

Chapter 5

BIOLOGY AND HOST RELATIONSHIPS OF PARASITOIDS

I. Definitions of Parasitoid and Host

A. Parasitoid: A parasitic insect that lives in or on and eventually kills a larger host insect (or other arthropod).

B. Host: Those animals attacked by parasitoids.

II. Characteristics of Parasitoids

A. Parasitoids usually destroy their hosts during development.

B. The parasitoid's host is usually in the same taxonomic class (Insecta).

C. Parasitoids are large relative to their hosts.

D. Parasitoid adults are free living while only the immature stages are parasitic.

E. Parasitoids develop on only one host individual during the immature stages.

F. With respect to population dynamics, parasitoids are similar to predatory insects.

III. Mode of Development of Parasitoids

A. With respect to the host

1. Endoparasitoid (internal): usually in situations where the host is exposed.

2. Ectoparasitoid (external): usually in situations where host lives within protected location (e.g., leafminers, in cocoons, under scale covers).

B. With respect to numbers of immature per individual host

1. Solitary parasitoid

2. Gregarious parasitoid

C. With respect to host stage

1. Egg

2. Larvae

3. Pupa

4. Adult

5. Combinations of the above (i.e., egg-larval parasitoid)

D. With respect to affect on host

1. Idiobionts: host development arrested or terminated upon parasitization (e.g., egg parasitoids)

2. Koinobionts: host continues to develop following parasitization (e.g., larval -pupal parasitoids)

E. With respect to other parasitoid species

1. Primary parasitoid

2. Secondary parasitoid (Hyperparasitism)

3. Tertiary parasitoid (Hyperparasitism)

F. Competition among immature parasitoid stages

1. Intraspecific competition: Superparasitism

2. Interspecific competition: Multiple parasitism

IV. Types of Hyperparasitism

A. Direct: The situation when a secondary parasitoid searches out and deposits its egg in or on the body of its parasitic host (a primary parasitoid), which may or may not be contained in the body of a living phytophagous insect.

B. Indirect: The situation when a secondary parasitoid searches out and deposits its egg in the body of an unparasitized, nonparasitic host. The egg usually remains

undeveloped until the nonparasitic host is subsequently parasitized by a primary parasitoid, which then serves as a host for the secondary parasitoid.

C. Facultative: Situation in which secondary parasitoid may develop as a primary parasitoid under the right conditions.

D. Obligatory: Situation in which secondary parasitoid can only develop within or on another primary parasite.

E. Autoparasitism: Situation in which the male of the species develops as a hyperparasite (sometimes of the female of the same species) and the female develops as a primary parasite. These species may be referred to as "heteronomous" because male and female develop on different hosts.

F. Cleptoparasitism: Not true hyperparasitism. Situation in which parasitoid preferentially attacks hosts already parasitized by another parasitoid species and then competes with first parasitoid for nutrients in the host. The cleptoparasite usually wins the competition.

V. Modes of Reproduction in Parasitic Hymenoptera

A. All hymenoptera display the phenomenon of haploid parthenogenesis. This means that the unfertilized egg undergoes parthenogenetic development to produce a normal, viable adult male which is haploid. All fertilized eggs develop into diploid females.

B. There are variations on the basic pattern which cause extremely important differences in the mode of reproduction.

C. The variations may be divided into 3 types of reproduction:

1. Arrhenotoky: This is the basic mode. Unfertilized eggs produce males and fertilized eggs produce females. May be referred to as "biparental" species. Male or female offspring can be produced through internal or external control of fertilization in some species.

2. Deuterotoky: Unmated females produce both male and female (mostly) progeny. Males produced are biologically and ecologically nonfunctional. Such species are called "uniparental". A diploid condition is produced in the female progeny through various cytogenetic mechanisms.

3. Thelytoky: Only female progeny are produced. Males are unknown. Also called "uniparental". Males can be produced when female adults are reared under extreme temperature conditions or if female adults are feed antibiotics to kill endosymbionts (e.g., rickettsia in the genus *Wolbachia*) that make them sterile through cytoplasmic incompatibility.

VI. Physiological and Behavioral Aspects of Reproduction in Parasitoids

A. Pre-mating Period. A pre-mating period after emerging from the pupal stage is generally not a necessary characteristic of the parasitic life. In most parasitoids mating is almost immediate after emergence from the pupa. This is aided in nature by the males of parasitic hymenoptera having a shorter developmental period than the females which allows them to precede the females to the adult stage by 1 or 2 days.

B. Mating Habits. In many species courtship behavior has been recorded (e.g., *Aphytis* species). In some species females tend to ignore males after mating occurs.

C. Pre-oviposition Period. This includes the interval between emergence of the adult female and deposition of the first egg. In some species it does not occur, in some it is facultative, and in some it is obligatory. Occurrence is usually associated with nutritional requirements of the adult female. With respect to egg production females can be divided into 2 groups:

1. Proovigenic: Those species of hymenoptera which reach the adult stage with a complete complement of ripe eggs which they deposit in a short time. No more eggs are produced during the parasitoid's life.

2. Synovigenic: Those species (most parasitoids) of hymenoptera which continue to produce eggs throughout the adult stage. Production of eggs is dependent on the nutrition of the adult female rather than on the metabolites retained from the immature stages.

a. Adult nutrition. A source of protein is required for continuous production of eggs. This protein may be provided by aphid honeydew, plant nectaries, and host feeding.

b. Host feeding and host mutilation. Wounds made by the parasitoid's ovipositor give rise to host body fluids which the parasitoid feeds upon. Actual "feeding tubes" may be formed by secretions from the ovipositor. Host mutilation may have been the first step in the evolutionary development of host feeding. Host feeding usually renders host unsuitable for development of immature parasitoids.

c. Ovisorption. When the synovigenic female does not obtain proteinaceous food or is unable to find hosts for a period of time, then ripe eggs in the ovarioles are absorbed. Eggs can be produced at a later time when food or hosts are found. The conservation of reproductive material is correlated with a high searching capacity.

D. Behavior in Host Selection

1. Host habitat finding.
2. Host finding.
3. Host acceptance.
4. Host suitability.

VII. Developmental Stages of Parasitoids

A. Egg types. Forms of eggs in entomophagous parasites are not uniform. Many adaptive modifications are superimposed on those differences due to phylogeny (Figs. 4.1–4.3).

B. Embryology. Usually the parasitoid deposits partially or completely incubated eggs in, on, or apart from the host and the larvae upon hatching commence to feed. These are monoembryonic eggs. A special exception to this is polyembryony.

C. Polyembryony: The production of many parasite larvae from a single egg. The polar nuclei give rise to an embryonic membrane called the "trophamnion". The trophamnion surrounds the embryonic area of the egg and functions in a nutritive fashion by extracting and concentrating nutrients from the host haemolymph to the embryonic area. The embryonic area divides into small groups of cells (morulae) within the trophamnion which lengthens into a chain-like structure. When the trophamnion breaks up the morulae form separate embryos. As many as 1500 embryos may be produced in *Copidosoma*. Characteristics of polyembryonic species are:

1. Oviposition into egg or young larvae of host with parasitoid maturity obtained in mature host larvae or pupae;
2. Exceptionally large numbers of progeny (1000 to 3000) develop within the host;
3. Simultaneous development and emergence of progeny from a single host individual; and
4. Major proportion of the broods consists of only 1 sex or mixed broods with widely varying sex ratios.

D. First-Instar Larvae. The most distinctive parasitic stage in the life cycle is the primary or first instar larva (Figs. 4.4–4.6). Subsequent larval stages are usually grub-

like without any conspicuous structures. The main types of first instar larvae recognized among the parasitoids or egg predators are:

1. triungulin 6. encyrtiform 12. caudate
2. planidium 7. eucoiliform 13. hymenopteriform
3. sacciform 8. mandibulate 14. chrysidiform
4. teleaform 9. microtype 15. agriotypiform
5. mymariform 10. muscoidiform 16. vesiculate
6. cyclopiform 11. vesiculate

E. Planidium larvae: First-instar larvae that have elongated setae arising from the thoracic or caudal regions to assist them in moving to their hosts after hatching from the egg (Fig. 4.7).

F. Triungulin larvae: First-instar larvae that have segmented legs that assists them in moving to their hosts after hatching from the egg (Fig. 4.8).

G. Intermediate and Mature Larvae (Fig. 4.9). The larva usually exhibits a change of form other than size as it develops through its various instars. The form change may be subtle, but because hypermetamorphosis is the general rule among endoparasitic larvae, there usually are conspicuous modifications between certain instars. Generally the larva loses any bizarre first-instar characteristics as it develops toward maturity.

H. Prepupae. Stage when the last larval instar ceases to feed prior to pupation and exhibits little movement (Fig. 4.10).

1. During this time the proctodaeum (hind gut) links up with the midgut. These have been separated during development to avoid fecal contamination of parasitoid's environment.

2. Connection of mid and hind gut allows excretion of fecal material. Fecal matter is referred to as meconia.

I. Pupae (Fig. 4.10). Most parasitic larvae pupate within the host remains. They may pupate within the host cocoon or puparium or in a mine or tunnel produced by a host.

VIII. Ovipositional Sites and Developmental Characteristics

A. Eggs or larvae deposited apart from host.

1. Eggs hatch or larvae deposited before host contact.
2. Eggs hatch after ingestion by host.

B. Eggs or larvae deposited on or near host.

1. Larvae develop externally on host.
 - a. Among eggs (egg predators)
 - b. In hosts concealed in cocoons, puparia, mines, galleries, galls, etc., or under scale covers
 - c. On exposed hosts
2. Larvae develop internally in host.
- C. Eggs, or more rarely larvae, deposited in host.

1. Deposited in host egg.

- a. Development completed in host
- b. Development completed on other eggs as egg predators
- c. Development completed in larva, prepupa, or pupa of host

2. Deposited in host larva or hemimetabolous insects.

- a. Development completed in host larva or in nymphs
- b. Development completed in host pupa
- c. Development completed in homopterous nymphs or adults

3. Deposited in host pupa.

4. Deposited in host adult.

D. Oviposition site correlated with sex of the egg.

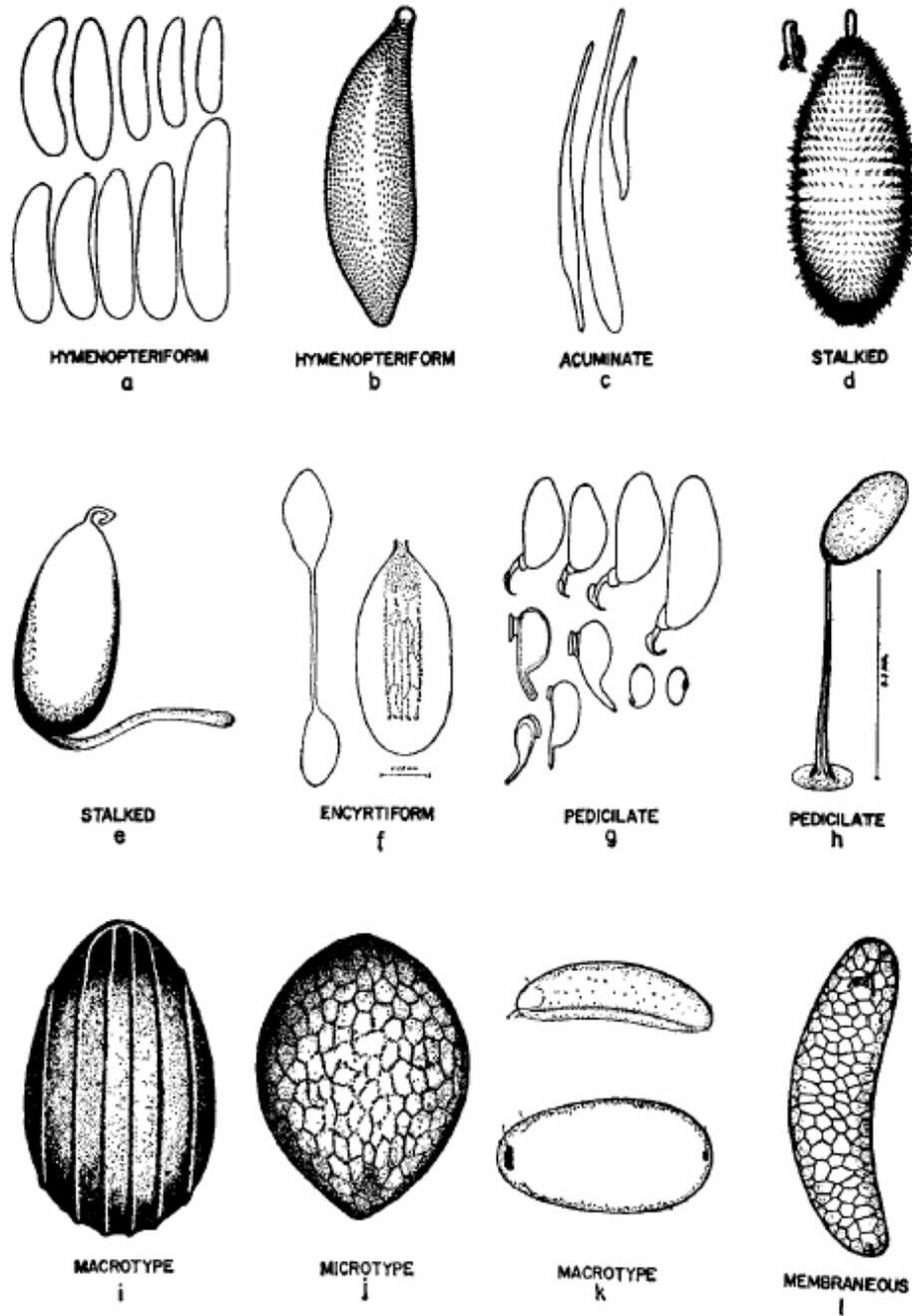


Fig. 4.1. Parasitic egg types: (a) ovarian eggs of Ichneumoninae; (b) *Monodontomerus dentipes* (Dal.); (c) Ephialtinae, Xoridinae; (d) *Eurytoma tylodermatis* Ashm.; (e) *Eupelmella vesicularis* (Ret.); (f) *Microterys flavus* (How.); (g) Tryphoninae, Ophioninae; (h) *Euceros frigidus* Cress; (i) *Poecilognathos thwaitesii* Westw.; (j) *Zenillia libatrix* Panz; (k) *Phorocera* sp.; and (l) *Bonnetia comta* Fall. Figures from Doult (1964).

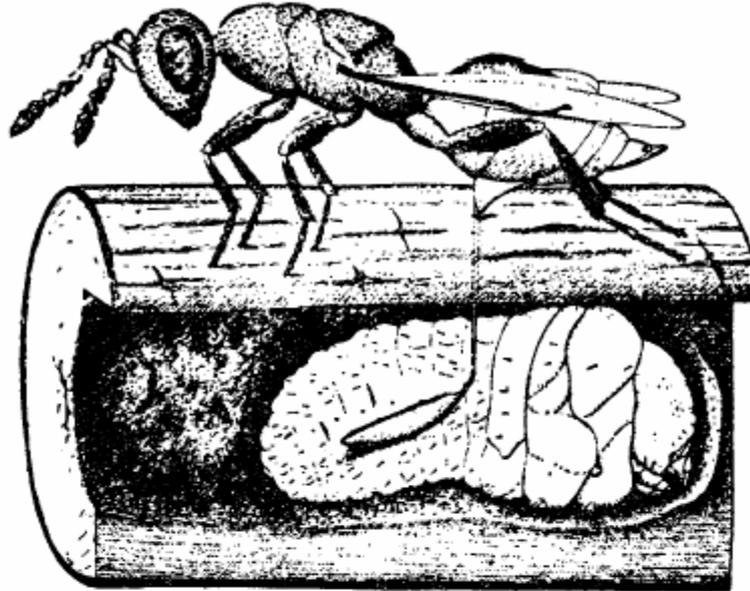


Fig. 4.2. *Eurytoma masii* Russo ovipositing externally on *Phloeotribus scarabaeoides* (Bern.) in woody branch. Figure from Doutt (1964).

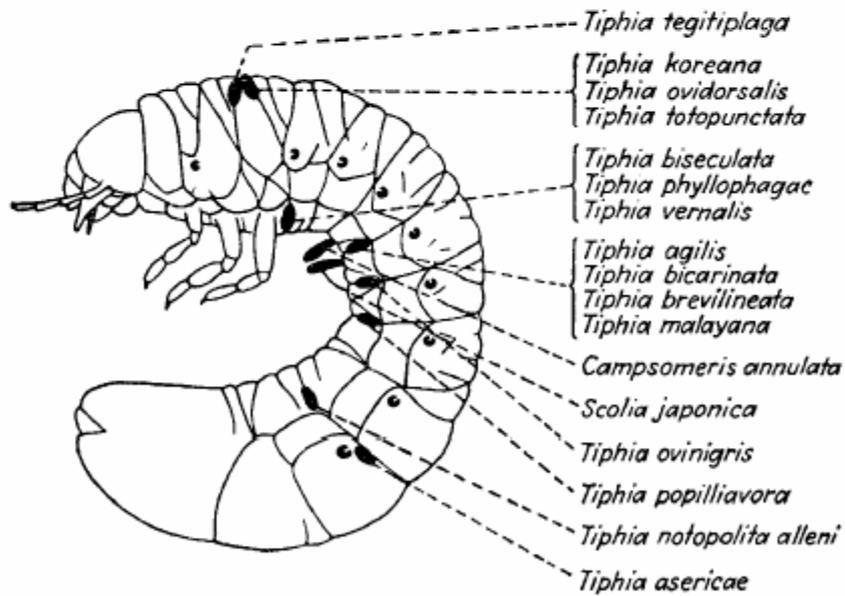


Fig. 4.3. Egg positions of a series of Tiphidae and Scoliidae on a scarab grub. Figure from Doutt (1964).

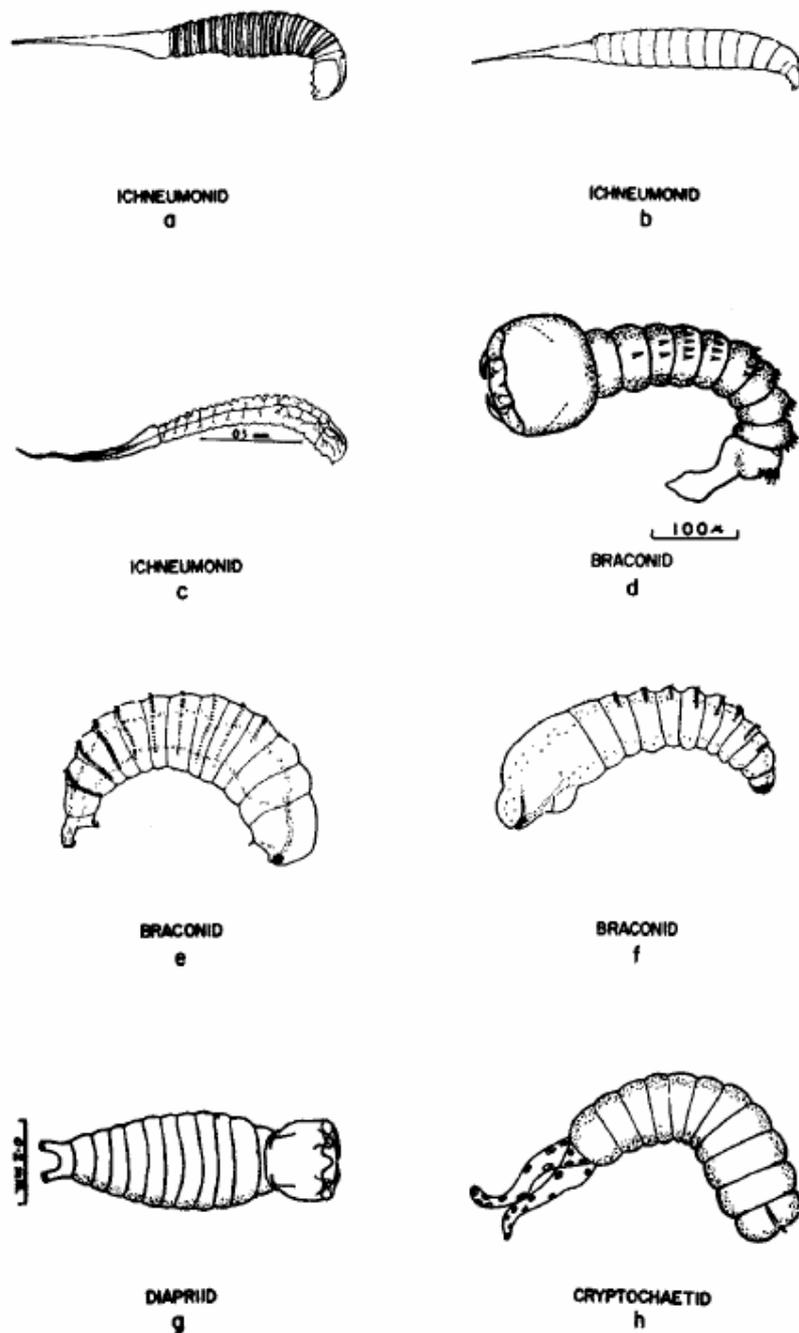


Fig. 4.4. Parasitoid first instars: a) *Zaleptopygus flavo-orbitalis* 96 hrs after oviposition; b) same species 240 hrs; c) *Cremastrus interruptor* early first-instar; d) *Apanteles medicaginis* first-instar larva; e) *Praon palitans* first-instar larva; f) *Trioxys utilis* first instar larva; g) *Loxotropa tritoma* first-instar larva; h) *Cryptochaetum grandicornis* late first-instar larva. Figures from Doutt (1964).

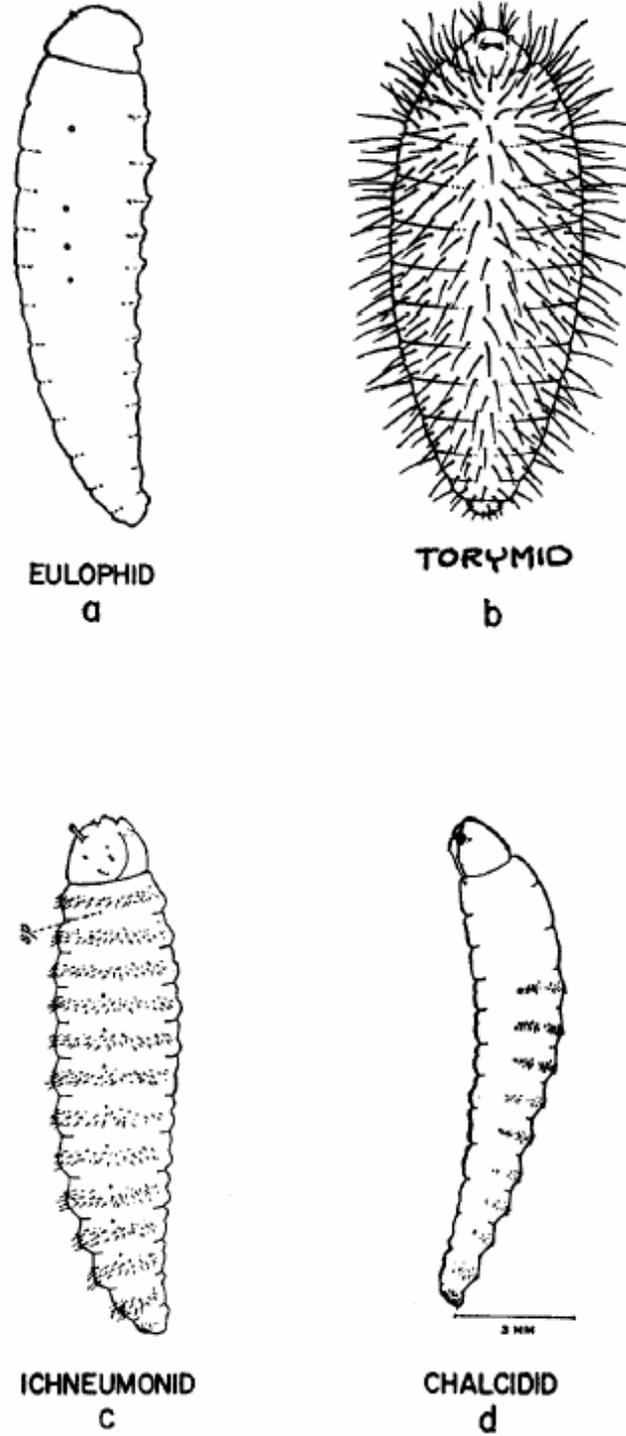


Fig. 4.5. Hymenopterous first-instar larvae: a) *Sympiesis* sp.; b) *Monodontomerus dentipes*; c) *Phanomeris phyllotomae*; d) *Spilochalcis side*. Figures from Doutt (1964).

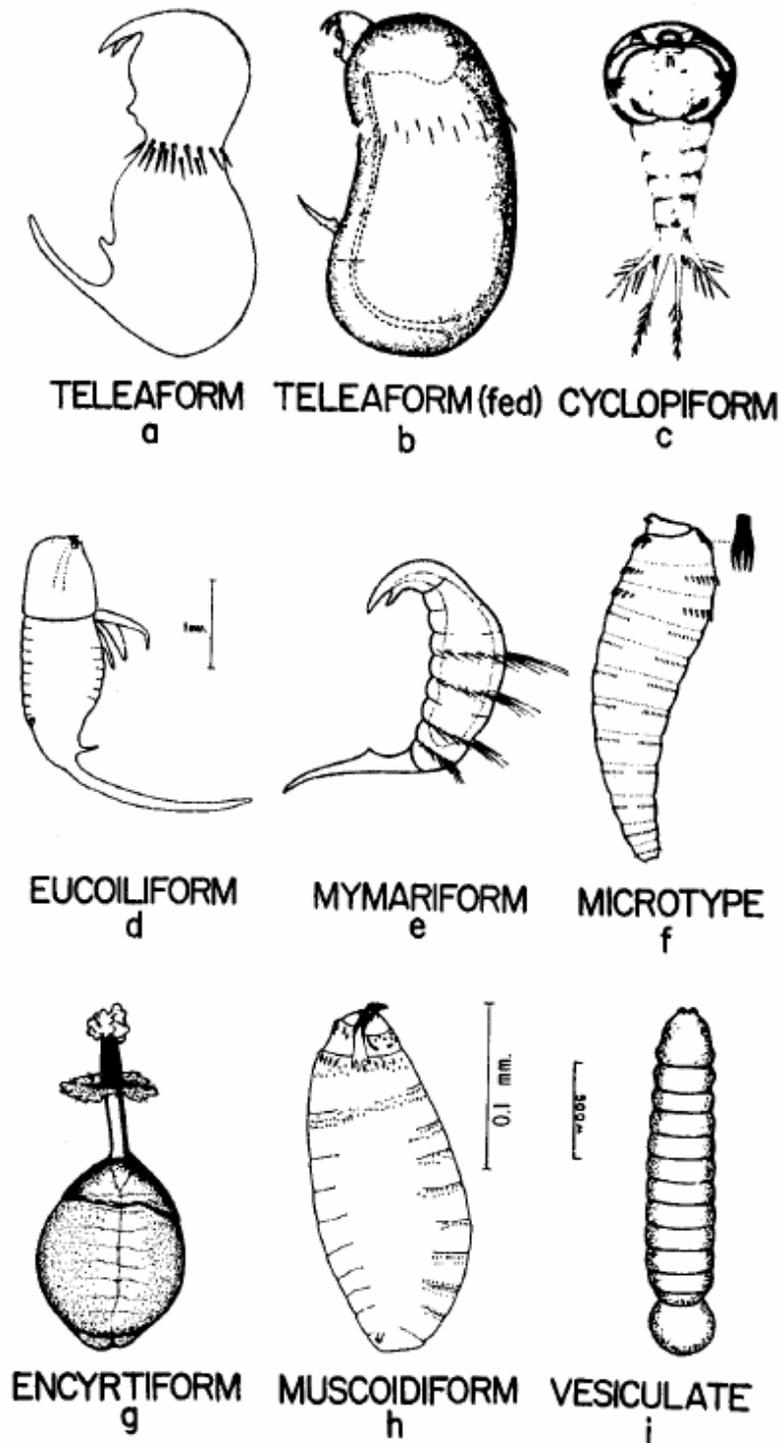


Fig. 4.6. Various types of parasitoid first-instar larvae: a) *Telenomus gifuensis*; b) engorged *Hadronotus ajax*; c) Platygasterid; d) *Hexacola* sp.; e) *Polynema striaticorne*; f) *Orthogonalos debilis*; g) *Isodromus niger*; h) *Phorocera incrassata*; i) second stage of *Apanteles medicaginis*. Figures from Doutt (1964).

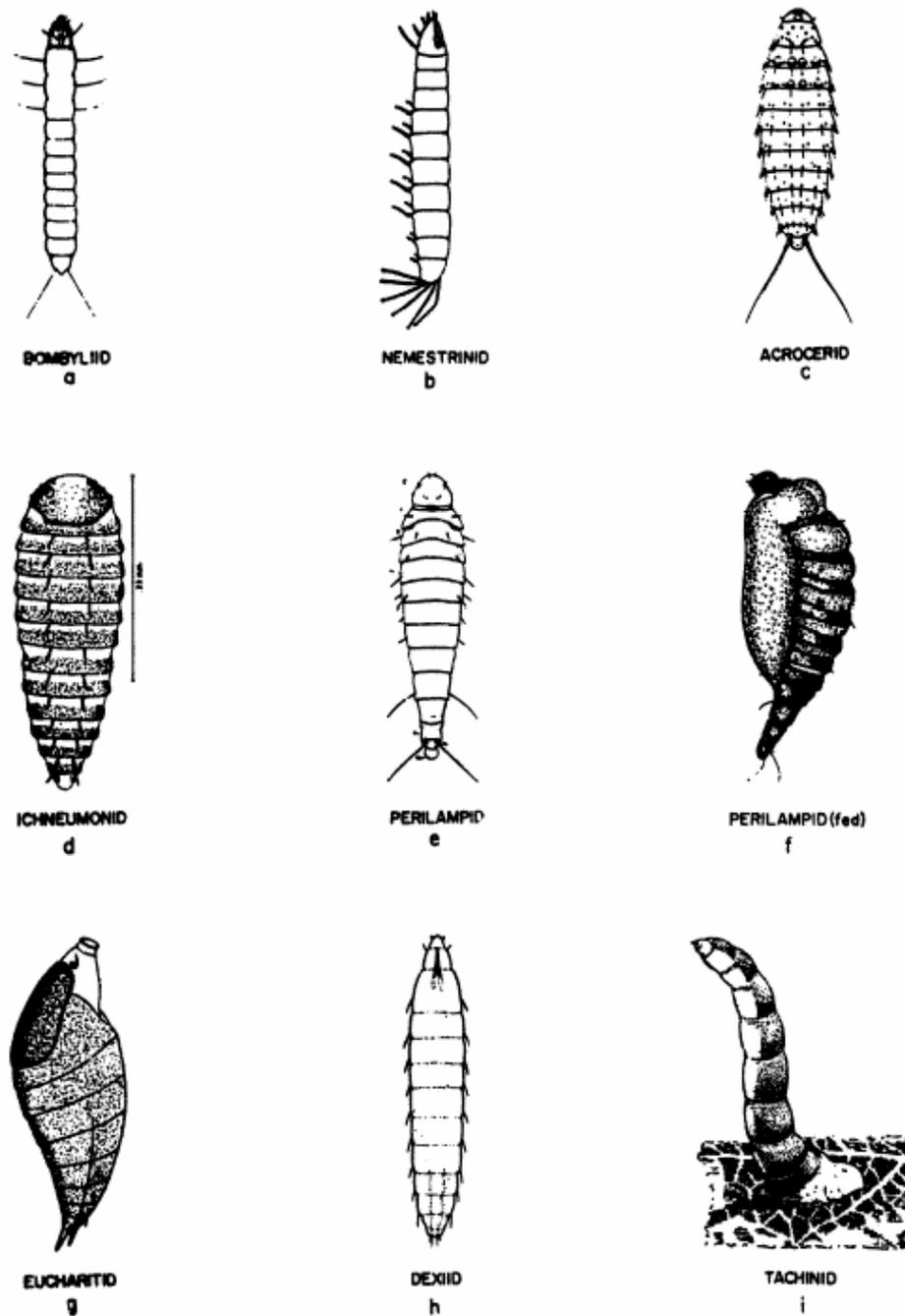


Fig. 4.7. PLANIDIUM TYPE first-instar larvae: a) *Hyperalonia oenomaus*; b) *Trichopsidea clausa* lateral view; c) *Pterodontia flavipes* dorsal view; d) *Euceros frigidus* dorsal view; e) *Perilampus laevifrons* dorsal view; f) *Perilampus chrysophae* engorged planidium, lateral view; g) *Schizaspidia tenuicornis* lateral view; h) *Callirrhoe siberita*; i) *Tachina magnicornis* showing the egg chorion serving as an attachment "cup" to leaf. Figures from Doutt (1964).

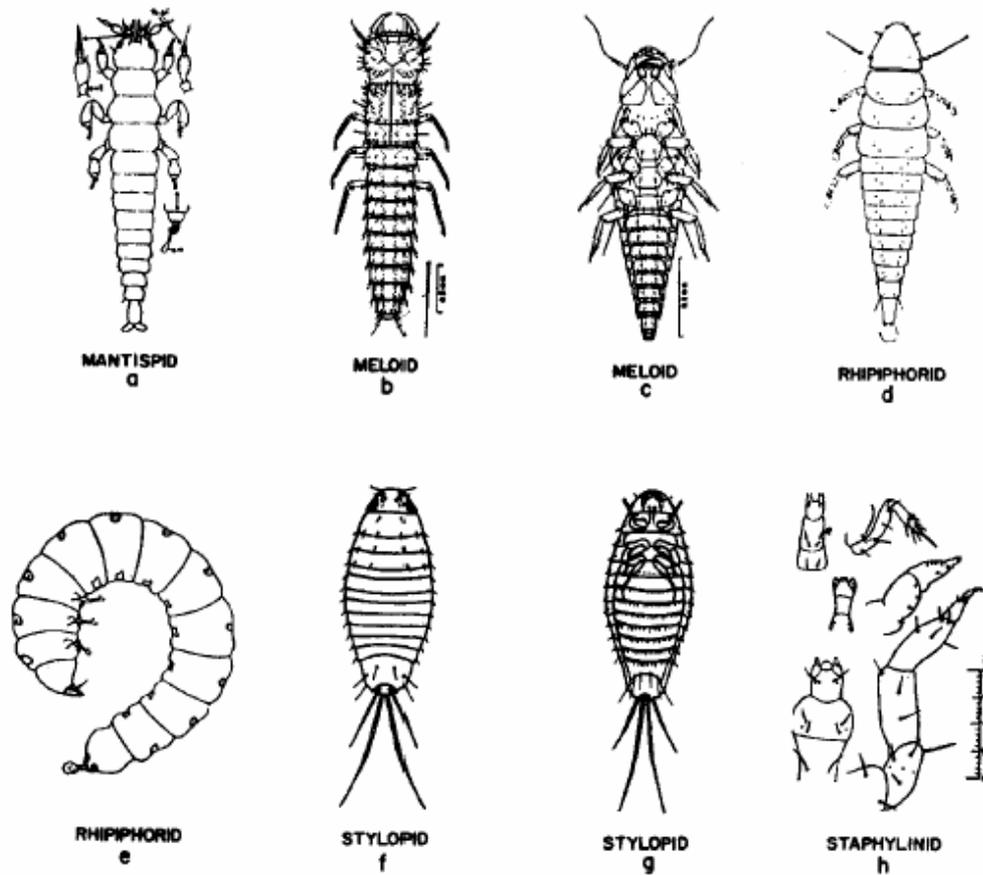


Fig. 4.8. TRIUNGULIN TYPE first instar larvae: a) *Mantispa interrupta*; b) *Epicauta pardalis*; c) ventral view *Zonitis bilineatus*; d) *Rhipiphorus smithi*; e) *R. smithi* first-instar endoparasitic phase; f) *Eoxenos laboulbenei* dorsal view; g) *E. laboulbenei* ventral view; h) *Aleochara sparsa* labium and leg of first, second, and third instar. Figures from Douitt (1964).

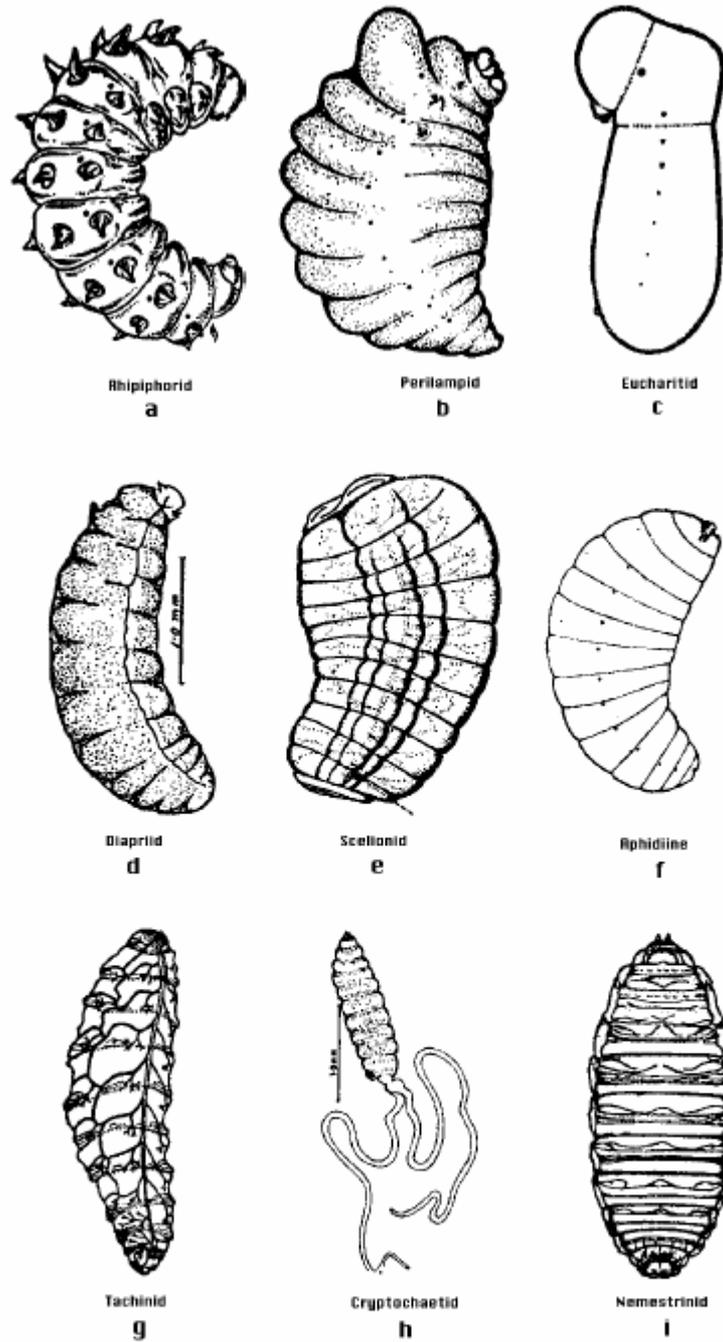


Fig. 4.9. Mature larvae of various parasitoids: a) *Rhipiphorus smithi* fully fed sixth instar; b) *Perilampus chrysopae* mature third instar; c) *Stilbula tenuicornis* third instar; d) *Loxotropa tritoma* third instar fully grown; e) *Hadronotus ajax* third instar larva; *Trioxys utilis* third instar; g) *Sturmia harrisinae* third-instar larva; h) *Cryptochaetum grandicorne* young third-instar larva; i) *Trichopsidea clausa* prepupal-larva dorsal aspect. Figures from Doutt (1964).

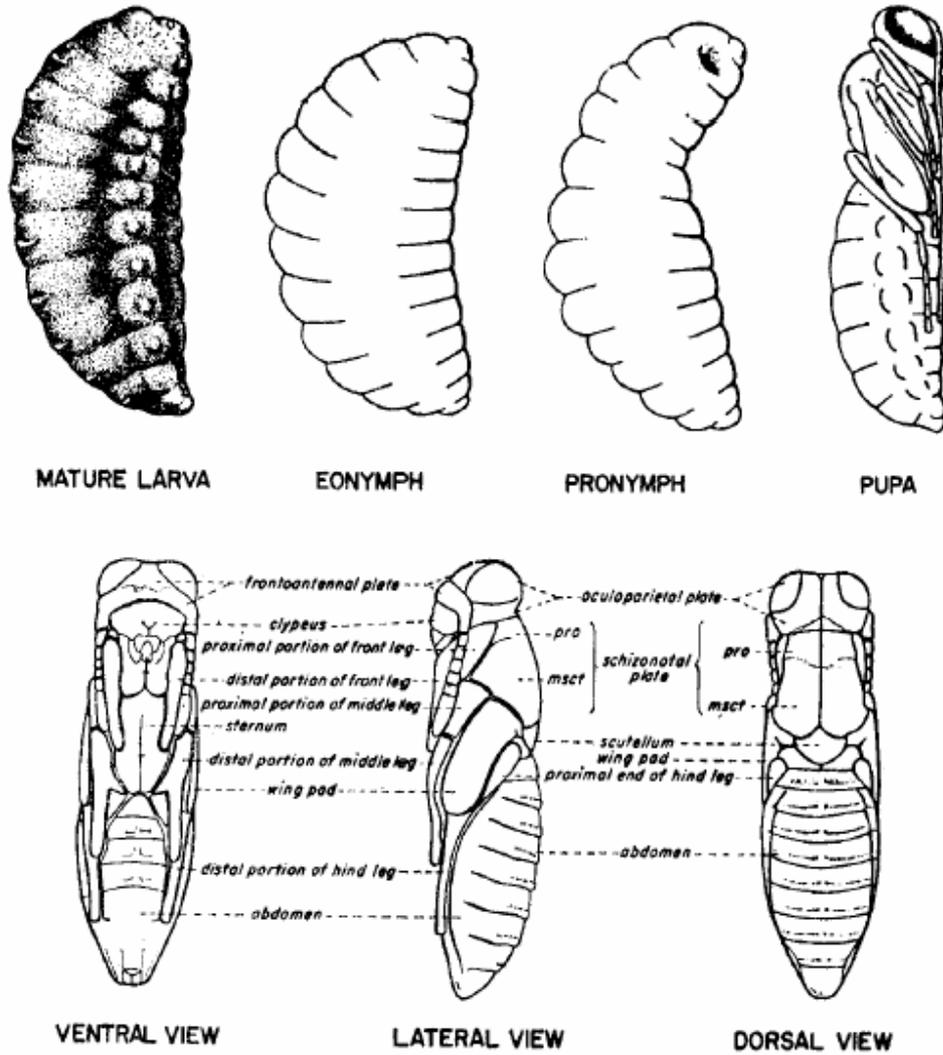


Fig. 4.10. Prepupal and pupal stages of parasitic Hymenoptera. Top figures are of *Exenterus abruptorius*. Lower figures are various aspects of *Eupelmus allynii*. Figures from Doult (1964).

Chapter 6

TRAITS COMMON TO PREDATORS AND PARASITIDS

I. Behavior in Host/Prey Selection

A. A natural enemy in nature limits its attack to a fraction of the suitable prey / hosts species that may be available to it.

B. Behavior, like morphological characteristics, is specific and adaptive, but the adaptive action is based on a foundation of specificity.

C. Several distinct and consecutive processes of host selection occur and through their operation the host list of a parasite or predator becomes restricted to fewer host species than are potentially available to it in nature.

D. Salt classified these processes into 3 broad categories which follow in proper sequence:

1. Ecological selection

2. Psychological selection

3. Physiological selection

E. These were later reclassified into:

1. Host habitat finding (initially ecological selection)

2. Host finding (initially ecological selection)

3. Host acceptance

4. Host suitability

F. S. Bradleigh Vinson (1975) added host regulation as a fifth step.

II. Host Habitat Finding

A. Parasites and predators initially and fundamentally seek a certain environment, and they do this irrespective of the presence of hosts.

B. Particular plant species may exert a strong attraction even though suitable hosts are not present on it. Conversely, the parasite / predator may ignore suitable hosts / prey growing on plants to which it is not attracted.

III. Host Finding

A. Once the parasite / predator is in the habitat of the host / prey, it still must be able to locate a host individual.

B. The most commonly reported senses used in detecting the host are tactile and olfactory (for parasitoids).

C. It has been proposed that a parasite / predator tends to search in the parts of its environment most likely to contain its host and that this is caused by a combination of pre-adaptation in habits and a specific attraction exerted by the portion of the environment concerned.

D. Some natural enemies display a distinct behavioral change when hosts are found in a location. This change is from a random search "mode" to a search mode of tight circles within the area of interest.

IV. Host Acceptance

A. Even though a parasite / predator actually finds or contacts a suitable host / prey, it still may not attack if the proper stimuli are lacking.

B. This step is truly host selection and is clearly a matter of innate behavior of a parasitic / predacious species.

C. van Lenteren (The Netherlands) has done some excellent work with regards to this area using the parasitoid *Encarsia formosa* and the greenhouse whitefly.

D. Hosts may be rejected because they are:

1. Too young or old; 2. Wrong size
3. Diseased; 4. Unhealthy
5. Already parasitized (by the same or another species)
6. Have been used for host feeding
7. Do not exhibit the correct reactions when investigated by the parasitoid

V. Host Suitability

A. Even though a parasite / predator has found the potential host / prey in its habitat and selected it for attack, the host/parasite or prey/predator relationship may still not succeed if the potential host individual is immune or otherwise unsuitable.

B. Oviposition by a parasite is not necessarily an index to host suitability and the attractiveness of the host is often independent of its suitability for parasitic development.

C. Studies have suggested that hosts may evolve some type resistance to parasites. The larch sawfly was heavily parasitized by *Mesoleius tenthredinis* in Canada. After some years the efficiency greatly decreased in Manitoba and Saskatchewan. Studies showed that the hosts were inhibiting the parasite's embryonic development

VI. Learning in Natural Enemies

A. Both parasitoids and predators have the ability to learn.

B. Learning has the ability to affect host preference.

C. Associative learning involves learning to link the perception of one (or two) stimuli with the presence of another object or event. Parasitoids may associate secondary stimuli (e.g., host plant odors) with hosts or food sources.

D. Mass reared natural enemies may be less effective in the wild because they have not learned to associate their hosts / prey with specific odors in nature. Exposure to the target host prior to release may improve this situation.

VII. Attributes of Effective Natural Enemies

A. **High searching capacity:** Searching ability is a composite of several qualities of the parasite which include:

1. Its power of locomotion;
2. Its power of perception (of the host);
3. Its power of survival; and
4. Its aggressiveness and persistence.

B. **Limited host specificity:** Most BC successes have resulted from the introduction of host-specific entomophagous species. A high degree of host-specificity indicates good bio-physiological adaptation to the host and a fairly direct dependence on changes in the host's population.

C. **High reproductive potential:** This includes a short developmental period and a relatively high fecundity.

D. **Wide environmental tolerance:** Ideally, the host and parasite would have absolutely equivalent distributions. This in turn means that the parasite would be well adapted to a broad range of climatic conditions.

E. **Restriction of oviposition to suitable hosts:** Oviposition in previously parasitized hosts or unhealthy hosts would limit the effectiveness of the parasite.

F. Amenability to insectary rearing: This would facilitate the breeding of material for colonization and distribution, and thus would make the early control of the pest more probable.

G. **Density-dependent performer**: Only those natural enemies that increase mortality levels in their host of prey populations as those populations increase are effective natural enemies. The cause of mortality alone does not mean that a natural enemy will 'regulate' a host or prey population.

H. **Good competitive ability**: Many natural enemy species may compete for the same host. A good natural enemy may be out competed resulting in inefficient control if less effective natural enemies lay their eggs first in suitable hosts.

I. **Synchronization with the host and its habitat**. Some natural enemies may not appear in sufficient numbers at crucial times of the year such as spring time, allowing the host to out distance it reproductively.