ENTOMOPHAGOUS INSECTS

BY

CURTIS P. CLAUSEN

Principal Entomologist, in Charge
Division of Foreign Parasite Introduction
Bureau of Entomology and Plant Quarantine
United States Department of Agriculture

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PREFACE

This has been termed the age of insects, and it has been said that they are the chief competitors of man for possession of the earth. As in the case of the human race, however, the insects are their own worst enemies, and it is to this relentless conflict that we owe a large measure of credit for the maintenance of equilibrium in the insect population at a sufficiently low level to permit of the existence of plant and animal life as we know it today. The entomophagous insects comprise a very considerable portion of the total insect population, as is readily realized when we consider that the great majority of species of other food habits have one or more species of parasites or predators which live at their expense.

Ever since the early days of entomology, when the study of habits followed the early attempts at classification of the adult insects, the phenomenon of one insect preying upon another and being dependent upon it for food has attracted attention. The latter half of the nineteenth century was productive of a great advance in our knowledge of this phase of entomology and the foundation was then laid for what we now call biological control, the utilization of parasites and predaceous insects in the control of crop pests. This method is generally recognized today as one of the promising lines of approach to the solution of a great many of our major insect problems.

The literature dealing with entomophagous insects is assuming formidable proportions, and the fieldworker or student has access to only an exceedingly small fraction of the publications relating to the subject. He is consequently unable to familiarize himself with the important contributions that have appeared in many countries and languages. The present volume represents, as nearly as possible, what the author himself would like to have had available while engaged in field work upon insect parasitology and the biological control of insect pests.

In the discussion of the biology and habits of the entomophagous insects, particular attention has been given to those groups which reveal a high degree of specialization in their host relationships and in the form of the immature stages to adapt themselves to this mode of life. The generalized predators, consequently, are dealt with briefly and only sufficiently to illustrate the host preferences and habits of each group.

It is with particular pleasure that the author expresses his appreciation to all of those who have contributed in various ways to the preparation of this book. First, to Prof. Harry S. Smith of the University of California, under whom the author served his apprenticeship and who has been a constant source of encouragement and advice since that time. Many members of the staff of the Bureau of Entomology and Plant Quarantine have given invaluable assistance. C. F. W. Muesebeck and the specialists of the Division of Insect Identification have made determinations of a number of species and have reviewed the manuscript informally. In justice to them, however, it should be stated that the groupings and names used do not always represent their opinions and are the author's own responsibility. Grateful acknowledgments are made to the staff of the Bureau library and to Carlo Zeimet, translator, J. G. Pratt, photographer, and Mrs. M. F. Benson, artist. Much of the laborious clerical work in the preparation of the manuscript was done by Miss L. L. Bennett, to whom many thanks are extended. Dr. S. E. Flanders of the University of California has kindly reviewed the section dealing with the Aphelinidae. The courtesy of J. D. Maple and D. W. Clancy in permitting inclusion of data and illustrations from unpublished manuscripts is particularly appreciated.

Thanks are extended to the many authors whose illustrations have been used, each of which is credited in the legend accompanying the figure.

CURTIS P. CLAUSEN.

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ENTOMOPHAGOUS INSECTS

The habit of feeding upon other insects is found in all the major orders of insects. It ranges from incidental feeding during times of scarcity of the normal food to obligate parasitism. The latter involves development upon a limited number of host species, and in occasional instances it extends to actual specificity. Sweetman (1936) lists 87 families, in 5 orders, which contain species of parasitic habit, while those which are predaceous are included in 167 families, representing 14 orders. Allowing for duplications in the two lists, there are 224 families, in 15 orders, which have adopted, in some measure, the entomophagous habit.

A consideration of the relationships between entomophagous insects and their hosts requires the employment of certain terms to designate specific relationships. These insects are broadly divided into two general classes, the parasites and the predators. The term parasite, in medical and veterinary entomology, has a very different meaning from that which it has in insect parasitology, and there appears to be little possibility of reconciling the two, nor is there any real need for doing so. When applied to an entomophagous insect, it refers to one that, in its larval stage, develops either internally or externally upon a single host individual, the latter eventually dying as a result of attack. The adults are, with very few exceptions, free-living, and their food sources are usually distinct from those of the larvae. A predator, on the contrary, is to a large extent free-living in the larval stage also; it kills the host immediately by direct attack and requires a number of individuals to provide sufficient food to bring it to maturity. The predator is of greater size than the prey, and the food sources of the adults and immature stages are often the same. Many instances might be cited of particular species that are intermediate between the two or that fail to meet entirely even the broad definitions given. No sharply defined line of demarcation can be drawn between the two.

It has been mentioned above that the food sources of the adults of parasitic insects usually differ from those of the immature stages, whereas among the predators they are usually the same. The greatest divergence in feeding habits of the adults and the larvae or nymphs is found in a few species that have parasitic or predaceous larvae, yet the adults are strictly phytophagous and are classed as crop pests.

In referring to a species or group as being parasitic or predaceous in habit, it should be borne in mind that it is the immature stages which are referred to unless otherwise specified.

The first effort to define the relationships between a host and its parasites and between the parasite species themselves was made by H. S. Smith (1916), and several later authors have proposed modifications or entirely new series of terms to designate the different relationships. The latter have, in part, some merit; but Smith's definitions are generally understood and are adequate for present purposes. There are, however, two general terms in wide use for which the distinction should be pointed out. "Host preferences" relate, as the term implies, to the choice of

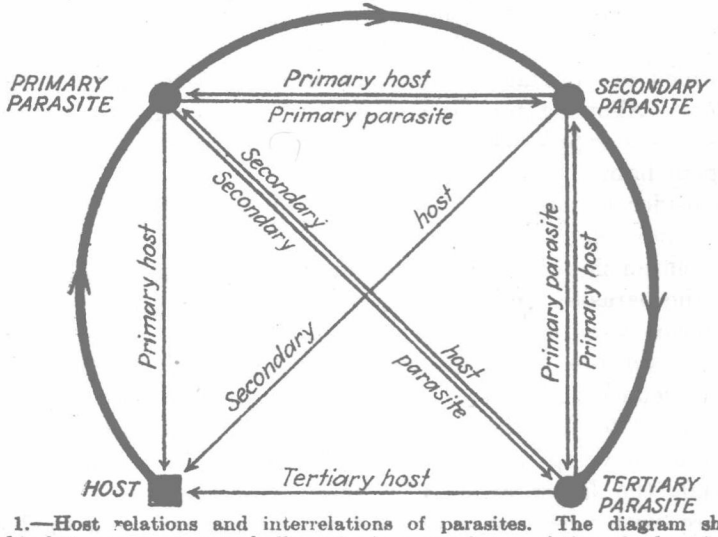

FIG. 1.—Host relations and interrelations of parasites. The diagram shows the relationship between any two and all species in a complex consisting of a host insect and parasites of the first, second, and third degree.

host species for attack, and under that heading we list the insects that are the normal hosts of species or higher groups in nature. "Host relationships," on the contrary, refer to the direct physical relationship between an individual parasite or predator and the individual host. The latter term is often erroneously used to cover the first as well.

In the discussion of the parasite complex associated with a given insect, there is often considerable confusion because of uncertainty or ambiguity in expressing the relationship between particular members of the series. This is especially true where the parasite series extends to the third degree. In Fig. 1, an attempt has been made to show in diagrammatic form the relationship between any two members of such a series. The third member, which is a tertiary parasite of the species designated as the host of the series, is a primary parasite of the secondary; and, conversely, the latter is its primary host.

HYMENOPTERA

The Hymenoptera are the dominant order among the entomophagous insects, both as regards the number of species having that feeding habit and in the frequency and effectiveness with which they attack the insect pests of agricultural crops. About half the families having entomophagous representatives are strictly parasitic in habit, one-fourth are predaceous only, and the remainder contain both parasites and predators. The most important and frequently encountered families of parasitic habit are the Ichneumonidae and Braconidae, which attack a wide variety of caterpillars, sawfly larvae, beetle larvae and adults, etc. The Encyrtidae and Aphelinidae are generally encountered as parasites of Homoptera, whereas the Scoliidae and Tiphiidae limit themselves to the grubs of Scarabaeidae. The Trichogrammatidae, Mymaridae, and Scelionidae are parasites of eggs only. In a great number of the families, a varying portion of the species is of hyperparasitic habit, this being particularly evident in the Ichneumonidae, Eulophidae, and Pteromalidae. The Formicidae are probably the most important of the predaceous groups and possibly of the entire order. Because of the exceedingly wide range of host preferences within the order, a detailed statement of this subject is not presented here but is included in the discussion of the respective superfamilies and families. There are, however, several biological topics that may be discussed with reference to the order as a whole, and an enumeration and description of the different egg and larval forms are also given below.

PLACEMENT OF THE EGG IN RELATION TO THE HOST

There is a great variety in the manner and place of oviposition by the Hymenoptera, ranging from the common internal placement of the egg to its deposition on foliage or in plant tissue far removed from the host. These variations in habit are often correlated with adaptations in form or structure of the egg, and they presumably serve a definite purpose, though frequently the relationship is not obvious. The following outline presents the different positions in which the eggs may be placed, with examples of species or groups having each habit.

A. Internal parasites, the egg deposited internally,

1. In egg of host, to develop in a later stage. (Several genera of Braconidae, Encyrtidae, and Platygasteridae, and occasional species of Ichneumonidae, Callimomidae, Eulophidae, and Cynipoidea.)

2. Free in the body cavity of the larva, pupa, or adult.
   a. In that of the primary host. (Of general occurrence.)
   b. In that of the primary host within the living secondary host. (*Mesochorus* spp., *Brachymeria dalmani* Thoms., *Aphidencyrtus aphidivorus* Mayr, etc.)
3. Regularly placed in a particular organ.
   a. In the brain or a ganglion. (Several Encyrtidae and Platygasteridae.)
   b. In the intestine. (*Platygaster zosine* Wlk., *Diversinervus elegans* Silv., *Microterys clauseni* Comp., etc.)
   c. In the embryo while still within the parent female. (Not definitely known to occur, but probable.)
4. Attached to the body wall.
   a. By its stalk fixed in the oviposition puncture in the host integument. (*Encyrtus*, *Microterys*, and other genera of Encyrtidae.)
   b. By an "adhesive disk" to the inner body wall. (*Therion morio* F. and *Heteropelma calcator* Wesm.)

B. Internal parasites, the egg deposited externally,
1. In contact with the host. (*Eretmocerus serius* Silv. and *Coccophagus ochraceus* How.)
2. Partially embedded in a puncture in the host integument. (Occasional in several species of Dryinidae.)
3. Entirely apart from the host. (All Trigonalidae, and *Orasema* spp.)

C. External parasites, the egg deposited externally,
1. Adhering to the host integument. (Of general occurrence.)
2. Attached to the host integument.
   a. Partially embedded in a wound in the host integument. (*Anisoctenion alacer* Grav. and several species of *Exenterus*.)
   b. The tip of the pedicel or stalk inserted in a puncture in the host integument. [Agriotypidae, many tryphonine Ichneumonidae, and occasional species of Eulophidae (*Elachertus* and *Euplectrus*) and Aphelinidae (*Euxanthellus* and the male eggs of several *Coccophagus*.)]
3. In immediate vicinity of host in cocoon, cell, burrow, etc. (of general occurrence).
4. Entirely apart from the host. (The great majority of Eucharidae and the parasitic Perilampidae.)

EGG-LARVAL PARASITES

Under this heading we include a relatively large group of parasitic Hymenoptera, distributed through a number of families, which oviposit in the host egg but complete their development in the larva or pupa. They are all true larval parasites in the sense that their development is primarily at the expense of that stage. Species having this habit are often referred to as egg parasites, but there is no more justification for so terming them than to designate a tachinid species an external parasite merely because its egg is deposited externally upon the host. So far as known at present, the above manner of oviposition and development is found only in the Hymenoptera, though in four superfamilies. These are the Ichneumonoidea (Ichneumonidae, Braconidae), Chalcidoidea (Encyrtidae, Callimomidae, Eulophidae), Cynipoidea (Ibaliinae), and Serphoidea (Platygasteridae). Oviposition in the egg, with development

in and emergence from a later host stage, was first suggested by Kirby in 1800, in the case of *Isostasius inserens* Kirby, a parasite of *Phytophaga*. Investigations since that time have substantiated this conclusion and have revealed that the habit is common to many members of the family Platygasteridae, though some of them will also attack the newly hatched larvae. All of these which have been studied in detail are parasites of the Cecidomyiidae, and the adults emerge either from the mature larva or from the puparium.

In the Cynipoidea, the single recorded instance of the above oviposition habit is for *Ibalia leucospoides* Hoch., which is parasitic in *Sirex*. In this species, oviposition may be in either the egg or the newly hatched larva and the host is killed in its late larval stage.

Among the Ichneumonidae, *Collyria calcitrator* Grav. oviposits in the egg of its sawfly host and completes its development in the mature larva, and *Sagaritis dubitatus* Cress. questionably has the same relationship to its lepidopterous host. Perhaps the best known representative of the family is *Diplazon laetatorius* F. and others of that genus, which oviposit either in the egg or in the larva of various Syrphidae, the adult emerging from the puparium. In the Tryphoninae, *Oocenteter tomostethi* Cush. places its egg in that of the host, and development is completed in the mature larva.

The Braconidae have a considerable number of species, particularly of the genera *Chelonus*, *Ascogaster*, and *Phanerotoma*, which oviposit in lepidopterous eggs and complete their development in the larvae. The habit is consistent in these genera. Several species of *Microgaster* attack lepidopterous hosts in the same way, and an occasional species of *Coelinidea* and *Sympha* oviposit in the eggs of their dipterous hosts and emerge from the puparium.

Among the Chalcidoidea, the family Encyrtidae contains a considerable number of species of *Ageniaspis*, *Copidosoma*, and closely related genera, which deposit their eggs in those of Lepidoptera and complete their development in the later stages. These comprise principally the species of polyembryonic habit. *Tetrastichus asparagi* Cwfd. places its eggs in those of the asparagus beetle, and maturity is reached only after the host larva has completed its feeding and formed the pupation cell in the soil. *Epimegastigmus brevivalvus* Gir. oviposits in the egg of *Megastigmus* and kills the host in its mature larval stage.

It is of interest that most if not all of the polyembryonic representatives of the Encyrtidae and Platygasteridae have the egg-oviposition habit, and this may possibly be explained by the longer period required for embryonic development. That requirement is lacking in the isolated instances occurring in other families. Thus *T. asparagi* represents a

striking departure in habit from other members of the same genus that attack similar hosts.

It has been mentioned that the dipterous hosts of some of the species referred to form the puparium before death, and occasional individuals of other species may likewise do so. This represents the final activity of the host, and death follows very quickly and without the attainment of the perfect pupal stage.

UNISEXUAL REPRODUCTION

The production, under normal conditions, of female progeny generation after generation without the intervention of the male is of much more frequent occurrence among the parasitic Hymenoptera than in other orders of entomophagous habit. Rather surprisingly, it has not yet been found to occur in the Serphoidea. In no family or even genus is the habit of general occurrence, and it is apparently a specific adaptation to meet particular conditions.

This manner of reproduction has been recorded in one or more of the entomophagous species of the following families and genera.

Ichneumonoidea:
- Braconidae (*Apanteles, Chelonus, Microctonus, Rogas*).
- Ichneumonidae (*Hemiteles, Nemeritis, Polyspincta*).

Chalcidoidea:
- Mymaridae (*Anagrus, Paranagrus, Polynema*).
- Trichogrammatidae (*Trichogramma, Oligosita*).
- Eulophidae (*Tetrastichus, Ootetrastichus, Pleurotropis, Thripoctenus*).
- Aphelinidae (*Aphelinus, Aphytis, Encarsia, Prospaltella*).
- Encyrtidae (*Achrysopophagus, Adelencyrtus, Anagyrus, Blepyrus, Habrolepis, Pauridia, Saronotum*).
- Eupelmidae (*Anastatus, Eupelmus, Eupelmella*).

Vespoidea:
- Bethylidae (*Sclerodermus*).
- Dryinidae (*Gonatopus*).

In the majority of species which reproduce unisexually, and of which sufficiently large rearings have been made, it has been found that occasional males appear. These may be degenerate forms incapable of mating or normal and able to accomplish mating readily. In the latter case, however, the progeny are again all female.

It has been recorded by Phillips and Poos (1921) that the spring brood of *Ditropinotus aureoviridis* Cwf. consists solely of females, whereas the progeny of these include a small proportion of males. The same authors (1927) state that virgin females of *Eridontomerus isosomatis* Riley produce progeny of both sexes.

POLYEMBRYONIC REPRODUCTION

Among insects the development of two or more individuals from a single egg has been demonstrated thus far only in the Hymenoptera, though in that order it occurs in no less than four superfamilies and a number of genera, as follows:

Hymenoptera.
Ichneumonoidea.
Braconidae (*Macrocentrus* spp.).
Chalcidoidea.
Encyrtidae (*Ageniaspis, Litomastix, Copidosoma,* etc.).
Serphoidea.
Platygasteridae (*Platygaster* spp.).
Vespoidea.
Dryinidae (*Aphelopus theliae* Gahan).

The literature dealing with polyembryonic reproduction in the Hymenoptera is becoming quite extensive. The embryological phases of the subject are too complex to permit of adequate treatment here, but the references cited in the discussion under the respective families may be consulted if detailed information is required. Several general reviews on the subject have been published, among which may be mentioned those of Howard (1906), Gatenby (1918), Leiby (1929), and Silvestri (1937).

In reviewing the host preferences of the various groups of polyembryonic habit, an exceptional consistency becomes evident. The Braconidae and Encyrtidae develop in Lepidoptera only, whereas the Platygasteridae parasitize the dipterous family Cecidomyiidae. Only in the Encyrtidae is more than one genus known to have this habit, and the several genera of that family are closely related and, being of common origin, naturally would show a consistency in host preferences.

Deposition of the egg in that of the host, together with the completion of larval development in the mature larva or pupa of the latter, is the habit of all polyembryonic Encyrtidae and Platygasteridae. A maximum period of time is consequently available for embryonic development; and this, as well as other undetermined requirements, has brought about the adoption of a habit that is uncommon among the species of the same families that reproduce monembryonically.

The number of individuals that are able to develop to maturity in a single host is, of course, in direct proportion to the size of the mature host larva, as the entire body contents are consumed by the parasite brood. Very frequently the number of young larvae present in a host is larger than the food supply can support and the surplus consequently die and are themselves consumed. The broods of *Macrocentrus gifuensis*

Ashm. in *Pyrausta nubilalis* Hbn. range from 16 to 24, whereas in *M. ancylivorus* Roh., which develops in larvae of *Grapholitha molesta* Busck, only a single individual emerges, even though the early stages of embryonic development show numerous morulae, germs, and pregerms, and several may even attain the first larval stage. Daniel (1932) expresses the belief that the latter species, at one period in its development, was parasitic in a host of greater size than *Grapholitha*, in which polyembryonic reproduction was successfully accomplished.

All the polyembryonic Encyrtidae are exceedingly small, though a number of them attack large hosts, and consequently the number that can reach maturity in a single caterpillar is very large. The maximum recorded is somewhat more than three thousand from a larva of *Phytometra brassicae* Riley.

The hosts of the Platygasteridae are of smaller size, and the number of *Platygaster* produced in cecidomyiid larvae ranges from only 2 to 18.

The habits of the polyembryonic *Aphelopus theliae* differ in several respects from those of other groups of similar habit. The egg is deposited in nymphs of any of the first three instars of the membracid host, and death of the latter takes place in the last nymphal or the adult stage. Forty to sixty individuals develop to maturity in each host. As in *Macrocentrus*, the mature larvae emerge from the host body for pupation.

The large numbers of individuals mentioned above from single hosts are not invariably, or even generally, the product of a single egg. Some species consistently deposit a single egg at each insertion of the ovipositor, whereas others deposit two or more. In *Copidosoma* and *Litomastix*, which produce the largest numbers, each egg may give rise to one or two thousand larvae, but the larger broods are quite consistently the product of a number of eggs from one or several parasite females.

The parasite brood from a single host may all be of one sex or it may comprise both sexes. There is a marked difference between species in this respect, as shown below:

Parasite	Approximate number per brood	Per cent male broods	Per cent mixed broods	Per cent female broods
Macrocentrus gifuensis	16–24	35.5	37.5	27.0
Copidosoma gelechiae	160	37.0	1.0	62.0
Litomastix floridanus	1,000–2,000	3.9	83.7	12.4
Litomastix truncatellus	1,000–2,000	11.3	87.0	1.7
Platygaster felti	11–18	0.0	95.0	5.0
Platygaster hiemalis	6	0.0	80.0	20.0
Platygaster variabilis	15	0.5	92.0	7.5