Dryinidae (Hymenoptera Chrysidoidea): an interesting group among the natural enemies of the Auchenorrhyncha (Hemiptera).

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Abstract

A survey on the family Dryinidae (Hymenoptera Chrysidoidea), an interesting group of natural enemies of the Auchenorrhyncha (Hemiptera), is emphasized. In particular, informations on evolution, biology, natural enemies, economic importance, Auchenorrhyncha-Dryinidae relationships and biological control of this group on Auchenorrhyncha taxa are provided.

Denisia 04,
zugleich Kataloge des OÖ. Landesmuseums,
Neue Folge Nr. 176 (2002), 549-556

Introduction

The Dryinidae are a small cosmopolitan family of Hymenoptera Aculeata parasitizing Homoptera Auchenorrhyncha. It includes about 1400 species belonging to 10 subfamilies (Anteoninae, Aphelopinae, Apodryininae, Bocchinae, Conganteoninae, Dryininae, Gonatopodinae, Laberitinae, Plesiodryininae, Transdryininae) and living in all terrestrial habitats from sea-level to the high mountains. Knowledge of the ecology and biology of Dryinid wasps is insufficient, the main gap regarding parasitoid - host interactions. Hosts are known only in 5 of the 10 above mentioned subfamilies (Anteoninae, Aphelopinae, Bocchinae, Dryininae and Gonatopodinae) (GUGLIELMINO & OLMI 1997). Usually Dryinids are both parasitoids and predators on their hosts, being very effective for the biological control of plant pests. Auchenorrhyncha, indeed, as well as causing direct damage to plant through their feeding, oviposition, and production of honeydew and wax, may be also vectors of several pathogen agents (virus, bacteria, spiroplasma, phytoplasma) and so may cause considerable economic damage.

Evolution and biology

In the evolution of Dryinidae, driving forces seem to be the host-capture and the host's reaction (OLMI 1994). They acted mainly on the female sex, the only one having any contact with the host, and involved changes of the prothorax (from very short and almost not visible in dorsal view to elongated and very mobile) and fore legs (from short and no raptorial to elongated and raptorial with robust and mobile chelae) (Figs 1-6). Regarding the 5 subfamilies known to have relationships with Auchenorrhyncha, the Aphelopinae females are the most plesiomorphic Dryinids; on the contrary Dryininae and especially Gonatopodinae females the most evolved. The modest male selection explains also why in several groups females and males are so different (Figs 7, 8).

Parallel with the evolution of these morphological characters, the Dryinidae females developed their predatory behaviour to obtain energy and nutrients necessary for egg production. Females feed on sugar solutions or on their hosts consuming haemolymph and tissue; in the last case, the prey may survive (non-destructive host-feeding) or die (destructive host-feeding) (JERVIS et al. 1996). Males do not feed or feed only on sugar solutions.

Polyphagy appears to be the rule within Dryinidae, as is the case in Strepsiptera and Pipunculidae which are other parasitoids of Auchenorrhyncha (WALOFF & JERVIS 1987). Only *Crovettia theliae* (GAHAN), species belonging to the subfamily Aphelopinae and parasitoid of *Thelia bimaculata* FABRICIUS (Membracidae), seems to be monophagous.

Dryinidae species parasitize adults and nymphs of Auchenorrhyncha. Usually the parasitized host does not exhibit fundamental changes, if it is parasitized in the adult stage. On the contrary, the parasitization on nymphal stages can have different effects. If the host's metamorphosis is not stopped by the Dryinidae (as in the case of *Crovettia* and *Aphelopus* species), the adult of the Auchenorrhyncha species exhibits fundamental morphological, anatomical and physiological changes (depigmentation, males similar in appearance to females, parasitic castration, ecc.). If the host's metamorphosis is stopped (as in Anteoninae, Bocchinae, Dryininae, Gonatopodinae species), the nymph does not reach the adult stage. According to PILLAULT (1951), the host's metamorphosis is stopped by substances produced by dryinid larva.

Dryinidae reproduction may be bisexual and/or parthenogenetic (thelytokous or arrhenotokous); the polyembryony is known only in *Crovettia theliae* (GAHAN) (Aphelopinae).

The females of many species of Dryinidae are similar to ants in their general appearance. This mimicry allows them to attack easily their hosts, because ants frequently feed on the honeydew produced by Auchenorrhyncha defending them from natural enemies. This phenomenon was observed mainly in apterous females of genus *Gonatopus*, but also in winged females like the Australian *Anteon myrmecophilum* (PERKINS), a myrmecophilous species parasitoid of *Ipo conferta* (Cicadellidae).

Knowledge on the biology of the Dryinidae is insufficient (see OLMI 1984 for a

Figs 1-5.
Evolution in Dryinidae females involving changes mainly of thorax and fore legs.

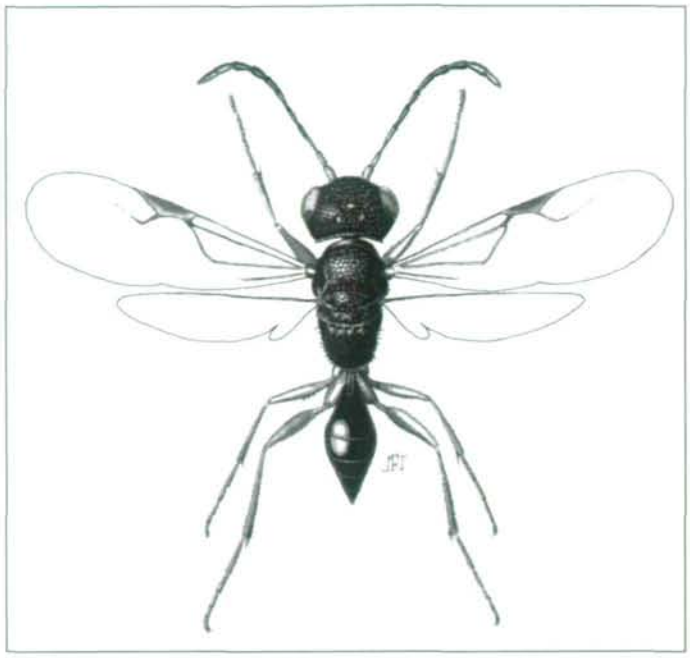

Fig. 1.
Crovettia masneri (OLMI 1984)
(= *Biaphelopus masneri* OLMI 1984) (Aphelopinae), (from OLMI 1984). Length 2.43 mm.

Fig. 2.
Anteon ephippiger (DALMAN 1818) (Anteoninae) (from OLMI 1999). Length 2,2 mm.

Fig. 3.
Bocchus scaramozzinoi OLMI 1984 (Bocchinae) (from OLMI 1999). Length 4.2 mm

Fig. 4.
Dryinus collaris (LINNAEUS 1767) (Dryininae) (from OLMI 1999). Length 5.9 mm.

Fig. 5.
Gonatopus lunatus KLUG 1810 (Gonatopodinae) (from OLMI 1999). Length 3,3 mm.

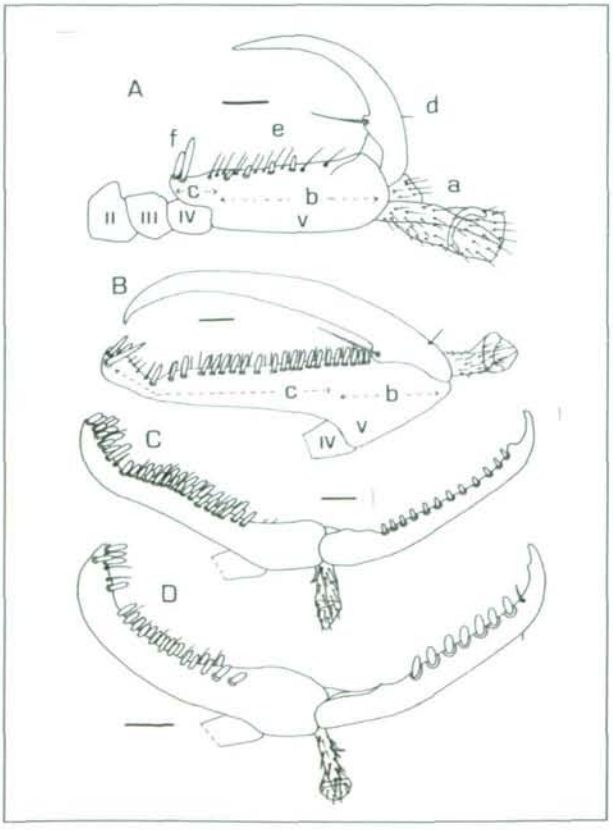

Fig. 6.
Evolution of the chelae in Dryinidae females (from OLMI 1999) showing an increase of the number of bristles and lamellae and a more elongated distal part of the 5th tarsal segment. A: *Anteon jurineanum* LATREILLE 1809. Scale = 0.07 mm; B: *Anteon fulviventre* (HALIDAY 1828). Scale = 0.04 mm; C: *Dryinus canariensis* (CEBALLOS 1927). Scale = 0.06 mm; D: *Gonatopus solidus* (HAUPT 1938). Scale = 0.05 mm. a: arolium; b: basal part of 5th segment; c: distal part of 5th segment; d: enlarged claw; e: bristles; f: lamellae.

review). In particular, few data are known on the postembryonic development. These insects are hypermetamorphic; their postembryonic development consists of 4 or 5 larval instars, the last of which is the mature larva (PERKINS 1905; BUYCKX 1948; BARRETT et al. 1965; HÉRNANDEZ & BELLOTI 1984; KITAMURA 1985; GIRI & FREYTAG 1988; ABRIL RAMIREZ 1992; VIRLA 1992; GUGLIELMINO & VIRLA 1998).

The immature larval instars are usually sacciform and endo-ectoparasitic. The anterior part of their body lies in the haemocoel of the host and the posterior part protrudes outside between two overlapping sclerites of the host (Fig. 9). The immature larvae of the polyembryonic genus *Crovettia* (Aphelopinae) are an exception being totally endoparasitic and developing inside the host haemocoel (KORNHAUSER 1919; OLMI 1994).

In each subfamily of the Dryinidae, the mature larva is hymenopteriform (sensu GAULD & BOLTON 1988); it is an eucephalous larva with developed mouth-parts. This larva kills the host by eating out all its internal organs; it then crawls out and pupates in a silk cocoon in the soil or on plants (Figs 9, 10) (see OLMI 1994 for a review).

Few data are known on feeding habits of the immature larvae of the Dryinidae and concern only the subfamilies known having relationships with Auchenorrhyncha.

The following are few hypotheses quoted for each subfamily.

In the Aphelopinae, the immature larval instars feed through a tissue which absorbs the substances from the host transforming them into high energy nutrients (KEILIN & THOMPSON 1915; FENTON 1918; BUYCKX 1948). How these nutrients are consumed by the Aphelopinae larvae is unknown. In addition, the nature of this tissue is not clear. According KEILIN & THOMPSON (1915) and FENTON (1918), this tissue is composed by hypodermal cells of the host body. These cells are stimulated to abnormal growth by the presence of the parasite. The early stages of the parasite develop inside of the host body and are enclosed by this tissue forming a «cyst». When the immature larvae assume a curved position and protrude outside of the host body, the cyst remains in intimate connection with the

attachement area of the larva and goes on absorbing and transforming the nutrients for the parasite. According to BUYCKX (1948), on the contrary, this tissue is formed by cells of the trophamnion, a membrane surrounding the embryo. After the eclosion, the trophamnion remains as a sac-like structure in front of the larval mouth, forming a barrier between the host and parasite. The cells of the trophamnion select the substances from the host haemolymph and transform them in nutrients for the parasite.

Regarding Dryininae and Gonatopodinae interesting data on the feeding habits were provided by PONOMARENKO (1975) and especially by CARCUPINO et al. (1998). Immature larvae of Dryininae and Gonatopodinae have a pair of vesicles in front of their head. They are generally considered to be involved in larval feeding. According to CARCUPINO et al. (1998), the vesicles are evaginations of the body wall , unrelated to the digestive apparatus of the larva. They are formed by large epithelial cells showing signs of intense protein synthesis and completely enveloped in one or more layers of transparent permeable cuticle. Besides, they are unrelated to the host gut.

Immature larvae of Anteoninae and Bocchinae seem to have a feeding habit intermediate between Aphelopinae and Gonatopodinae (PONOMARENKO 1975). The part of the larva body lying into the host body is surrounded by a tissue which is not as wide as in

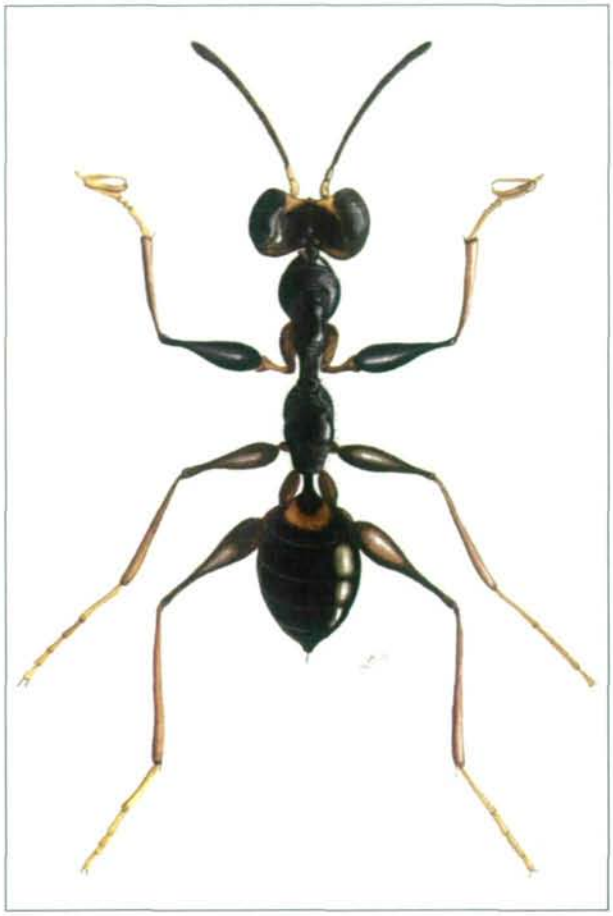

Fig. 7.
Gonatopus clavipes **(THUNBERG) (from OLMI 1999): female. Length = 3.3 mm.**

Fig. 8.
Gonatopus clavipes **(THUNBERG) (from OLMI 1999): male. Length =2.5 mm.**

Fig. 9.
Immature larva of Dryinidae on the host.

the Aphelopinae. It is composed by a layer of hypodermal cells of the host lined by a membrane on the larva side. The larvae have a pair of small conical processes which emerge from the oral cavity and are in contact with the above tissue. According to PONOMARENKO (1975), these processes are probably homologous to the oral vesicles of Dryininae and Gonatopodinae.

Fig. 10.
Mature larva of Dryinidae just after emergence from the host

Fig. 11.
Cocoon of Dryinidae

Natural enemies of Dryinidae

The main natural enemies both parasitoids and predators of Dryinidae (OLMI 1999) are listed (Tab. 1, 2). The activity of these may greatly reduce the efficiency of this group.

Auchenorrhyncha-Dryinidae relationships

Up to now about 800 relationships to different systematic levels between the two groups are known (GUGLIELMINO & OLMI Dryinidae species has relationships with more Auchenorrhyncha species belonging to the same or several systematic levels; only few cases of monospecific taxa are known (for instance the Aphelopinae *Crovettia theliae* which seems to parasitize only the Membracidae *Thelia maculata* F.), but this probably could be due to scarcity of research. Regarding the number of species involved, these relationships include just 320 Auchenorrhyncha and 230 Dryinidae species. This number is insignificant when compared with the number of known Auchenorrhyncha (over 40.000 species) and Dryinidae (about 1.400 species). From a biogeographical point of view, the most studied regions are the Palaearctic and Nearctic. Moreover, it is important to point

Tab. 2.
Predators known to attack Dryinidae

DRYINIDAE stage attacked	PREDATORS
Adults	Ants
Larvae	Crabonidae Sphecidae
Cocoons	Insects Birds Rodents

Tab. 1.
Predators known to attack Dryinidae

	Aphelopinae	Anteoninae	Bocchinae	Dryininae	Gonatopodinae
Aphelinidae					+
Ceraphronidae					+
Chalcididae				+	
Diapriidae	+	+			
Encyrtidae				+	+
Ichneumonidae					+
Pteromalidae					+

out that at least one case of Auchenorrhyncha parasitization by Anteoninae, Aphelopinae, Dryininae and Gonatopodinae is known in each zoogeographical region; on the contrary, the records of parasitization by Bocchinae are known only in the Palaearctic and Nearctic regions. In spite of insufficient knowledge of the Auchenorrhyncha-Dryinidae relationships, some apparent constant links at several systematic levels emerge from these data. While Auchenorrhyncha-Dryinidae relationships are certainly the result of a co-evolution between the two groups, the scarce knowledge of the interactions (from both qualitative and quantitative points of view), the biology and the phylogeny of both taxa does not presently allow us to theorize on how the relationships evolved. For the same reason, up to now we are not able to understand the sensory and biological bases of Auchenorrhyncha-Dryinidae links. Any hypothesis on a phylogenetic congruence should be premature.

Biological control

Dryinidae have a high potential as biological control agents. The predatory and parasitic efficiency of this family has been studied in many species. In fact, females of many taxa, mainly of Gonatopodinae, kill significant numbers of hosts by feeding as well as by parasitism. At least within 4 subfamilies (Gonatopodinae, Dryininae, Bocchinae and Anteoninae) predation is almost as important as parasitization (OLMI 1994). Gonatopodinae are very active in predation (WALOFF 1974; CHUA & DICK 1982; KITAMURA 1982; GIRI & FREYTAG 1988; ALMA & ARZONE 1994). Anteoninae show a lower activity of predation than Gonatopodinae (WALOFF 1974). Dryininae and Bocchinae, both very scarcely investigated, surely have predation activity, while Aphelopinae have none (OLMI 1994). As previously mentioned, the host-feeding can be «non-destructive» or «destructive», if the wounds inflicted by the dryinid female permit the host to survive or not. From an applied point of view, the destructive host feeders are valuable because they kill their prey more rapidly than not feeder parasitoids, i.e. they give the pests less chances of damaging plants directly or transmitting pathogen agents.

Unfortunately, little is known on the role of dryinids and other parasitoids in limiting Auchenorrhyncha populations. Indeed many factors, like the parasitoid interference, the heterogeneous parasitism rates, the presence of refugia, the presence of invulnerable developmental stages, can influence Auchenorrhyncha population control (GUGLIELMINO 2000). According to WALOFF & JERVIS (1987), it is very difficult to evaluate the factors which can determine the outcome of a biological control attempt in terms of parasitoid-hopper population dynamics.

Presently, Dryinidae are used in some biological control programmes. In Italy, France and Switzerland, *Neodryinus thyphlocybae* (ASHMEAD) is used in the control of *Metcalfa pruinosa* (SAY) (in Italy, a second dryinid, *Thaumatodryinus danieli* OLMI, is being reared for the same purpose); in New Zealand, *Neodryinus nelsoni* PERKINS to control *Scolypopa australis* (WALKER); in Nigeria, at the I.I.T.A. (Ibadan) control projects using Dryinidae against *Cicadulina* spp., dangerous to maize, are being studied.

Acknowledgements

I would like to thank Prof. M. Olmi of Viterbo, E.J. Brill (Leiden, The Netherlands) and Calderini Edizioni (Bologna) for their kind permission to reproduce figs 1-8, first published in OLMI 1999. I wish to thank again Prof. M. Olmi for his valuable suggestions and Mr. M. Vollaro (Viterbo) for his nice photographs.

This study was supported by a grant of the University of Tuscia: 60%.

Zusammenfassung

Die Familie Dryinidae (Zikadenwespen; Hymenoptera Chrysidoidea), eine interessante Gruppe natürlicher Feinde der Zikaden, wird überblicksartig vorgestellt. Informationen zu Evolution, Lebensweise, natürlichen Feinden und wirtschaftlicher Bedeutung werden dargestellt und Beziehungen zwischen Zikaden und Dryiniden erläutert.

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