise during the season of release, but winter conditions were unfavorable to them and they declined and disappeared in a few years. Only one species has been able to maintain itself, and that in small numbers in one locality in New Jersey.

Before undertaking the importations from the Far East, entomologists knew that a native parasite, *Macrocentrus ancylivorus*, frequently attacked the pest in New Jersey and Delaware. Its normal host is the strawberry leaf roller, but the new pest was just as suit-
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able. Investigations revealed that the parasite, although limited in its distribution, was adaptable to most of the area infested by the fruit moth. Colonization in the infested orchards

in the spring reduced the later fruit injury as much as 80 percent. That benefit continued year after year. Large numbers were reared and distributed widely. It was the most dependable means of control before the development of the new insecticides. It is one of the few instances in which a native parasite has proved to be effective in combating an introduced pest.

The Comstock mealybug, of Asiatic origin, has become a serious pest of apple in the Northeastern States since 1930. After a search for its parasites in Japan, two species, *Allotropa burrelli* and *Pseudaphycus malinus*, were imported and established. They and another parasite, *Clausenia purpurea*, which already had found its way to the United States, have been highly effective in bringing the pest under control throughout the infested area.

Disappointments can arise in a biological control project. Efforts with the Mexican bean beetle furnish an example. A promising parasite, *Paradexodes epilachnae*, was found in central Mexico and was imported, reared, and released in large numbers in the 1920's. The field colonies increased rapidly. Some destroyed 80 percent or more of the beetle larvae the first season. The problem appeared to be solved. But the following season revealed a discouraging situation. Not a single individual of the hundreds of colonies released in 19 States had survived the winter. The parasite is evidently adapted only to tropical or subtropical places, where it can breed throughout the year. In the United States the bean beetle hibernates as an adult, and consequently no larvae are available to the parasite for more than 6 months. Its survival under such conditions is obviously impossible.

A serious threat to our citrus industry is the citrus blackfly, which occurs in the West Indies, Central America, and Mexico. It is native to tropical Asia and was first found in the Western Hemisphere in Jamaica in 1913. Its occurrence near our borders caused apprehension and a realization of the need to adopt all possible measures to prevent its entry. One practical measure, of benefit both to us and to the nearby infested countries, was the reduction of the heavy existing infestations. Accordingly the United States Department of Agriculture and the Cuban Department of Agriculture, Labor, and Commerce undertook to import its natural enemies from Asia. A parasite, *Eretmocerus serius*, and a predaceous beetle, *Catana clauseni*, were established in Cuba between 1928 and 1931. The parasite increased rapidly. Within 2 years the pest was brought under full commercial control. No other measures have since been required against it. Equally effective control followed the establishment of the parasite in Jamaica, the Bahamas, Haiti, Panama, and Costa Rica.

The citrus blackfly, discovered in destructive numbers on the west coast of Mexico in 1935, has spread rapidly. It is now approaching our borders on both the east and west coasts. Here again a cooperative effort was required. The parasite was introduced and colo-
nized at many points on the west coast in 1943 and was widely distributed thereafter. It was a surprise and a disappointment to find later that the expected degree of control, such as was attained in Cuba and elsewhere, did not materialize. Semi-arid conditions in Mexico, with rainfall only in summer, prevented the parasite from attaining maximum effectiveness. Other natural enemies better adapted to those conditions therefore had to be brought in.

A search during 1949 and 1950 through western India and Pakistan, where the climate resembles that of Mexico, brought to light several effective parasites, two of which appeared to be responsible for holding the pest in control in nearly all areas. All have been shipped to Mexico and widely colonized. Three species have become established, but the outcome in terms of control was not known in 1952.

Another activity involving international cooperation is the sending of shipments of effective parasites and predators to foreign countries. It began in the early 1890's, shortly after the results of the work on cottony-cushion scale in California became generally known. Most of the shipments have comprised species that have been notably successful in biological control, such as the vedalia for cottony-cushion scale, the Australian lady beetle and a number of parasite species that control mealybugs, Alphelinus mali, an effective parasite of the woolly apple aphid, and others. More than 350 shipments have been made to 56 countries since 1890. Among them were 138 species of parasites and predators for use against 55 insects.

Work in California in biological control has been conducted by the University of California since 1923 and previously by the State Department of Agriculture and the State Commission of Horticulture. The first importations exclusively under State auspices were in 1904. In 1911 the work was placed on a permanent basis under the direction of Harry S. Smith. He has been responsible for the development and expansion of the State work from that date to 1951. Most of the work has been with pests of citrus, although it has been extended recently to include pests of other crops.

Conspicuous successes in California have been with the black scale, citrophilus mealybug, citrus mealybug, and long-tailed mealybug.

The black scale was for long the most destructive of all citrus pests in California. A search for effective natural enemies lasted more than 50 years and covered nearly all tropical and subtropical countries. Forty or more parasite and predator species were imported and released in infested orchards. Some showed promise for a time, but not until 1937, when Metaphycus helvolus was received from South Africa, was success finally achieved. In a few years the parasite brought the black scale under satisfactory commercial control in all sections except a part of the orchards in the even-hatch, or single-generation, area, although outbreaks sometimes follow unusually cold winters. The successful outcome of the long search has saved citrus growers several million dollars annually. The parasite also has been strikingly effective in eliminating a related scale insect, Saissetia nigra, which was destructive to ornamental plants in southern California.

The Australian lady beetle, which was introduced in 1891, has already been mentioned. For many years it persisted in the citrus orchards of California but was not conspicuously successful against mealybug pests. It was discovered that its ineffectiveness was due mainly to its inability to withstand winter conditions. Methods were then developed for the large-scale rearing of the beetles in the insectary, and releases were made in the orchard each spring at intervals as the infestations made necessary. The citrus mealybug and the citrophilus mealybug were satisfactorily controlled by this means for many years. State, county, and private organizations were engaged in produc-
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The need for this program became less acute in the 1930's because of the introduction of highly effective internal parasites of several of the mealybug species.

The citrophilus mealybug was first observed in southern California in 1913. It spread rapidly and quickly became a major pest in a number of sections. Two parasites, Coccophagus gurneyi and Tetracnemus pretiosus, were introduced from Australia in 1928, and the pest was brought quickly under control.

The long-tailed mealybug only occasionally becomes a serious pest of citrus but is better known for its attack on avocado. The internal parasites, Anarhopus sydneyensis (obtained from Australia in 1933) and Tetracnemus peregrinus (brought from Brazil in 1934), have brought about satisfactory field control.

The citrus mealybug, a serious pest for many years, was the species against which the Australian lady beetle was originally introduced. In 1914 an internal parasite, Leptomastidea abnormis, was imported from Sicily. It brought about field control in most sections, although releases of Cryptolaemus are still necessary in some orchards.

The California red scale is the most destructive of all the citrus insects in some sections of southern California and the search for effective natural enemies has been as long as that on the black scale. An effective parasite or predator has not yet been found, although nine species have been introduced. The yellow scale, a close relative of the red, has been controlled in some parts of the citrus-producing area by Comperiella bifasciata, introduced from China and Japan.

An attempt to utilize a virus disease of the alfalfa caterpillar in California is interesting. Scientists learned in 1948 that extensive outbreaks of the disease could be brought about by artificial dissemination of the virus. Field tests in the use of a virus for control of the alfalfa caterpillar, begun in 1947, demonstrated that the spray application of a suspension of virus material resulted in commercial control of the pest within 8 to 10 days. Also, the application of a water suspension of spores of a parasitic bacterium brought about similar control in only 2 days. The effect of the virus is more persistent than the bacterium, however, as the diseased caterpillars die and disintegrate on the foliage when killed by the virus, insuring infection of following broods of caterpillars, whereas those killed by the bacterium fall to the ground.

An outstanding contribution to biological control in California by Harry S. Smith and his coworkers has been in the development of methods for mass production of the imported parasites and predators. The procedure has permitted the widespread colonization of species within a short time after their importation and hence the advancing of the date on which control is accomplished.

The key to mass production is usually the rearing of adequate numbers of the pest insects themselves in the insectary, rather than the parasites and predators. The pest insects must, of course, be reared on plants, but use of citrus or other trees for the purpose was obviously impractical. The first big step was the discovery that the mealybugs could readily be reared on potato sprouts. The production of enormous numbers of Cryptolaemus beetles thus was made possible. Enough mealybugs can be reared on the sprouts from a ton of potatoes to produce more than 125,000 Cryptolaemus. The output of internal parasites is vastly greater than that.

It was later discovered that potato sprouts would serve equally well for the rearing of the black scale—the production of Metaphycus helvolus and other parasite species was thereby facilitated.

Equally successful results have been
obtained with the armored scale insects (California red scale, yellow scale, San Jose scale, and others). Potato tubers, squash, and several kinds of melons are used for insectary production rather than citrus or other plants.

A more recent use of potatoes to produce a host insect was in connection with the oriental fruit moth. The parasite, Macrocentrus ancylivorus, will develop as readily upon the potato tuberworm as upon the fruit moth. An elaborate production technique was developed that yielded approximately 235,000 parasites for each ton of potatoes used; 29 million parasites were produced in 1946.

The most consistent results in the biological control of insect pests have been obtained in Hawaii—the mild climate there interposes no obstacles to the development of parasites at any season. The absence of a cold winter eliminates the long hibernation period, and there is no need for an alternate host to bridge this season. Those factors have been responsible for the ineffectiveness of many promising species in the continental United States. Also, Hawaii has no prolonged dry periods of high temperatures, which handicap the natural enemies by requiring a period of inactivity in summer.

As a result, the sugar industry of Hawaii is now free from serious attack by any insect pest. Several major pests and a number of lesser importance have been adequately controlled by imported parasites and predators.

The importation of parasites and predators of insect pests into Hawaii began in 1893, stimulated by the outcome of the work with the cottony-cushion scale. Albert Koebele, who had found the vedalia in Australia, was appointed to the staff of the Territorial Board of Agriculture and Forestry in that year. In the following decade he was responsible for the introduction and establishment of 18 or more beneficial insects from Australia and Asia. Most of these were general predators on scale insects and mealybugs. The Territorial Board has continued its activities and has introduced many natural enemies of miscellaneous agricultural pests other than those of sugarcane. Among them are the melon fly, Mediterranean fruit fly, taro leafhopper, and Asiatic fruit fly.
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beetle borer quickly followed the establishment of the fly in Hawaii.

While the leafhopper and weevil were the outstanding pests of cane, many others have caused appreciable damage and have necessitated the importation of natural enemies. The outcome has been successful with the oriental beetle, several species of armyworms, the Chinese grasshopper, a mole cricket (*Gryllotalpa africana*), a cane aphid (*Aphis sacchari*), and two species of mealybugs. Many parasites of miscellaneous pests also have been imported, some with conspicuous benefit, such as those against the fern weevil, torpedo bug, a scale on coconut (*Pinusapsis buxi*), the coconut mealybug on avocado, and cockroaches.

The work in Hawaii may be brought up to date by mention of the work on fruit flies, including the oriental fruit fly. First found in the Islands in 1945, it quickly demonstrated its destructive capabilities. Its habits and its large numbers in Hawaii are a serious threat to the fruit industry in California, through the possibility of entry in aircraft or by other means. The importation of natural enemies was undertaken in a cooperative effort of the Hawaii Agricultural Experiment Station, the Board of Commissioners of Agriculture and Forestry of Hawaii, the Hawaiian Sugar Planters' Association Experiment Station, the Pineapple Research Institute, the University of California, and the Bureau of Entomology and Plant Quarantine.

The first shipments of parasites were brought from Malaya and the Philippines by the Board of Commissioners of Agriculture and Forestry in 1948. Since then the exploratory work by the cooperating agencies has extended to South and East Africa, India, Thailand, China, Formosa, Australia, and several islands of the South Pacific. Between 30 and 50 species of parasites have been imported for testing. Many have been released in large numbers. The importation program was completed in 1951. Four or more parasitic species are established in Hawaii. Two of them, originally imported from Malaya, have brought about commercial control on the island of Oahu and prospects of similar control on the other islands appeared excellent.

Many of the introduced parasites and predators I have mentioned have held the pest insects under control for many years and other control measures have not been required. Since 1945, however, complications have arisen because of the new insecticides, beginning with DDT and followed by a series of others, some of which are more toxic than DDT. The use of DDT in the orange orchards of California for control of the citruscola scale was followed by widespread outbreaks of the cottony-cushion scale, the first since 1890. This was due to the destruction of the vedalia by the insecticide.

In other instances, the use of the new insecticides against a specific crop pest has upset the natural balance of minor pests of the same crop, likewise apparently due to elimination of their natural enemies. The application of DDT and some other chemicals to vegetable and fruit crops frequently brings heavy infestations of aphids and spider mites—pests that at times become more destructive than the ones against which the insecticide was applied. This upsetting of the natural equilibrium has created a serious situation in pest control and is being investigated. The solution may be found in a combination of remedial measures involving a change in the insecticide used, its formulation, the time of application, or in some other change in current practices.

This account of biological control of insect pests has described only the more important achievements in the United States. The same method has been employed with conspicuous success in other countries, notably Australia, New Zealand, Fiji, and Canada. At least 30 major insect pests have been fully controlled in one or more countries through the use of parasites and
Infectious Diseases of Insects

Edward A. Steinhaus

Like human beings and other animals, insects are susceptible to a variety of infectious agents, which infect and kill hordes of them every year. Most of this mortality goes unnoticed, although at times outbreaks—epizootics—of disease are so spectacular as to claim considerable attention among growers and entomologists everywhere.

The possibilities of using disease agents to help control insect pests have excited entomologists and others periodically since infectious organisms were first detected in insects. As I explain in a later paragraph, however, that is only one of the applications that may be made of our knowledge of insect diseases, because insect pathology has already contributed greatly to other branches of entomology and to medicine, agriculture, and biology generally.

The infectious agents responsible for diseases in insects belong to the same major groups as those that cause diseases in other animals: Bacteria, fungi, viruses, protozoa, and nematodes. In general, however, insects are not very susceptible to those particular microorganisms that cause diseases of other animals and of plants. Furthermore, most of the micro-organisms that cause fatal diseases in insects are harmless to plants and higher animals.

The resistance shown by insects to pathogens of higher animals is largely a normal or innate one. Nevertheless insects often can ward off infection by virtue of mechanisms of immunity similar to those exhibited by other animals. Antibodies against foreign materials may be produced in the body fluids of the insects, thus giving a humoral immunity against infection. Cellular immunity frequently is evidenced by the predators and substantial reductions brought about in the infestations of a much larger number.

C. P. Clausen was leader of the division of foreign parasite introduction, Bureau of Entomology and Plant Quarantine, from its establishment in 1934 until 1951, when he retired and became chairman of the division of biological control at the University of California. His training was obtained at the University of California. In 1916–17 he conducted a search for natural enemies of citrus scale insects in Japan, China, Formosa, and the Philippines for the California State Commission of Horticulture. After joining the Department of Agriculture in 1920 he spent the following 11 years in a search for natural enemies of the Japanese beetle in Japan and India and of the citrus blackfly in Malaya.

For further reading on insect parasites and predators, Dr. Clausen suggests:
