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Evolution of Parasitoidism in Hymenoptera

Sevda Hastaoğlu Örgen[1,a,*], Mehmet Gülmez[2,b]

[1]Sivas Cumhuriyet University, Vocational School of Health Services, 58140, Sivas-Türkiye
[2]Sivas Cumhuriyet University, Faculty of Science, Department of Molecular Biology and Genetics, 58140, Sivas-Türkiye
*Corresponding author

ARTICLE INFO	ABSTRACT
	Insects, the most diverse group of animals, are known to benefit society for a sustainable future. By focusing on the use of natural enemies of pests, including parasitoids and predators, the need for biological pest control for the conservation of agricultural crops has been emphasized. Parasites are organisms that live in the body of another organism and feed on it without killing it, while predators hunt, kill and eat their prey. Parasitoids, on the other hand, live in or on another organism and feed on it, ultimately killing the host. Our study highlights the use of parasitoids to control pests in agriculture and describes the parasitoid lifestyle as an evolutionary transition between parasitism and predation. It also notes that parasitoid larvae typically require only one host to complete their development and can be used to control a wide range of pests. The aim of this study was to determine the origin of the parasitic life form of order Hymenpotera, the mechanisms revealed by the parasitic life form, the importance of life strategies, the types of parasitism and to evaluate the important insect groups belonging to the order Hymenoptera used in biological control.

[a] hastaoglu@cumhuriyet.edu.tr   https://orcid.org/0000-0001-8313-2946   [b] mgulmez26@gmail.com   https://orcid.org/0000-0001-6547-7190

Introduction

Insects, the most diverse group of animals in the world, provide many benefits to our society as we work toward a more sustainable future. Although they are terrestrial creatures, they can be found in all types of ecological environments except deep sea bottoms. Many of them are harmful, but some groups are extremely beneficial. Pests are responsible for about one-third of the world's crop losses. Due to the destructive environmental effects of pesticides and development of insect resistance to these pesticides, alternative control strategies have become crucial in the fight to preserve agricultural plants. The most important of these strategies is biological pest control, which employs natural enemies of pests. Beneficial organisms consisting of predator and parasitoid insect groups are used in this struggle. Certain species can be very important in controlling pest populations because many parasitoid hosts are insects and other arthropods that are, or have the potential to be, significant pests in the real world. In most cases, control occurs naturally, and the host only becomes a pest when the natural control agent is absent, such as when a potential pest moves artificially or naturally into an area lacking its natural enemies. However, the deliberate introduction of parasitoids—known as classical biological control—into new regions can have major positive effects on the environment and the economy (Polaszek and Vilhemsen, 2023).

What is Parasite, Predator and Parasitoid?

Predators and/or parasitoids have been used in biological control programs around the world to control a wide range of pests and have become an important tool in conservation efforts. Today, the terms parasitoid and parasite are often used interchangeably. Parasites are a group of organisms that live and feed on the body of another organism (host) (Fernandes and Waquil, 2018). Host acceptance, host suitability etc.. are important for host selection. Parasitic organism can rarely kill their hosts, but rather affect the health of the host. Predators are organisms that feed on another organism by hunting, killing, and eating it (Abrams, 2000). Since predators use their prey for food, the prey eventually dies. Many organisms have a predatory lifestyle and play an important role in the ecosystem.

The concepts of parasites and parasitoids in insects are important for ecosystem dynamics and interactions between organisms. The differences between these two terms help to understand the transition between parasitism and predation. Here are the main differences between parasites and parasitoids:

- Parasitoids can often be larger than their hosts. For example, some parasitoid insects can reach sizes larger than the host insect, whereas parasitoids are usually similar or smaller in size to the host (Price, 1980).

- While parasites spend some or all of their life cycle inside the host, parasitoids usually develop inside the host and eventually complete their life cycle by killing the host (Begon, Townsend, & Harper, 2006).
- Parasites usually have a long-lasting effect on the host and can weaken the host's health. Parasitoids, on the other hand, have a shorter but more destructive effect by killing the host (Godfray, 1994).
- While parasites live by taking nutrients from the host, parasitoids usually consume tissues inside the host, leading to the death of the host in the process (Eberhard, 1990).
- Examples of parasites include intestinal worms and some plant parasites, while examples of parasitoids include insect parasitoids (e.g. some species of flies) (Thacker, 2006).
- Parasites usually lay large numbers of eggs within the host, while parasitoids usually develop on a single host, causing the death of the host in the process (Price, 1980).
- Parasites play an important role for ecosystem balance, while parasitoids can serve a critical function in terms of population control (Begon et al, 2006).
- While parasites generally have a wide range of hosts, parasitoids can be specific to particular hosts and therefore have a more specialised life cycle (Godfray, 1994).

This transition between parasitism and predation is an important factor shaping ecosystem dynamics.

A parasitoid is a group of organisms that live inside the body of another organism (the host) and feed on that host but differs from a parasite in that it kills the host (Godfray, 1994). The parasitoid lifestyle can be viewed as an evolutionary transition between parasitism and predation. The parasitoid life cycle can be defined by the feeding behavior of the parasitoid larva. The larva feeds entirely on or in another arthropod, resulting in the death of the host. The parasitoid larva usually requires only one host to complete its development. Parasitoids can be found in many different species and are used to control many pests. The terms parasitic insect, parasitic Hymenoptera, and parasitic bee are used synonymously with the term parasitoid, although there are significant differences between parasitism and parasitoid life forms (Polaszek and Vilhemsen, 2023).

Parasitoid Groups in Insects

Parasitoidism occurs in the following seven holometabolous insect orders: Coleoptera, Diptera, Hymenoptera, Lepidoptera, Neuroptera, Strepsirtera and Trichoptera (Yu et al., 2016; Labandeira and Li, 2021; Bolu et al., 2022). However, among all insect orders, Hymenoptera have the greatest species diversity and numerical abundance (Heraty, 2017). Parasitoids are present in almost every ecosystem in terms of species and numbers of individuals. Parasitoid bees make up 10% to 20% of the order Hymenoptera (Godfray, 1994; Ouicke, 1997; Whitfield, 1998; 2003). Approximately 50,000 parasitoid species of Hymenoptera and 16,000 parasitoid species of Diptera are known, with a total of approximately 3,000 species in all other parasitoid insect orders (Godfray, 1994; Feener and Brown, 1997). The number of identified insect species in the world is more than one million, of which approximately 68,000 species are parasitoids (Godfray, 1994; Stork, 2018; Bánki et al., 2023), representing 6.8% of insects, and Hymenoptera account for 80% of these parasitoid insect species (Ouicke, 1997).

Hymenoptera

The incredibly diverse insect order Hymenoptera, with its wide range of life-history traits such as phytophagy, parasitism, predation, pollination, and eusociality, provides an excellent model for studying the evolutionary origin and transition of several important traits. Hymenoptera serves as an excellent model for studying the evolutionary transition between different lifestyles (Branstetter et al., 2017; Peters et al., 2017). It consists of two suborders, Symphyta (the basal lineage of the order) and Apocrita as a derived suborder. Orussidae is the only family in Symphyta that has the parasitic lifestyle. The derived suborder Apocrita is divided into two groups: Parasitica and Aculeata. Almost all members of the Parasitica and some members of the Aculeata have a parasitoid lifestyle. The parasitoid species of Hymenoptera play an important role in the control of agricultural pests and are therefore often used in biological control.

Diptera

The order Diptera contains an estimated 16,000 species as parasitoids, or about 20% of the total number of species with this lifestyle (Feener and Brown, 1997). The order consists of two suborders: Nematocera and Brachycera. The Dipteran parasitoid families are Cecidomyiidae, Acroceridae, Bombyliidae, Nemestrinidae, Phoridae, Pipunculidae, Conopidae, Sarcophagidae, and Tachinidae (Godfray 1994).

Coleoptera and Other Orders

Only five families in the order Coleoptera are parasitic: Carabidae, Staphylinidae, Ripiphoridae, Melonidae, and Stylopidae (Godfray, 1994). The parasitic lifestyle is also observed in two families of Lepidoptera and one family of Neuroptera.

Parasitoid Hymenoptera

Hymenoptera is one of the major orders of insects, including honeybees, wasps, and ants. It is called membranous winged insects because they have two pairs of membranous wings. In Symphyta, the 8th and 9th abdominal segments are transformed into a saw-shaped ovipositor. The female's ovipositor is specialized into a saw-like shape for depositing eggs in plant tissue. The internal component facilitates the expulsion of the egg from the body. The plant is damaged when the hatching larva feeds on the nearest plant tissue. They are therefore considered economically as agricultural and forest pests. In particular, the larvae of *Nematus* sp. (Tenthredinidae) use the leaves of plants as a food source. Although some of them lay eggs on a single plant species, others can lay eggs on many species. *Cephus pygmeus* (Cephidae), which is a widespread species, lays its eggs in Poaceae stems. The hatching larvae hollow out the stem from the inside and prevent grain formation in the plant. Even if grains are formed, they remain hollow. The only parasitoid family in Symphyta is the Orussidae (Godfray, 1994).

The suborder Apocrita consists of two groups, Parasitica and Aculeata. Their larvae are legless, i.e. they have no legs on the thorax. In Apocrita, the ovipositor has evolved into a needle or piercing organ. The diet of Apocrita is very diverse, ranging from an exclusively animal diet to an exclusively plant diet. The larvae of *Apis mellifera* (honeybees) feed solely on pollen and nectar, while the larvae of *Vespa* sp. (wasps) feed on a mixed diet. Still others eat only animal foods. Feeding takes the form of parasitism in or on some other insects and spiders. However, unlike other parasites in the animal kingdom, these parasites eventually kill their hosts, becoming parasitoid rather than parasitic.

When the evolution and some characteristics of parasitoid Hymenoptera and other orders of parasitoid insects are compared, significant differences are observed (Eggleton and Belshaw 1992, 1993). In Hymenoptera, the parasitoid lifestyle probably evolved first in families such as Siricidae and Xiphydriidae, which are related to Orussidae (the only known parasitoid Symphyta family) and exhibit an endophytic-mycophagous diet. However, the parasitoid lifestyle is thought to have appeared independently at least 14 times in Coleoptera and 21 times in Diptera. The main route to parasitism in Diptera is through saprophagous feeding, but it has also been shown to evolve from predation (Quicke 1997).

Although some Diptera species are parasitic on Gastropoda, Hirudinea and Centipedes, no Hymenoptera select these groups as hosts. It is noteworthy that almost all hymenopteran hosts are evolutionarily newer insect groups (e.g., Coleoptera, Lepidoptera, and Diptera). Many parasitoid Diptera (23 families), Coleoptera (11 families) and some Lepidoptera and Neuroptera lay their eggs in the host environment. Thus, the encounter between the egg and the host depends either entirely on chance or on the ability of the first larval stage of the parasitoid to find the host. Parasitoid Hymenoptera, however, take no chances and lay their eggs on, in, or very close to the host. While a few families in the order Hymenoptera have been observed to lay their eggs in the host environment, these are exceptions and represent a secondary specialization rather than an ancestral behavior.

The Origin of The Parasioid Lifestyle in Hymenoptera

Except for the parasitic sawfly family Orussidae, the ancestral Hymenoptera, members of the suborder Symphyta, are phytophagous, so it is of great interest to discuss how parasitic and predatory life forms have evolved. Hardlirsch (1907) was one of the first to discuss the evolution of the parasitoid lifestyle, and his hypothesis is generally accepted. According to this hypothesis, a primitive saw bee (Siricoidea or similar), which was phytophagous and laid its eggs in wood tissue, began to lay eggs in woodworms (Coleoptera larvae) in the same microhabitat. However, it did not explain what possible steps it went through during this transition. Today, two alternative scenarios have been developed based on this idea. According to one scenario, the parasitoid ancestor had the advantage of choosing an oviposition site close to the eggs or larvae of another insect. This is because it provides a more nutritious resource for its offspring than plant material. Over time, with some behavioral and biological specialization, a dependency will evolve that allows the parasitoid to thrive on an increasingly large and valuable host. An alternative scenario can be suggested by observing the biology of members of the Orussidae, the only living parasitoid Symphyta family today. *Guiglia schauinslandi* (Ashmead), a species of Orussidae found in New Zealand, is parasitic on another Symphyta, Sirex, a member of the Siricidae (Nuttall 1980). Siricidae and Xiphydriidae, whose larvae feed on dead wood tissue, have a symbiotic relationship with fungi. They cannot feed on wood tissue that is not contaminated with fungi. Therefore, during oviposition, they inject fungal spores, which they carry in special sacs in their abdomen, into the tree tissue. The wood tissue digested by the developing fungus can be used as food by the hatched larvae of these families. Some members of these families do not carry fungi. In order for their larvae to develop, they must lay their own eggs in the wood tissue where the fungus-bearing species lay their eggs. Based on these data, a credible hypothesis for the evolution of the parasitoid life history can be formulated as follows:

- Of the larvae of fungus-carrying and non-fungus-carrying members of the Siricidae and Xiphydriidae families encountered in the tree tissue where they lay eggs, the larvae of the non-fungus-carrying species should have evolved to kill larvae of the fungus-carrying species.
- The second step in the parasitoid life path is not only to kill these larvae, but to start using them as food, which is an advantage in the competition for food, so there must have been selection in this direction.
- In the next stage, the egg must have been laid on the host larva, a mechanism that leaves the hatching larva no chance of finding its host.

In addition to Hymenoptera, many parasitoid Coleoptera are known to have descended from a mycophagous ancestor that fed on dead wood (Godfray 1994). The most important environmental pressure forcing this transition is the increase in the population of species that colonize wood tissue. This is because spawning, egg deposition, and subsequent larval development in tree tissue provide complete protection from predators and ensure the persistence of the species. However, the occupation of this microhabitat by an insect community beyond its carrying capacity has led to competition for food between species. Here, selection pressure would favor species whose survival depends on their ability to exploit the richer animal food (Rasnitsyn 1980).

This idea of Handlirsch is not accepted by everyone. There are few hypotheses as Eggleton and Belshaw 1992, Malyshew 1968. According to Malyshew (1968), Apocrita and the parasitoid lifestyle originated from a Cephidae-like ancestor that formed gal. A secretion released by the female bee during oviposition caused isolated but nutrient-rich deformations in plant tissues. The availability of such a rich food source gradually led the larvae to settle there. This nutrient-rich tissue became attractive to other insects that laid their eggs in this environment. These larvae, initially feeding only on plant tissue, gradually acquired a carnivorous or parasitoid lifestyle. However, there is serious debate about the validity of this hypothesis. Phylogeny of Hymenoptera shows that the closest group to Apocrita is Orussidae and Siricidae + Xiphydriidae clade.

For Malyshev's hypothesis to be valid, the parasitoid lifestyle must have evolved several times independently in Hymenoptera.

Mechanisms Revealed by the Parasitoid Lifestyle

Concurrent with or immediately following the parasitoid lifestyle, several mechanisms have evolved to make this lifestyle competent. These can be grouped under the following headings.
- Host Selection
- Egg Laying Strategy
- Reproductive Strategy

Host Selection

The place where the insect can lay its egg is the place where the larva will feed. Almost all ancestral Hymenoptera have phytophagous larvae (Gauld and Botton, 1988), meaning that the egg is laid in useful plant tissue and this ancestral behavior is still maintained. The host is usually phytophagous but can also be a predator or a scavenging arthropod.

Parasitoid eggs are laid by different species on different hosts, or the host may be specialized for different stages of a host's life cycle. At the same time, each natural enemy species can attack a series of hosts ranked from high quality to low quality. Some parasitic bees have evolved from predators rather than parasitoids, which make greater use of a host to complete their development. Presumably parasitoid life has evolved either by a decrease in the size of a predator or an increase in the size of a prey (Godfray, 1994).

Egg Laying Mechanism

The ovipositor is formed by differentiation of the 8th and 9th abdominal segments. In parasitoids, the host is usually found by females that lay their eggs directly in or on the host. The eggs are placed in the host by the ovipositor. The ovipositor has two functions. These are oviposition and venom injection. Both functions are seen in all Apocrita except the Aculeate group, but in later groups the ovipositor is not used for oviposition but only for venom injection. Many hosts are found under the bark of trees or between the leaves, where the parasitoid cannot reach them directly. For this reason, there has been a great deal of differentiation in the ovipositor. For example, many parasitic bees have specialized ovipositors that can easily pierce the host's cuticle and deliver their eggs to the host located between tree trunks or leaves (Onstad and McManus 1996; Strant and Obryeki, 1996).

The ovipositor is usually strong enough to pierce wood tissue and long enough to reach deep places. Studies of the order Hymenoptera have revealed the presence of zinc or manganese in the ovipositors and mandibles of species that can only bore holes. The presence of these metals has been associated with reduced abrasion by causing cuticular hardening (Quicke et al., 1998; Morgan et al., 2003). There are also various specializations in identifying egg-laying sites on the host, for example, it has been shown that members of the Orussidae use a vibration sensing method to locate suitable oviposition sites (Vilhelmsen, 2001). During oviposition on the host, the vibrations generated by striking the wood with the antennae are converted into nerve impulses that are picked up by the forelimbs via the basitarsal spurs and transmitted along the basitarsi to thin-walled areas on the tibia and through the hemolymph to the subgenital organs.

At the same time, most of the venom injected into the host through the venom injecting ovipositor paralyzes the host without killing it. It is important for the parasitoid that the host be immobile. A moving host can harm the parasitoid. The immobilized host is vulnerable to all kinds of predatory attacks. To prevent this, the parasitic bee lays its eggs in a protected or semi-protected host.

Reproductive Strategy

Darwin observed that in animals, females do not immediately mate with the first males they meet but find a way to select high quality males. The selection of high-quality males has adaptive value because it allows more offspring to be produced and the offspring produced are of higher quality. If females are selective in mating, then males are high quality mates. Natural selection has favored the evolution of behaviors that maximize the reproductive success of males and females (Bahceci, 2000; Freeman and Herron, 2009). The recognition and selection of a superior male increases the chances of growth and survival of an animal's offspring (Bahceci, 2000).

Classification of Parasitoids

Parasitoids are classified according to the host in which they live as parasitoids and in which their offspring develop. Some parasitic flies (Diptera) lay their eggs directly in or on the host, while others lay their eggs close to the host. If the eggs are laid near the host, the host may eat the eggs, or the mobile larvae that hatch from the eggs may enter and infect the host. Many parasitoids attack the host only at a particular stage.

Species that lay egg, larva, pupal and complete their development in the egg stage of the host are called egg parasitoids. Parasitoids that attack in other life stages are called larval, pupal and adult parasitoids. In other words, those that complete their development in the larval stage are called "larval parasitoids", those that complete their development in the pupal stage are called "pupal parasitoids", and those that complete their development in or on an adult insect are called "adult parasitoids".

There are also parasitoids that lay eggs in one stage of the host but complete their development in another stage. These are known as egg-larval, larval-pupal parasitoids. In egg-larval parasitoids, the parasitoid lays its egg in the egg of the host, but the host completes its development when the host enters the larval stage. A similar situation occurs in the larval-pupal parasitoid. The parasitoid lays its egg in or on the larva of the host, and the host completes its development when the host reaches the pupal stage.

Parasitoids are also classified according to where the offspring feed. Species that develop inside the host are called "endoparasitoids", while those that feed outside the host are called "ectoparasitoids". Also, there are two type of parasitism, these are superparasitism and multiparasitism. Superparasitism is a form of parasitism in which the host (typically an insect larva such as a caterpillar) is attacked more than once by a single species of parasitoid. Multiparasitism or coinfection, on the other hand, occurs when the host has been parasitized by more than one species.

If only one individual develops in a host, it is called a solitary parasitoid; if more than one individual develops in a single host, it is called a gregarious parasitoid.

A primary parasitoid is a single individual that develops in the host. Secondary or hyperparasitoids are species that develop within or above the primary parasitoid and infect it. There are heterenome parasitoids in the family Aphelinidae of Hymenoptera. Among them, female wasps develop as primary parasitoids on Homoptera, while males develop as hyperparasitoids on females of their own or other species (Onstad and McManus 1996; Strant and Obryeki, 1996).

Today, two new categories of parasitoids have been added to the literature. These are coidiobionts and idiobionts. In the case of the coidiobiont, the host can continue to develop after being infested, whereas in the case of the idiobiont, the host cannot develop after being infested, i.e. the host is permanently paralyzed. In fact, it is more accurate to consider choidiobionts, idiobionts, ectoparasitism and endoparasitism as life strategies and the others as types of parasitism. Also, a feeding tactic known as kleptoparasitism involves an animal purposefully stealing food from another. Theft from individuals of the same species might be intraspecific, or it can be interspecific, including members of different species (Broom et al., 1998; Furness, 1987).

Life Strategies

The transition between ectoparasitism and endoparasitism is a critical stage in the evolutionary adaptation of parasitoids. Over time, ectoparasites can evolve into an endoparasitic lifestyle by moving into the internal organs of their hosts (Quicke, 1997). This transition allows parasites to exert more control over their hosts and develop a more efficient feeding strategy. Similarly, transitions between idiobiont and koinobiont play an important role in the evolution of parasitoids. While idiobiont parasitoids become more resistant to the defences of their hosts, koinobiont parasitoids have the opportunity to feed for longer periods of time, affecting the life span of their hosts (Vinson, 1990). These transitions can affect the balance in ecosystems by increasing the diversity of parasitoids. The evolution of parasitoidism in insects has been shaped by transitions between ectoparasitism and endoparasitism and between idiobiont and koinobiont. These transitions play an important role in ecosystems by determining the effects of parasites on their hosts and their feeding strategies. Future research will contribute to a better understanding of these processes and elucidate the evolutionary dynamics of parasitoids.

Idiobiont Strategy

In Hymenoptera, the ancestors of parasitoid species probably had larvae that fed endophytically (feeding within plant tissue) and consumed other larvae they encountered (Gauld and Bolton, 1988). The next evolutionary step toward a parasitic lifestyle may have been for the adult female to deliberately seek out shoots or plant stems containing other immature insects that would serve as a food source for her larvae, and to lay the eggs near that food source (Gauld and Bolton, 1988). This strategy probably evolved into the widespread and relatively unspecialized parasitoid behavior seen today. The hymenopteran egg consumes its host to develop, then pupates and emerges from the host as a larva. Such a parasitoid, i.e. a parasitoid that stops host development when it lays its eggs on the host, is called an "idiobiont". An idiobiont immediately paralyzes/kills its host and is estimated to have lower fecundity (Pennacchio and Strand, 2006; Yadav and Borges, 2018). Ectoparasitoids, endoparasitic eggs, and pupal parasitoids that develop (outside/on) the host by permanently paralyzing it are usually idiobionts. The idiobionts that attack larval host stages are almost always ectoparasitoids (Yadav and Borges, 2018). Egg, pupal and adult parasitoid are usually idiobionts. Egg-larval and larval-pupal parasitoid are koinobionts. Ectoparasitoids typically immunosuppress their hosts (Pennzcchio and Strand, 2006). Most hosts in the idiobiont strategy are either hidden or protected. Specialization of the parasitoid ovipositor has occurred in order to reach the host. Thus, most ectoparasitic idiobionts are highly specialized. Ectoparasitic idiobionts inject venom into the host during oviposition, causing death, paralysis, or developmental arrest. This prevents the developing parasitoid from falling off the host and the host from harming or killing the parasitoid.

Some idiobionts may lay eggs on exposed hosts. Since the ectoparasitic larvae would be very vulnerable to crushing and damage in this situation, these idiobionts have an "endoparasitic" lifestyle. Recent studies have shown that the ancestor of Ichneumonoidea was an idiobiont ectoparasitoid (Sharanowski et al., 2021), in which the parasitoid larva feeds inside the host and secures itself. On the other hand, this strategy exposes them to the host's immune defense system. Endoparasitic idiobionts stop or reduce host responses to their larvae. They use toxins or physically paralyze the host by laying eggs in vital organs such as the brain. In the case of egg parasitism, the host's eggs are lysed. Except for this natural parasitism, there is kleptoparasitism. Kleptoparasitism, "parasitism" by theft (not true parasitism). Kleptoparasites steal food (e.g., prey) from another animal as their main feeding strategy, but do not feed directly from a host's body.

In the idiobiont strategy, the parasitoid is usually outside the host and can be thought of as an unprotected piece of flesh. Idiobiont ectoparasitoid larvae are vulnerable because they are immobilized after venom injection and open to attack by many predators. For this reason, idiobionts are often found in places that are not easily accessible, such as between the bark of trees.

The parasitoid spends a lot of time searching for, finding, and laying eggs on these hosts. Because of this, the female idiobiont tends to live a long time. During their lifetime, these species lay many eggs to maturity. This is called "synovigenic". In the idiobiont strategy, the parasitoid must complete its development on the host without being noticed by other organisms. The production of such eggs is more difficult for the adult female parasitoid. This is because the parasitoid female must feed more in order to produce nutritious eggs. These species generally exhibit feeding behavior on the host to provide protein for egg production. The family Dryinidae (Chrysidoidea) has several interesting biological features (Olmi, 1984; Guglielmino, 2002). These wasps are both parasitoids and predators of Auchenorrhyncha hosts

belonging to the order Hemiptera. Female wasps lay eggs on the hosts and their pupa develop outside the hosts (ectoparasitoid). Female wasps also capture and feed on hosts. Male wasps, however, do not hunt or feed on hosts. Parasitoid wasps with both predatory and parasitoid behavior are rare in Hymenoptera. In addition, no other wasps with predatory behavior are found in the Chrysidoidea (Melo et al., 2011). Therefore, the origin of predatory behavior in Dryinidae is likely to be an independent trait that has gained events in the evolution of Hymenoptera (Yang et al. 2021). Some idiobiont parasitoids protect the host by hiding it after paralyzing it. For example, some bethylids protect their paralyzed host by dragging it into their shelter. Others, such as pompilids and sphecids, overcome this problem by building a nest before finding the host (Gauld and Bolton, 1988).

Koidiobiont Strategy

If the host can continue to develop after the eggs are laid, such parasitoids are called "choidiobionts". Coidiobionts are thought to have higher fecundity (Pennacchio and Strand, 2006). Egg-larval, larval pupal koinobionts is proovogenic. Almost all coidiobionts are endoparasitoids. Endoparasites complete their development inside the host. They are expected to encounter a strong host immune defense response, but they usually overcome the immune defenses (Schmidt et al., 2001). Unlike the idiobiont strategy, hosts in the choidiobiont are not hidden. The host is usually unprotected on plants. Since it is easier to reach the host, i.e. to lay eggs, there is not much specialization here. Since the endoparasitic choidiobionts lay their eggs inside the host, the parasitoid is prevented from falling off the host or the host from directly damaging the parasitoid, but the host is open to predation. For this reason, choidiobiont ectoparasitoids can carry many eggs at the same time and lay them when they find a suitable host (Gauld, 1988; Sharanowski, 2009).

Types of Parasitoidism

Primary Parasitoidism

Primary parasitoids complete their development by laying their eggs inside the host. The best studied species is the aphid bee *Aphidius smithi*, which has demonstrated control of the exotic pea aphid *Acyrhosiphon pisun* in North America. The female bee lays eggs inside the aphid, and over a period of about 8 days, the parasitic larvae gradually eat the aphid from the inside, killing it. The fourth instar larva weaves a cocoon inside the dead aphid while the outer shell forms and changes from green to light brown (this is called the "mummy"). After about 4 days when the larva pupates (or about 12 days after the original oviposition), the new adult primary parasitoid cuts the circular exit hole on the dorsal side of the mummy and expels itself.

Secondary Parasitoidism

It occurs when the primary parasitoid is parasitized by another parasitoids. Aphid hyperparasitism has been studied extensively. They divided aphid hyperparasitoids into two categories based on adult oviposition and larval feeding behavior.

- The female bee of the endophagous species lays her egg inside the primary parasitic larva while it is still developing inside the living aphid before the aphid mummifies. The egg does not open until after the mummy has formed and then the hyperparasitic larva feeds internally in the primary larval host.
- The female bee of the ecdophagous species lays her egg on the primary parasitoid larva after the aphid has been killed and mummified. The hyperparasitic larva feeds externally on the primary larval host while both are still inside the host. The 8 taxonomically listed genera that are basic (essential) in these behavioral criteria are arranged as shown below. Endophagus hyperparasitoid species in *Alloxysta*, *Phoenoglyphis*, *Lytoxysta*, *Tetrastichus*, ectophagus species in *Asophes*, *Dendrocerus*, *Pachynwon* and *Conna*.

Tertiary Parasitoidism

A secondary parasite occurs when it is parasitized by another parasite. For example, the larvae of Apanteles inhabit caterpillars (primary parasite), while certain species of Chalcidoidea (Mesochorus and Tetrastidus) infest the larvae of the primary parasite and lay eggs (secondary parasite). The larvae of this secondary parasite develop on or in the larvae of the primary parasite. These secondaries are beneficial insects to humans (if the primary parasitized insect is harmfull). Pleurotropis of Chalcidoidea also lives on this secondary parasite (tertiary parasite) and is considered harmful to humans (Demirsoy, 1995).

Facultative Parasitoidism

Some parasitoids behave as both secondary and primary parasitoids. These are called facultative parasitoids. *Pachyneuron coccolar* can develop as tertiary parasitoids on members of its own species or on other Chalcidoids that develop as secondary parasitoids on encyrtid hosts. Despite this, an interesting feature that has been demonstrated is that *P. concolar* is a true facultative hyperparasitoid but develops as a primary parasitoid on butterfly pupae. The choice of host is based on the fly pupae in the puparium or the one localized on the soft body inside the hard dry container, regardless of whether it is the primary parasitoid on the mummified host. Unfortunately, when *P. concolor* acts as a primary parasitoid, it attacks the beneficial aphidophagous butterflies. *P. concolor* is therefore detrimental to biological control programs (Sullivan, 1987).

Parasitoids as Biological Control Agents

The history of parasitoids has progressed in parallel with the evolution of agricultural practices. The first applications of biological control date back to ancient times. The Egyptians used natural enemies in the control of pests. However, modern biological control practices started towards the end of the 19th century. The first systematic use of parasitoids occurred during the red spider (*Tetranychus* sp.) infestation in Australia in the 1880s. During this period, parasitoids brought to Australia were effective on pests. In the early 1900s, important developments were experienced in the field of biological control. In particular, Trichogramma sp. parasitoids were effective in the control of many pests by targeting eggs.

This species was widely used in the USA in the early 1900s (Van Driesche & Bellows, 1996). Trichogramma sp. has been recognised as an effective tool to reduce pest populations in agricultural fields.

In the 1950s, other parasitoid species, such as *Cotesia glomerata*, were also introduced for biological control. This species was effective against important pests such as cabbage moth (Godfray, 1994). In the same period, *Encarsia formosa* was also used in the control of whiteflies. These species contributed to the widespread use of biological control methods in agriculture. Today, the parasitoid species used in biological control have become more diversified. Research is focussed on the discovery of new species and increasing the effectiveness of existing species. The use of parasitoids has become an important strategy for sustainability in agriculture.

The superfamilies and families containing parasitoid species of the order Hymenoptera can be listed in order of availability as follows (Godfray, 1994; Quicke, 1997).

- Superfamily Ichneumonoidea: Ichneumonidae: Braconidae
- Superfamily Chalcidoidea: Eulophidae : Chalcidoidea
- Superfamily Cynipoidea: Cynipidae
- Superfamily Platygastroidea: Platygastridae
- Proctotrupoidea: Proctotrupidae

Parasitoids are frequently used as biological control agents against harmful insects. *Torymus sinensis* (Hymenoptera: Torymidae), a solitary ectophagous parasitoid species that has recently been used in biological control, can be given as a good example of this control method. This species is used against the chestnut gall wasp (*Dryocosmus kuriphilus*), which causes loss of productivity and quality in chestnut trees, which has important economic and ecological importance. *D. kuriphilus* is a Chinese gall wasp that was introduced to the United States in 1974 (Rieske, 2007). It was first reported in Europe in 2002 (Brussino et al., 2017) and in Tukiye in 2014 (Cetin et al., 2014) from chestnut trees in forested areas in Yalova. In the following years, it was observed that the population density increased rapidly in the Marmara, Aegean and Black Sea Regions. *D. kuriphilus* is considered to be one of the most harmful organisms for plants of the genus *Castanea*, by causing galls on buds and leaves, reduced branch growth and fruit formation (Lobo et al., 2024). The resulting galls reduce photosynthesis and therefore can cause plant death in heavy infestation (Payne et al., 1975; Anagnostakis and Payne, 1993).

To control *D. kuriphilus* are used various methods such as biological, chemical and mechanical/cultural. However, since it lays its eggs inside the fruit, the success rate of chemical control is very low. In a mechanical control method, shoots with gal formation are cut. However, the most effective method on the pest species is biological control. The *T. sinensis* parasitoid bee is used as a biological control agent. This species was identified for the first time in Turkey in the Marmara region (Cetin et al., 2014). In the following years, the population increased rapidly and was recorded from different regions (Yıldız et al., 2020; Akyuz et al., 2022; Kok et al., 2023). These natural enemies are ectophagous parasitoids of the pest *D. kuriphilus* and have a solitary life form (Quacchia et al., 2013). *T. sinensis* females lay eggs on *D. kuriphilus* gals

(the body of the host *D. kuriphilus* or the wall of the larval chamber) in early spring. Several eggs per larva have been observed in a single compartment under natural conditions. However, only one parasitoid larva completes its development among *T. sinensis* larvae due to cannibalism (Amorim et al., 2022). The parasitoid larva feeds ectophagously on the host larva. In late spring, the mature larvae stop feeding, but do not pupate until winter, and adults emerge the following spring. By eating the gall wasp larvae, they help control the pest population.

Moriya et al. 2024 conducted a study on the long-term effect of *T. sinensis* on *D. kuriphilus* in Japan between 1982 and 2023. This study showed that the density of the pest fell from 42.5% to 0.7% in the first 10 years, a reduction of about 61-fold, and remained at low levels for the next 30 years. However, it was observed that pest density occasionally exceeded the economic damage threshold. Over the same time period, the density of *T. sinensis* was also found to be synchronized with fluctuations in pest density. These results show that *T. sinensis* has played an important role in suppressing *D. kuriphilus* for 40 years and that biological control is an effective method. In this context, effective control of the pest *D. kuriphilus* allows chestnut trees to produce more fruit (Luo et al., 2014) and minimizes the negative impact on the environment by reducing the use of chemical pesticides (Gehring et al., 2018).

Conclusion

The order Hymenoptera exhibits interesting evolutionary patterns and adaptations related to parasitism. The parasitoid insects within this order are organisms that live on or inside other organisms, feeding on them and ultimately killing the host organism. Hymenopteran parasitoids have developed various adaptations for locating their prey, accessing them, and laying eggs. For example, Hymenopteran parasitoids possess keen olfactory abilities to locate host organisms. They also have specialized structures and behaviors for oviposition. Some species deposit their eggs inside the host organism, while others lay their eggs externally, employing different adaptation strategies. For instance, some species secrete chemical substances to alter the behaviors of host organisms or suppress their immune systems. These adaptations enable the successful habitation and reproduction of the parasitoids on their host organisms. Furthermore, these adaptations are crucial for understanding the evolutionary relationships of parasitoids with host organisms. In addition, there are many parasitoid species used as biological control agents. It is especially important for economically important plant species.

Declarations

Ethical Approval Certificate
Not applicable.

Author Contribution Statement
Sevda Hastaoğlu Örgen: Methodology, Validation, Writing - original draft, Investigation, Review and editing.
Mehmet Gülmez: Investigation, Conceptualization, Data curation, Review and editing.

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