

## PARASITOID WASPS, NATURAL ENEMIES OF INSECTS

**A. Bonet**

*Department of Entomology, Instituto de Ecología A. C., Mexico*

**Keywords:** Augmentative biological control, ectoparasitoid, endoparasitoid, endosymbionts, idiobiont, koinobiont, mitigation, multitrophic interactions, natural enemies, ovigeny index, parasitism, parasitoids, polydnviruses, provigeny, synovigeny, *Trichogramma*, *Wolbachia*

### Contents

1. Introduction
  2. Parasitoidism (= parasitism), important mode of life in Hymenoptera
  3. Evolution of Hymenoptera parasitoids
  4. Parasitoid biology
    - 4.1 Developmental Strategies of Parasitoids
      - 4.1.1 Ectoparasitoids
      - 4.1.2 Endoparasitoids
  5. Parasitoid Behavioral Ecology
    - 5.1 Foraging and Optimization Theory with Parasitoids
    - 5.2 Parasitoid Interactions through Infochemicals
  6. Multitrophic interactions in natural and modified communities
  7. Augmentative biological control with parasitoids in the Neotropics
    - 7.1 A Success Case Study, Biological Control of Agricultural Pests with *Trichogramma* in Brazil, 20 Years of Research, Maintenance and Release of *Trichogramma*
    - 7.2 Search for New Parasitoids against Bruchid Pests in one of the Domestication Centers of Beans (legume pulses), a Mexican Example
  8. Digital information resources about parasitic wasps
  9. Conclusion
- Acknowledgements  
Glossary  
Bibliography  
Biographical Sketch

### Summary

Parasitoid wasps are important insects in the Neotropics. They are consumers (third and fourth trophic level) in the food web and play a vital role, in a multitrophic interaction context, in natural communities. Their high diversity (240,000 species) and major radiation in Hymenoptera relies on the successful parasitism mode of life. Notorious representative families are in Chalcidoidea and Ichneumonoidea (200,000 species). Here, we address recent developments in parasitoid evolutionary history, developmental strategies, endosymbionts, behavioral ecology, and their role in natural and modified communities. Lastly, the increasing use of parasitoid wasps in augmentative biological control in Latin America is discussed.

### 1. Introduction

Parasitoid wasps (belonging to insects of the Hymenoptera order) are important organisms in the natural and human modified environments of the Neotropics. They are the natural enemies of arthropod hosts in natural ecosystems and can be used as biological control agents against insect pests in agro-ecosystems. At least half of all animals have parasitism as their lifestyle and up to 20% of all insects account to be parasitoid wasps.

Hymenoptera have around 320,000 species, mostly more than 75% (240,000) are parasitoids. Parasitoid wasps are highly diverse and specialized to attack a particular host life stage (egg, larvae, pupae and adults) of most arthropods, mainly insects. They are highly specialized due the tight intimate relationship with their respective hosts. The diversity and radiation of the Hymenoptera relies on the successful parasitoid mode of life, which is present in the majority of families of this order. Within terrestrial ecosystems, parasitoids covered the third (primary parasitoids) and fourth (hyperparasitoids) trophic level attacking mainly phytophagous hosts which are on or inside host plants.

Parasitoid wasps need the presence of hosts for their feeding, survival and reproduction; this agonistic interaction between parasitoid and host is the result from a long co-evolutionary process and specialization in time. Extreme specialization and geographic differences on the specialization of both interacting organisms are favored, because of the need to complete the parasitoid development at expenses of one host. The parasitoid wasps depend on a series of adaptations to the ecology and physiology of their host plants for survival. This has been possible due the stable conditions of climate in specific natural ecosystems like the tropics. So changes in environmental conditions, makes them more susceptible than other organisms to changes, e.g. extreme temperature can reduce the presence of endosymbiont populations inside parasitoids. Parasitoids mitigate and control the abundance of different pests, mainly other insects that could grow exponentially without the presence of them.

In this chapter we will write about parasitoid wasps, their evolutionary history, biology, developmental strategies, behavioral ecology, and multitrophic interactions. Their use as biological control agents against insect pests in the Neotropics is explored in the last part of the chapter. Novel approaches using web sites for diffusion of parasitoid wasp knowledge are described.

## **2. Parasitoidism (= parasitism), Important Mode of Life in Hymenoptera**

In practical terms parasitoidism is equal to parasitism, in which parasitic wasps feed and damage an unrelated bigger species host, eventually the host is killed. Only a single host is required for the parasitoid to complete its development, and often a number of parasitoids develop gregariously on the same host.

### **Definition of parasitoid**

The term parasitoid is an adjective first devised by Reuter in 1913 to characterize a range of feeding behavior intermediate between the parasite (which harms the host but

generally does not kill) and predator (which kill the prey or host) behaviors. A parasitoid larva feeds like a true parasite on or inside a unique living host, obtaining from it all the necessary nutrients required to complete its development up to the pupal stage, eventually the host dies. Sometimes, the host is killed by the ovipositing female through the injection of paralyzing substances; the parasitoid larvae feed only on the resulting host's dead tissue. Askew (1971) used the term "protelean parasites" to name parasitoids and true parasites, but it has been dropped out. At present the term 'parasitoid' is used more often to describe an organism using this mode of life.

Parasitoid wasps have evolved a wide spectrum of interactions with their host (Godfray 1994). Different interactions have been classified in relation to their biology. From the simple solitary (at most one offspring is able to complete development to adult on or in a host) and gregarious parasitoid species (more than one offspring can successfully complete development on or in a host) to the koinobiont and idiobiont parasitoids which emphasized the developmental strategy of the parasitoid.

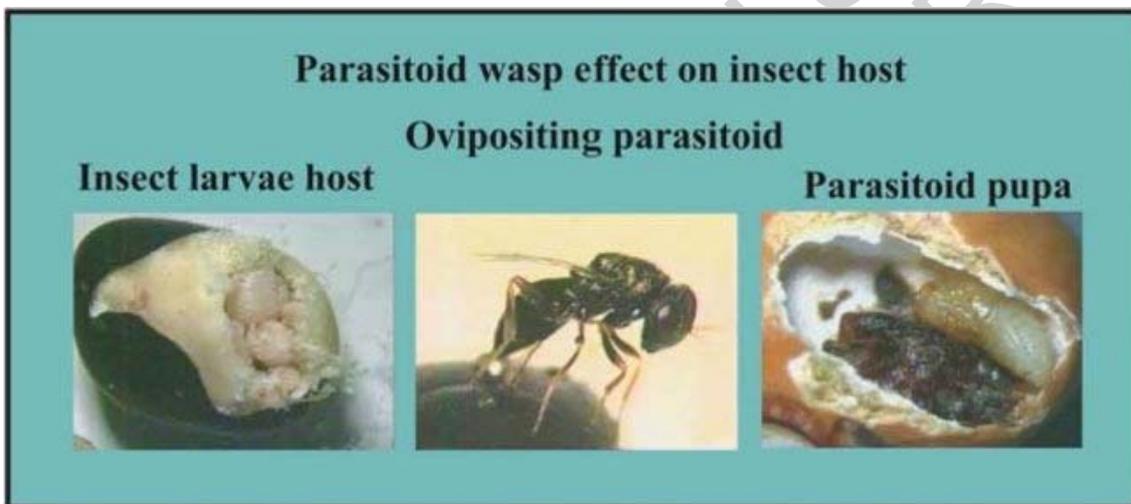


Figure 1: Insect host (*Acanthoscelides obtectus* pupa), female *Dinarmus basalis* parasitoid ovipositing on host and parasitoid pupa (*D. basalis*) developing inside seed legume (dry bean, *P. vulgaris*); (Photos by Carlos Morales and Cesar Rojas)

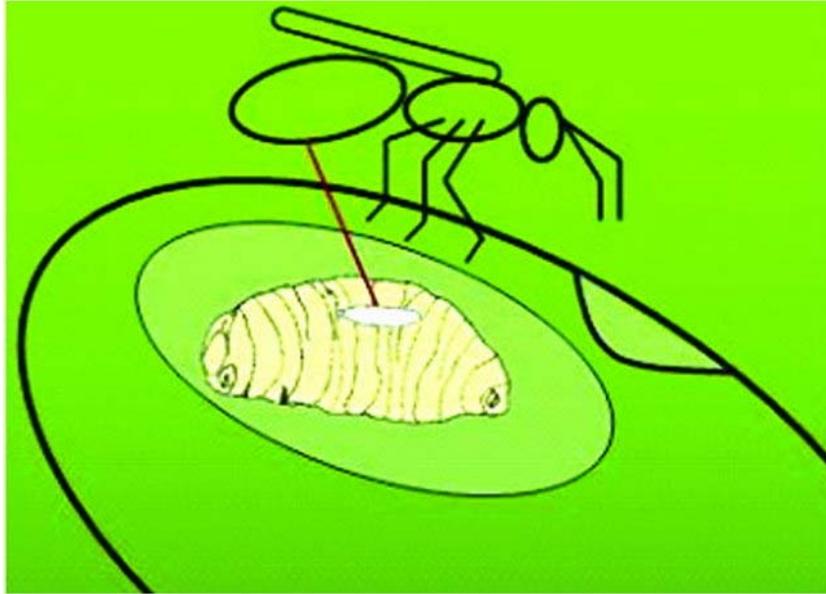


Figure 2: Schematic drawing of an idiobiont ectoparasitoid ovipositing on a concealed bruchid host inside a bean seed; (*Drawing done by Cesar Rojas*)

In a broad sense, Askew & Shaw (1986) categorized parasitoids as koinobiont and idiobiont parasitoids due to their developmental behaviors. After oviposition, koinobiont parasitoid offspring allows its hosts to continue developing, eventually the host is killed when the parasitoid emerge as an adult. The majority of koinobionts are endoparasitoids that attack hosts exposed to open environments, whereas idiobionts use hosts which are more concealed and less exposed to the open environment. Idiobiont parasitoid either paralyzes permanently or kills its host immediately at oviposition or dies shortly thereafter. A simple practical category is the host site where the female mother oviposits its progeny eggs, on (ectoparasitoid) or inside (endoparasitoid) the host. The first and more basal lineages of parasitoid wasps are in the Orussidae family, they have a slender and long ovipositor and are ectoparasitoids for wood-boring beetles and other wasps.

### 3. Evolution of Hymenoptera Parasitoids

Hymenoptera (320,000 species) is one of the four hyper-diverse insect lineages (group of insects) current today, the other three are Coleoptera (350,000) species, Lepidoptera (150,000) and Diptera (120,000). Although today Coleoptera has the major number of species, Hymenoptera may eventually rival in the future to the total diversity with respect to other hyper-diverse lineages, the most conservative potential estimates ranges are in the 600,000 to 1,200,000 species, with many unknown, yet undescribed microhymenopterans species (Proctotrupoidea, Chalcidoidea, Platygastroidea) remaining to be discovered in the tropics (Grimaldi & Engel 2005).

Hymenoptera is a recent monophyletic order and its success is due to their body structure with small hind wings that are linked to the forewings by the hamuli (minute hooks), the haplodiploid sex determination and the appearance of the parasitoid mode of life. Additionally, the transition from phytophage to parasitoidism conditions was

favoured by the development of the mesosoma and the metasoma on the wasp body and the acquisition of the sting ovipositor. The Hymenoptera parasitoids represent the single largest radiation of parasitic arthropods. Other habits like gall forming, pollen (pollination) and nectar feeding, predation with nest provisioning (sociality) in Hymenoptera are more derived and recent, they are present in the Aculeata, Ichneumonoidea, Chalcidoidea and Cynipoidea.

The first hymenopterans appeared in the Triassic (230–200 million years ago) of Australia, Central Asia and Africa. Although the origin of the Euhymenoptera and parasitoidism is 210 million years ago near the Triassic-Jurassic boundary. It is in the next era, the Jurassic (200 - 140 millions year ago) that Hymenoptera with the Apocrita (“true wasps” and parasitoid wasps) irradiated throughout the terrestrial environment and the first parasitoid lineage appeared near the Triassic – Jurassic boundary about 210 millions ago. In the Cretacic (145 – 65 million years ago) all of the major hymenopterans lineages (like ants and bees) present today irradiated in parallel with the angiosperms (85 million years ago), as well as other insect taxa (Grimaldi and Engel 2005). All the important parasitoid wasp families are present with the exception of Cynipoidea which originated later towards the end of the Cretacic era. In the Tertiary (65 – 2 million years ago) more radiation within family lineages occurred, up to recent times with a high diversity in terrestrial ecosystems.

Parasitic wasps are found in the following 12 superfamilies (No. of species in parenthesis) of Hymenoptera: Orussoidea (70), Stephanoidea (100), Trigonalioidea (100), Megalyroidea (100), Evanioidea (1,200), Ceraphronoidea (2,000), Proctotrupeoidea (6,000), Platygastroidea (10,000), Cynipoidea (4,000), Chalcidoidea (100,000), Ichneumonoidea (100,000), Chrysoidea (6,348) and Vespoidea (11,124) (Nieves Aldrey & Fontal-Cazalla 1999, Pennacchio & Strand 2006). Major species richness is in Ichneumonoidea 100,000 (Braconidae 40,000 and Ichneumonidae 60,000) and Chalcidoidea (100,000).

Rasnitsyn (1988) postulate the first hypothesis that parasitoidism appeared for the first time in the common ancestor of Orussidae and Apocrita, whose host probably was a xylophage insect inside tree trunk galleries. All indications point out that the ancestral parasitoid wasp was an ectoparasitoid while endoparasitism arises later. Ectoparasitism is found in the ancestral basal clades of Orussoidea, Stephanoidea, Ichneumonoidea and Aculeata, they are ectoparasitoids that attack hosts living inside plants, mainly tree trunk galleries. The superfamily Megalyroidea and many constituents of the superfamily Evanioidea, Chalcidoidea and Ceraphronoidea are also ectoparasitoids.

Endoparasitism is more extended in the more recent evolutionary groups of Ichneumonidae and Chalcidoidea, as well as, all Proctotrupeoidea and Platygastroidea, also endoparasitism is present in some primitive macrocypinids attacking hosts inside tree trunk (wood) galleries. Idiobiont behavior is also a primitive condition, meanwhile koinobiont parasitoids are of more recent origin. The induction of permanent host paralysis or even host killing, after the injection of poisonous substances (by idiobiont parasitoid), is primitive with respect to the temporal paralysis caused by koinobiont parasitoids.

-  
-  
-

TO ACCESS ALL THE 23 PAGES OF THIS CHAPTER,  
Visit: <http://www.eolss.net/Eolss-sampleAllChapter.aspx>

### Bibliography

Arakaki, N., H. Noda and K. Yamagishi. 2000. *Wolbachia*-induced parthenogenesis in the egg parasitoid *Telenomus nawai*. *Entomologia Experimentalis et Applicata* 96: 177 – 184. [Confirmation of *Wolbachia* inducing thelytoky in Scelionidae].

Askew, R. R. and M. R. Shaw. 1986. Parasitoid communities: their size, structure and development. In: Waage, J. and D. Greathead (Eds.). *Insect Parasitoids*. Academic Press, London. 225-264. [Classic contribution that categorize idiobiont and koinobiont parasitoids]

Barbosa, P. 1998. *Conservation Biological Control*. Academic Press. 396 pp. [Good book that refers to the importance of conserving parasitoids in natural and modified communities. Preservation of natural fields adjacent to cultivate land is essential for the permanence of parasitoids].

Barbosa, P. and I. Castellanos. 2005. *Ecology of predator-prey interactions*. Oxford University Press. 394 pp. [Excellent book on direct and indirect impact natural enemies have on other organisms; their importance on top-down or bottom-up effects in structuring communities].

Delgado, A., A. Bonet and P. Gepts. 1988. The wild relative of *Phaseolus vulgaris* in Middle America. In: Gepts, P. (Ed.). *Genetic Resources of Phaseolus beans*. Kluwer Academic Publishers. Dordrecht: 163-184 [Describe the entomofauna present on wild type populations and cultivated forms of *Phaseolus vulgaris* L. (beans)].

Dicke, M and M. W. Sabelis. 1988. Infochemical terminology: based on cost-benefit analysis rather than origin of compounds? *Functional Ecology* 2: 131-139. [The authors develop new infochemical terminology related to the previous Nordlund & Lewis (1976) semiochemical terminology].

Godfray, H. C. J. 1994. *Parasitoids, Behavioral and Evolutionary Ecology*. Princeton University Press. 473 pp. [Excellent contribution to our knowledge of the behavioral and evolutionary ecology of parasitoids. The book emphasized the different reproductive strategies this organisms have, treating them in relation with: searching for a host, host selection, clutch size, sex ratio, evolutionary aspects of physiological interactions between parasitoid and host, mating strategies, life history theory and community ecology].

Gonzalez-Hernández, A., R. A. Wharton, J. A. Sánchez-García, V. López-Martínez, J. R. Lómeli-Flores, I. Figueroa de la Rosa and H. Delfín-González. 2003. *Catálogo ilustrado de Braconidae (Hymenoptera: Ichneumonoidea) en México*. CD-rom. Universidad Autónoma de Nuevo León. [First data base in Spanish that covers initial efforts to digitize aids for identify and determination of Braconidae from México].

Grimaldi, D. and M. S. Engel. 2005. *Evolution of Insects*. Cambridge University Press. 758 pp.

[Latest and complete synthesis of the evolutionary history of fossil and recent insect orders].

Jervis, M. A., G. E. Heimpel, P. N. Ferns, J. A. Harvey and N. A. C. Kidd. 2001. Life-Histories strategies in parasitoid wasps: a comparative analysis of 'ovigeny'. *Journal of Animal Ecology* 70 (3): 442-458. [They devised a comparative of early-life concentration of egg production in parasitoids].

Jervis, M. A., J. Ellers and J. A. Harvey. 2008. Resource Acquisition, Allocation, and Utilization in Parasitoid Reproductive Strategies. *Annu. Rev. Entomol.* 53: 361-385. [Excellent review related to the integration of resource allocation, acquisition, and utilization to models of pro-ovigenic and synovigenic

parasitoid species].

van Lenteren, J. C. and V. H. P. Bueno. 2003. Augmentative biological control of arthropods in Latin America. *BioControl* 48: 123-139. [Important review on biological control of arthropods in Latin America].

Maddison, D. R. and K. S. Shutz (eds.) 2007. *The Tree of Life Web Project*. Internet Project. <http://tolweb.org> [Excellent web site with good taxonomical information].

van Meer, M. M. M., J. Witteveldt and R. Stouthamer. 1999. Phylogeny of the arthropod endosymbiont *Wolbachia* based on the *wsp* gene. *Insect Molecular Biology* 8 (3): 399-408. [This phylogeny emphasized the importance of *Wolbachia* inducing reproductive alterations in their hosts].

Nieves-Aldrey, J. L. and F. M. Fontal-Cazalla. 1999. Filogenia y evolución del orden Hymenoptera. *Bol. S. E. A.* 26: 459-474. [Good review of Spanish of Hymenoptera evolution and phylogeny].

Noyes, J.S. 2003. *Universal Chalcidoidea Database*. World Wide Web electronic publication. [www.nhm.ac.uk/entomology/chalcidoids/index.html](http://www.nhm.ac.uk/entomology/chalcidoids/index.html) [accessed 05-Sep-2003]. [Excellent database which covers more than 31,000 taxonomical names from more than 40,000 references. It is an obligate reference for Chalcidoidea students].

Parra, J. R. P. and R. A. Zucchi. 2004. *Trichogramma* in Brazil: Feasibility of Use after Twenty Years of Research. *Neotropical Entomology* 33 (3): 271-281. [It brings to our attention the excellent research done in Brazil on *Trichogramma*, from basic research in the laboratory to applied experiences in field conditions].

Quicke, D. L. J. 1997. *Parasitic wasps*. Chapman & Hall, UK. 470 pp. [Excellent contribution of the 90's, treating with depth our parasitoid biology understanding with emphasis on the genetics, development biology, life history strategy, morphology, anatomy and physiology, as well as, many aspects of ecology and phylogeny. With emphasis on life history strategy and phylogeny].

Pennachio, F. and M. R. Strand. 2006. Evolution of Developmental Strategies in Parasitic Hymenoptera. *Annu. Rev. Entomol.* 51: 233-258. [They give us an excellent update on parasitoids life history strategy and phylogeny].

Soler, R., T. Martijn Bezemer, W. H. van der Putten, L. E. M. Vet and J. A. Harvey. 2005. Root herbivore effects on above-ground herbivore, parasitoid and hyperparasitoid performance via changes in plant quality. *Journal of Animal Ecology* 74: 1221-1130. [First paper to report the role of soil organism with effects on above-ground herbivores and parasitoids].

Soler, R., J. A. Harvey, A. F. D. Kamp, L. E. M. Vet, W. H. van der Putten, N. M. van Dam, J. F. Stuefer, R. Gols, C. A. Hordijk and T. M. Bezemer. 2007. Root herbivores influence the behaviour of an aboveground parasitoid through changes in plant-volatile signals. *Oikos* 116: 367-376. [This article report the effect of infochemicals from below-ground herbivores to the presence of parasitoids above-ground].

Vet, L. E. M. and M. Dicke. 1992. Ecology of infochemical use by natural enemies in a tritrophic context. *Annu. Rev. Entomol.* 37: 141-172. [Good review on infochemicals and their importance in a multitrophic context to the function of natural and modified communities].

Wajnberg, E., C. Bernstein and J. van Alphen. 2008. *Behavioral ecology of insect parasitoids: from theoretical approaches to field applications*. Blackwell Publishing Ltd. 445 pp. [The most recent and excellent book on behavioral ecology of parasitoids, it continues with the seminal tradition of the books authored by Godfray and Quicke].

### Biographical Sketch

**Arturo Bonet** is an associate researcher in the Department of Entomology in the Ecological Institute, Xalapa, Veracruz, Mexico. For a number of years he has dedicated his time to the study to biological interactions (parasitoid-bruchid host –host plant) and biological control of insect pests. His interest is in Bruchidae attacking bean pulses and their interacting parasitoids. He has promoted native parasitoids for biological control of bruchids in small farmer pulses storage.