

REVIEW

A review of the biology of the pincer wasps (Hymenoptera: Dryinidae)

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Abstract

Because of their frequency, abundance, and unique morphological and biological traits, the Dryinidae (pincer wasps) are among the most important parasitoids of nymphs and adults of Hemiptera: Auchenorrhyncha. This contribution offers a summary of the knowledge about the main biological characteristics of the Dryinidae gained over more than 130 years. Among other topics, the information provided covers the interactions with their hosts and other organisms, as well as their development, behaviour, natural enemies and economic importance.

KEYWORDS

Auchenorrhyncha, biological traits, economic importance, host relationships, life cycle, parasitoids

INTRODUCTION

Dryinidae (Hymenoptera: Chrysidoidea) are a widespread family, present in all zoogeographical regions, except Antarctica. They are parasitoids and predators of Hemiptera: Auchenorrhyncha, with over 1900 species (Martins & Domahovski 2022; Olmi et al. 2020). Dryinidae, commonly known as pincer wasps, include species living in a wide range of habitats (from Patagonia to northern Europe beyond the Arctic Circle), from sea level to altitudes over 3000 m (Olmi 1999). By having usually genera with worldwide distribution (except subfamilies Apodryininae and Plesiodryininae), the family seems to present no greater biogeographic interest (Olmi 1999; Olmi et al. 2019; Olmi, Onore, Guglielmino 2022; Olmi & Virla 2006).

The family is composed of small wasps that are easily distinguished from the other members of Chrysidoidea by the 10-segmented antennae inserted near the clypeus and the female chelate protarsus (chela not present only in the subfamilies Aphelopinae and Erwiniinae), composed of an enlarged claw and protarsomere 5 (Figure 1) (except the fossil Cretaceous genus *Raptodryinus* having a chela composed of a proximal lobe of the fifth protarsomere opposable on a complex composed of protarsomere 5 + arolium + both claws); information on the chelae, their function and evolution can be found in Olmi et al. (2020). The Dryinidae have usually two pairs of wings. The forewings have a pterostigma and one to four cells fully

enclosed by pigmented veins (Figure 2). Females are apterous, micropterous or brachypterous, whereas in others, they are macropterous. Males are almost always fully winged (Figure 2), rarely brachypterous.

Within the Dryinidae family, 17 subfamilies (12 extant) and 53 genera have been reported using morphological characters (Martins & Domahovski 2022; Olmi et al. 2020; Olmi, Onore & Guglielmino 2022). About 90% of the dryinid species in the world belongs to the subfamilies Anteoninae, Aphelopinae, Bocchinae, Dryininae and Gonatopodinae (Olmi & Virla 2014). The genera *Anteon* Jurine, *Dryinus* Latreille and *Gonatopus* Ljungh contain more than half of the described species (Martins & Domahovski 2022; Tribull 2015). The works that gathered the taxonomic information available about the family are the world review by Olmi (1984) and its supplement (Olmi 1991). Recently, the full lists of known species for different biogeographic regions, including descriptions, keys, known hosts, natural enemies and references, have been updated in different revisions: Oriental (Xu et al. 2013), Neotropical (Olmi & Virla 2014), Eastern Palaearctic (Olmi & Xu 2015) and Afrotropical (Olmi et al. 2019).

The phylogeny of Dryinidae was debated by Olmi (1994, 1999), Carpenter (1999), Tribull (2015), Millán-Hernandez (2018), Martins (2018) and, recently, Olmi et al. (2020), using morphological and molecular data. Dryinids evolved at least 129 Mya during the Lower Cretaceous (Martynova et al. 2019; Olmi et al. 2010, 2020; Perkosky et al. 2019).

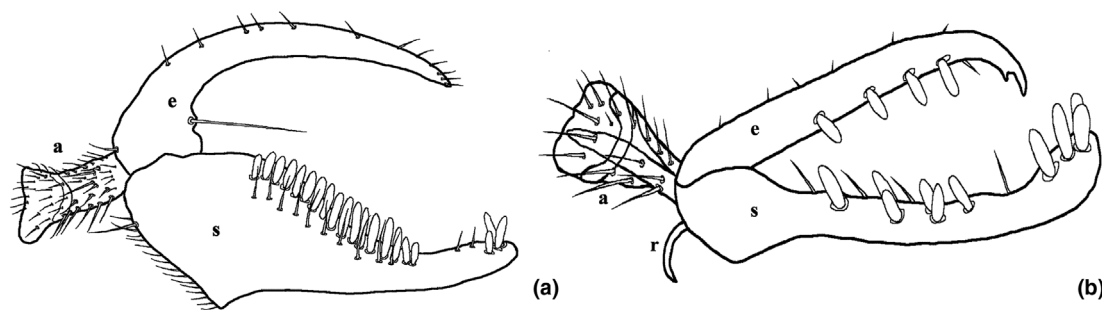


FIGURE 1 Chelate protarsus. (a) Chela of *Anteon* sp.; (b) chela of *Haplogonatopus* sp. (a, arolium; e, enlarged claw; s, protarsomere 5; r, rudimentary claw) (adapted from Olmi & Virila 2014; © Magnolia Press, reproduced with permission from the copyright holder).

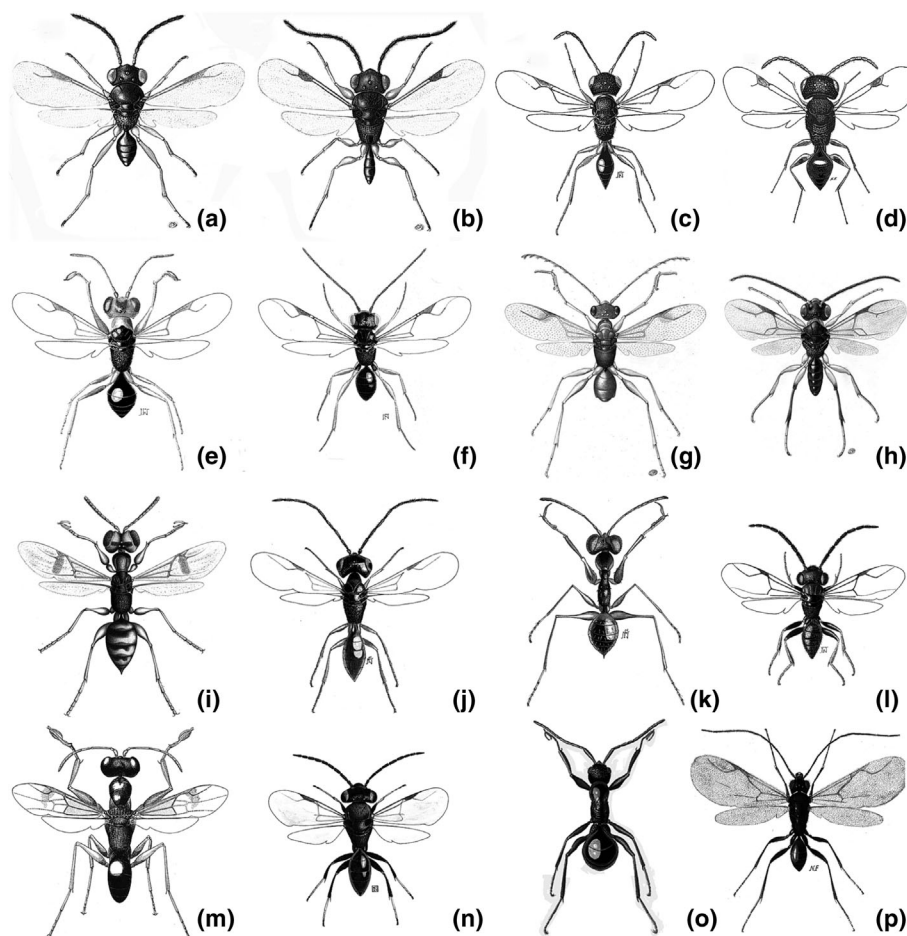


FIGURE 2 Habitus of different representatives of Dryinidae (dorsal view). (a) *Aphelopus* sp., female (length 1.7 mm); (b) *Aphelopus* sp., male (length 1.8 mm); (c) female of *Crovettia* sp. (length 2.4 mm); (d) male of *Crovettia* sp. (length 2.6 mm); (e) *Metanteon aerias* (Walker), female (length 4.0 mm); (f) *Metanteon aerias*, male (length 2.5 mm); (g) *Thaumatomyrinus* sp., female (length 3.5 mm) (from Xu et al. 2013); (h) *Thaumatomyrinus* sp., male (length 2.9 mm) (from Xu et al. 2013); (i) *Echthrodelphax* sp., female (length 2.2 mm); (j) *Echthrodelphax* sp., male (length 1.2 mm) (from Olmi 1984); (k) *Gonatopus* sp., female (length 3.5 mm); (l) *Gonatopus* sp., male (length 2.7 mm) (from Olmi 1984); (m) *Neodyrinus* sp., female (length 4.2 mm); (n) *Neodyrinus* sp., male (length 3.0 mm) (from Olmi & Virila 2014); (o) *Apodyrinus masneri* Olmi, female (length 3.4 mm); (p) *Apodyrinus masneri*, male (length 2.4 mm) (adapted from Olmi & Virila 2014; © Magnolia Press, reproduced with permission from the copyright holder).

Eighty-three fossil species of Dryinidae have been described (Olmi et al. 2020; Olmi, Eggs, et al. 2022).

As sexual dimorphism in the Dryinidae is so extreme that associations between opposite sexes are difficult

without rearings or DNA analysis, the classification is based primarily on females (Olmi & Virila 2014) (Figure 2e–p). Sexual dimorphism is not very extreme only in representatives of the subfamily Aphelopinae

(Figure 2a–d). During field studies, adult females are rarely collected and, due to the presence of many undescribed males, identification of males collected via traps is often difficult. In former times, males could be identified only when observed in copula or reared from the offspring of a wild mother composed by both sexes and from unfertilised eggs (Martins et al. 2021). But recently, due to the progress in the techniques of molecular biology, it is possible to classify male specimens using mitochondrial COI sequences (Mita & Matsumoto 2012) and DNA barcoding (Olmí et al. 2021; Olmi, Chen, et al. 2022).

Auchenorrhyncha hosts can cause serious problems in various crops, and pincer wasps are promising agents to be used to reduce their populations. They are common in agroecosystems, with rates of parasitism that can exceed 20%. In addition to their good performance as parasitoids, most of their females practise host-feeding, which adds another factor of mortality to their hosts' populations (Olmí 1999, 2000b).

Their immature larval instars are usually ectoparasitic (except for the endoparasitic larvae of the genus *Crovettia* and the first endophagous larval instar of *Aphelopus*), with the larva's head partly immersed in the coelom of the host and the rest of its body protruding between two of the host's sclerites. The mature larva empties the host's body, consuming the hemolymph and tissues. Then, the hopper dies, and the larva pupates in a silk cocoon spun in the soil or on the host plant.

Knowledge of various aspects of the biology of the group (e.g., host relationships and life cycle studies) is not comparable across biogeographic regions and depends largely on the presence (current or historical) of Dryinidae specialists in different areas. Dryinidae has been poorly studied, and the information referring to fundamental biological aspects is published in a scattered manner in various works published from 1889, by Giard, to the present. The aim of the present article is to compile a comprehensive review of the knowledge on the biology of dryinids based on literary records and our own observations after more than 30 years of working with these parasitoids. When discussing a particular topic, we normally turn to the literature that goes into more detail about it and includes prior references.

We provide data about the interactions between pincer wasps and their hosts, as well as information about their development, behaviour, natural enemies and economic significance as parasitoids. We also highlight some of the current gaps in the knowledge of these topics and, consequently, suggest future avenues of research.

BIOLOGY

Host relationships

Dryinidae parasitise nymphs and adults of Auchenorrhyncha Fulgoromorpha (~21 extant families) and

Cicadomorpha (12 extant families), except for the superfamilies Cercopoidea and Cicadoidea. The host–dryinid relationships are poorly known and are recorded for a limited number of species. The lack of knowledge about the relationships is due to the fact that host records can only be obtained by growing wasps to adulthood from parasitised hosts (Guglielmino et al. 2013; Martins & Domahovski 2017a, 2017b). Millán-Hernández (2018) tried to advance in the knowledge of the dryinid–host relationships by using larvae obtained directly from the hosts; his studies found new host hoppers, but he was unable to provide pincer wasp identification to a specific level. The known host–dryinid relationships, at subfamily and family levels, are summarised in Table 1. Comprehensive listings of known hosts for various species of Dryinidae can be found in the contributions of Guglielmino and Olmi (1997, 2007), Guglielmino et al. (2013) and Martins et al. (2021), and the most recent relationships in the biogeographic region-level reviews of the family mentioned above in the Introduction section.

The analysis of Dryinidae–Auchenorrhyncha relationships known reveals that each Dryinidae taxon could parasitise multiple host species from the same genus, different genera or, in some cases, different subfamilies; records of monospecific species seem to be only the result of insufficient research (Guglielmino & Olmi 1997). Furthermore, these authors highlight the host specificity at higher taxonomic levels (genus/tribes, genus/subfamily and genus/family). According to Waloff (1975), from an ecological point of view, the wide range of host species utilised by these parasitoids leads to greater stability of the large complexes of hopper populations. As an example, we can mention the contribution of Becerra-Chiron et al. (2017) who studied a community of six species of leafhoppers in the margins of corn crops in Mexico and found that all of them were attacked by five species of Dryinidae, suggesting that these species are mostly generalists.

A recent study (Klejdzys et al. 2018) stated that the dryinid *Haplogonatopus oratorius* (Westwood), a well-known parasitoid of Delphacidae, parasitised *Macrosteles laevis* (Ribaut) (Cicadellidae) in Poland because of the unstable ecological conditions in the vicinity of fields, which could induce settling on an accidental host. Another previous study (Olmí & Xu 2015) reported a similar example of atypical parasitoid–host relation for *Gonatopus lunatus* Klug (a Deltocephalinae parasitoid) that was recorded developing in young nymphs of *Ommatidiotus inconspicuous* Stål (Caliscelidae).

The developmental stage of the host to be parasitised varies according to the Dryinidae subfamily and the genus (Olmí 2000a). The choice of the host's developmental stage for parasitisation differs throughout the Dryinidae subfamilies and is largely influenced by the size of the female dryinid and its capacity to capture and paralyse the host. In general, Gonatopodinae prefer last nymphal instars and adults, whereas younger nymphs are preferably preyed upon. Among the Aphelopinae, *Aphelopus* spp. parasitised

TABLE 1 Summary of Dryinidae host records (Hemiptera: Auchenorrhyncha), considering only those subfamilies with known hosts (modified from Millán-Hernandez 2018).

Host infraorder	Host family	Host subfamily	Aphelopinae	Anteoninae	Bocchinae	Dryininae	Gonatopodinae	Thaumatomyzinae	Unknown	
Fulgoromorpha	Acanaloniidae					X	X			
	Caliscelidae				X		X			
	Cixiidae					X	X			
	Delphacidae					X	X			
	Dictyopharidae					X	X			
	Flatidae					X	X	X		
	Fulgoridae					X				
	Issidae					X	X			
	Lophopidae					X	X			
	Meenoplidae					X	X			
	Nogodinidae					X	X			
	Ricaniidae					X	X			
	Tropiduchidae					X	X			
	Eurybrachidae					X			??	
	Cicadomorpha	Cicadellidae	Aphrodinae					X		
			Cicadellinae					X		
			Coelidiinae					X		
		Deltocephalinae	X		X					
		Eunymelinae	X							
		Iassinae	X							
		Ledrinae	X							
		Megophthalminae								
		Tartessinae	X							
		Typhlocybinae	X							
	Membracidae	X								

only the nymphs of Typhlocybinae and never adults and, as far as is known, the same behaviour is found between *Crovettia* spp. and Membracidae species.

Most Gonatopodinae species whose hosts are Delphacidae (i.e., belonging to the genus *Gonatopus*, *Echthrodelphax* and *Haplogonatopus*) have a well-developed subapical tooth on the enlarged claw of the chelae (Figure 1b). The presence of this tooth seems to be intimately linked to the capture of the host. Delphacidae may be more reactive than Cicadellidae at the time of capture, and it is likely that the subapical tooth and enlarged claw's lamellae would work to strengthen the grip on the host (M. Olmi, personal communication, September 8, 2022).

The hosts have a very strong influence on biological traits and on the behaviour of the pincer wasps. Espinosa et al. (2019) stated that despite being able to develop on different species of Delphacidae, females of *Gonatopus bonaerensis* Virla faced with its usual host, lived longer and killed more planthoppers by parasitism than by host-feeding, but in front of its occasional host, host-feeding prevailed. *G. bonaerensis* has a marked association and the highest fitness with its most habitual host and could use other species as occasional hosts, especially when field populations of the main host are scarce.

Adult stage

Emergence

Pincer wasps emerge from the cocoon, where they pupated, through a hole made by the mandibles (Abril Ramirez 1992). In the empty cocoon, there is the exuvia of the mature larva, including its mandibles, and in some species, the meconium (Guglielmino et al. 2017; Virla 1995).

It seems that the pincer wasps are diurnal insects (Olmi 2000a) (rarely, they are captured at light during the night). The emergence of the adults can occur at any time of the day, as observed in *Haplogonatopus hernandezae* Olmi (Hernandez & Belloti 1984), or preferably at certain times of the morning, as reported for *Haplogonatopus oratorius* (= *Haplogonatopus atratus* Esaki & Hashimoto) (Kitamura 1989). The Gonatopodinae become inactive and repose after being kept in complete darkness for 1 or 2 h. If the temperature rises beyond 9°C, *Gonatopus desantisi* Olmi & Virla females become active (Virla 1995).

Adults, especially females, spend a lot of time cleaning their bodies (mainly the antennae). According to Lindberg (1950), Virla (1995) and Guglielmino et al. (2007), this behaviour was observed in females of the majority of *Gonatopus* species and in other subfamilies that the authors have bred in the lab. Females perform thorough cleaning after eating, after laying eggs or if the environment is dirty with dust.

Longevity

Adult longevity is variable and depends on the species. Unfortunately, few data regarding only species belonging to two subfamilies (Aphelopinae and Gonatopodinae) are known. Males normally live a few days after mating and die soon after. Among *Aphelopus* species (Aphelopinae), the males live 4–14 days, and females can reach 16 days of longevity (Jervis 1980). In Gonatopodinae, males have a mean longevity of 2–3 days or less, and this does not seem to change whether or not they have received a honey supplement (Rios-Reyes & Moya-Raygoza 2004; Virla 1995), whereas females live more than 18 up to 44 days, depending on the breeding conditions (Virla 1995).

Feeding and host-feeding

The performance or fitness of parasitoid wasps can be remarkably influenced by the uptake of nutrients obtained when adults feed on hosts and/or non-host resources (Benelli et al. 2017). The feeding behaviour of Dryinidae in the field is practically unknown. It was not recorded in literature that they feed on nectar of plants (both from flowers and from extrafloral nectaries), although this food resource is surely exploited by dryinid adults.

In the laboratory, females feed sugary solutions (especially the honeydew of their hosts) and host blood and tissues (host-feeding) (Figure 3); males do not feed or feed only sugary solutions, especially honeydew.

For Aphelopinae, the only observations on adult nutrition are by Jervis (1980) and refer to *Aphelopus melaleucus* (Dalman) and *A. camus* Richards. According to this author, the adults of these species court and mate immediately after the emergence, without feeding. Jervis does not say whether they feed after mating; however, it seems plausible to think that they do not feed at all.

The consumption of host-derived food (host hemolymph and tissues) was defined as 'host-feeding' by Jervis and Kidd (1986). The host-feeding is a common behaviour among insect parasitoids and has been reported in at least 17 Hymenoptera families and in Tachinidae flies (Kidd & Jervis 1989). Host-feeding is highlighted as a way to supply amino acids and other compounds to the adult diet, which increase the egg production and/or prolong longevity (Burger et al. 2005; Heimpel & Collier 1996; Jervis et al. 1996; Jervis & Kidd 1986). The males of all species and the females of Aphelopinae do not practise host-feeding. As far as known today, dryinid females with chelae are host-feeders (Olmi 1999, 2000b; Sahragard et al. 1991; Waloff 1974). Jervis et al. (1987) stated that females with claws practise predation on their hosts, capturing them with their chelae, and, after having made a hole with their mandibles in the integument of the hosts, they suck the hemolymph and consume tissues. According to Waloff and Jervis (1987), host-feeding is an

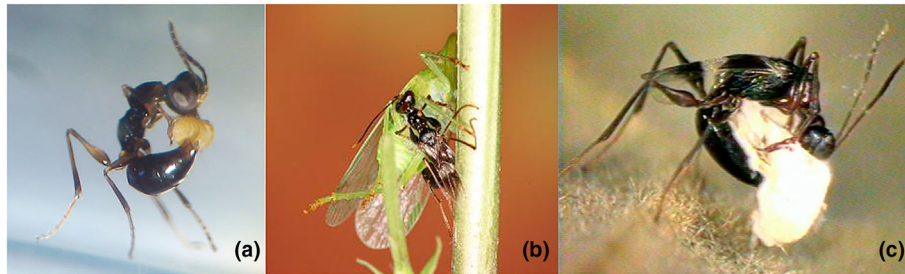


FIGURE 3 Host-feeding by pincer wasp females. (a) Female of *Gonatopus bonaerensis* Virla preying a small nymph of *Delphacodes sitarea* Remes Lenicov & Tesón; (b) female of *Dryinus tarraconensis* (Marshall) preying on a dictyopharid; (c) female of *Neodryinus typhlocybae* (Ashmead) preying on a nymph of *Metcalfa pruinosa* (Say).

acquired behaviour that developed in conjunction with the evolution of chelae. This may explain why the phenomenon has not been observed in Aphelopinae, which lack chelae (Olm 1999).

As far as known, host-feeding almost always takes place at the expense of their own hosts; for example, if a species of pincer wasp has Delphacidae as hosts and if in its environment there are also Cicadellidae, host-feeding occurs only at the expense of the planthoppers. However, rarely (maybe only in the case of long famine and in the laboratory), non-host leafhoppers can also be attacked in absence of the main hosts. For example, Chua and Dyck (1982) report the case of *Gonatopus flavifemur* (Esaki & Hashimoto), which, despite having available planthoppers as hosts, can attack (but only for host-feeding, not for oviposition) the leafhopper *Nephotettix virescens* (Distant). Sahragard et al. (1991) stated that Gonatopodinae species had never been recorded feeding on an individual host more than once and this was corroborated by Espinosa et al. (2019).

For the Gonatopodinae, it was stated that *G. bonaerensis* females display an active host-feeding behaviour and can benefit by eating the honeydew excreted by their hosts as well, using those nutrients for egg maturation (Espinosa & Virla 2018). Recently, Espinosa et al. (2021) reported for the same species that the addition of alternative food sources (i.e., pollen, bee honey and vitamin E), provided throughout parasitoid adult lifetime, affected its longevity, fecundity and both host-feeding and parasitism rates. The addition of pollen to the diet significantly increased the longevity of females. When females had access to additional food sources, their host-feeding decreased and their parasitising activity increased. For example, females feeding honey plus vitamin E parasitised significantly more host nymphs, produced more eggs and lowered host-feeding if compared with females feeding other diets. Waloff (1974) observed for two species of Anteoninae that they performed low predatory activities and rarely killed their hosts. Lower levels of host-feeding in Anteoninae may be due to a combination of morphological characteristics (a not-so-flexible body, wings and short forelegs with chelae) that make them less suited to grasp. According to Richards (1939), the greater predatory activity of the Gonatopodinae could be associated with a better

adaptation to host-feeding, resulting from a jointed body, and the greater length of the forelegs, with which hosts are caught. Following these criteria, the lack of predatory activity in the Aphelopinae is probably due to the stockier body, normal development of the wings and forelegs and the lack of chelae.

In the more specialised subfamilies of pincer wasps (Dryininae and Gonatopodinae), the host usually dies as a result of host-feeding; in this case, host-feeding is defined as ‘destructive’ (Jervis & Kidd 1986). In less specialised subfamilies (Anteoninae), the host generally survives after the host-feeding (non-destructive according to Jervis & Kidd 1986). Depending on whether the host-feeding is followed by oviposition or not, it can be defined as ‘concurrent’ or ‘non-concurrent’ (Jervis & Kidd 1986). Concurrent destructive host-feeding was registered for some species of Gonatopodinae (Espinosa et al. 2019; Kitamura 1982). Non-destructive concurrence was only observed in two species of dryinids: *Lonchodryinus ruficornis* (Dalman) and *Anteon pubicorne* (Dalman) (both Anteoninae) (Jervis & Kidd 1986; Waloff 1974). Jervis et al. (1987) and Kidd and Jervis (1989) made a list of the types of host-feeding known for various species of Dryinidae up to those dates. The data on host-feeding behaviour (i.e., concurrent or non-concurrent, and destructive or non-destructive) probably vary depending on the host. In fact, females of *Haplogonatopus oratorius* (as *Haplogonatopus atratus* Esaki & Hashimoto) when attacking *Laodelphax striatella* have a non-concurrent and destructive behaviour, whereas if they attack *Nilaparvata lugens* (Stål), they have a concurrent and non-destructive behaviour (Abe & Koyama 1991).

The first activity that the females perform after emergence is host-feeding. Indeed, the first host is always preyed upon rather than parasitised. Many species feed on very small and young hosts, in which the females cannot oviposit (Jervis et al. 1992; Kidd & Jervis 1991).

According to Jervis and Kidd (1986), newly emerged females of Gonatopodinae need to feed in order to increase egg production and thus the rate of parasitism. In a study on *H. oratorius* feeding on *Laodelphax striatella*, Kitamura (1986) found that the female produced more eggs with a higher rate of host-feeding.

Mora-Kepfer and Espinoza (2009) discovered that the proportions of parasitised and preyed-on host nymphs from *Haplogonatopus hernandezae*, affecting the rice planthopper *Togasodes orizicolus* (Muir), did not vary with the age of the adult female. However, Sahragard et al. (1991) discovered that as this Gonatopodinae grew older, their host-feeding activity increased and the number of hosts parasitised decreased. Espinosa and Virla (2018) observed that females of *G. bonaerensis* older than 4 days and feeding only honey and water showed a considerable decrease in egg laying; this suggested that host-feeding is important for egg maturation.

Giri and Freytag (1988) in the United States observed that the females of *Gonatopus americanae* Olmi (mentioned as *Dicondylus americanus* (Perkins)) practise 100% host-feeding on the first captured host, 90% on the second and 60% on the third, and all females lay eggs on the captured fourth host. According to Sahragard et al. (1991), in species such as *G. flavifemur* in which the females emerged with some mature eggs in their ovaries, it is evident that there is no need for host-feeding to produce the eggs. Nevertheless, the authors consider *G. flavifemur* an obligatory host-feeder because the host-feeding in this species acts as a 'releaser' to initiate oviposition, because they have insufficient metabolic reserves to ensure the maturation of successive eggs. A different condition was described by Espinosa and Virla (2018) and Rios-Reyes and Moya-Raygoza (2004) who demonstrated for *G. bonaerensis* and *G. bartletti* Olmi, respectively, that their females are autogenic (maturing some eggs without a first feeding) and laying eggs the first day after the emergence.

Jervis and Kidd (1986) affirmed that honeydew serves as a maintenance diet and host-feeding to produce eggs in hymenopteran parasitoids, but this may not be valid for Dryininae. According to the observations of Subba Rao (1957), females of *Dryinus pyrillae* (Kieffer) (named as *Lestodryinus pyrillae*) show a tendency towards host-feeding when they are fed with sugary solution and grapes, but they do not tend to practise host-feeding if they are fed with honeydew. This author suggested that this is because the host's honeydew contains the nitrogenous substances needed for the development of the eggs. Conversely, they are lacking in the sugar solution and in the grapes, so that the female is forced to practise host-feeding to obtain them. Subba Rao deduces that the cause of host-feeding is the lack of nitrogen in food.

Host-feeding is not always practised with the same intensity by the females of the dryinids along the day. Kitamura (1989) recorded that the females of *H. oratorius* practised host-feeding daily especially between 6 and 9 in the morning and between 12 AM and 3 PM. No predatory activity took place during the night.

It should be noted that host-feeding could be proportional to the density of hosts, as in the case of parasitism; in fact, Sahragard et al. (1991) observed in *G. flavifemur* that the more hosts there are, the greater the number of predated hosts. This fact was corroborated also for

Dicondylus indianus Olmi attacking the rice brown planthopper; Sahragard et al. (1991) concluded that the host availability has a strong influence on the rates of oviposition, host-feeding and longevity of Gonatopodinae.

Gonatopus females have often been observed to feed on the bodies of recently dead hosts (yet containing fresh tissues and hemolymph); this is seen in isolation (lab conditions) and when no live hoppers are available (M. Olmi, personal communication, September 8, 2022). Also, it is common to see the *Gonatopus* females 'stalking' an exuvia from their hosts, but after inspecting it, they continue looking for other hosts (Virla, personal observation).

Jervis et al. (1996) stated that destructive host-feeders parasitoids of 'Homoptera' are probably better biological control agents than other parasitoids. In the [Dryinid efficiency and functional response](#) section, the consequences of the host-feeding practice will be discussed.

Sexual cannibalism

Sexual cannibalism is a phenomenon that has been reported in a wide variety of invertebrate predators, especially in arthropods (Fisher et al. 2018). Virla and Espinosa (2019) described for the first time the occurrence of sexual cannibalism in Dryinidae. They observed that young and starved females of *Gonatopus chilensis* (Olmi) after mating occasionally caught the male and devoured his gaster, but they said that this behaviour would be an occasional action in this species (Figure 4b,c). Cannibalising a male may allow a female to avoid starvation or to produce a larger number of eggs.

Adult dispersal via hosts

Early in the dryinid larva's development, parasitised hoppers do not appear to have any difficulty moving around, jumping as freely as a healthy one (Olmi 1999). Nevertheless, smaller nymphs, especially those affected by Gonatopodinae, could show lateral displacement (Virla 1995). According to Giordano et al. (2002), the polyphagy and the major capacity of adaptation compensated the reduced potential of dispersal of the dryinid populations compared with those of their phytophagous hosts. It has been pointed out that in species with apterous females, whose dispersal capability seems reduced, their dispersion depends mainly on the migrations of their hosts when they carry eggs or young larvae of the Dryinidae (Olmi 1999; Raatikainen 1967). Mita et al. (2012) documented the annual long-distance migrations of Asian rice planthoppers (*Sogatella furcifera* Horvath and *Nilaparvata lugens*) and confirmed the overseas long-distance passive migration (as eggs and larvae) of two apterous Gonatopodinae (*Haplogonatopus apicalis* R. Perkins and *H. oratorius*) via their parasitised hosts.

Reproduction and development

Parthenogenesis (arrhenotoky and thelytoky) and sex proportion

Dryinids are mostly known for their females; males are uncommon or unknown due to the extreme sexual dimorphism (see the [Introduction](#) section). For example, in the Neotropical region, more than 80% of species are known only from one sex (Virla & Olmi 2008); 83 of 123 species (67.5%) of the genus *Gonatopus* found in this region are only known through their females (Olmi & Virla 2014).

The Dryinidae are reproduced by parthenogenesis and by biparental reproduction (Waloff 1974). There are several reports of species exhibiting thelytokous parthenogenesis (virgin females that produce females), but some of them can have populations with biparental reproduction as well; an example of this phenomenon is the species *Gonatopus chilensis* in Argentina (Olmi & Virla 2014). As in other Hymenoptera with sexual reproduction, virgin females can produce also only males (arrhenotokous parthenogenesis) (Normark 2003; Waloff 1974). Kornhauser (1919) stated that mated females produce female progeny and virgin females produce male progeny in the Aphelopine *Crovettia theliae* (Gahan).

Espinosa et al. (2017) established that the thelytoky in *Gonatopus bonaerensis* was due to the presence of the endosymbiont bacteria *Wolbachia* sp. wRi strain. Infected specimens treated with an antibiotic solution determined the normal arrhenotokous parthenogenesis and the production of male offspring. *Wolbachia* bacteria are a common symbiont of insects and were found infecting other species of Dryinidae (Gan et al. 2002; Noda et al. 2001).

In species showing biparental reproduction, the sex proportion is variable. Virla (1992) described for *G. chilensis* a field proportion of 4.4/1 females/male. The sex proportion may vary among different dryinid populations in a particular area. For example, in *G. desantisi*, some populations in Argentina were 100% constituted by females, other are female biased (2.8:1) and other are 1:1 (Virla 1995). Herlin et al. (2019) observed for *Echthrodelphax fairchildii* R. Perkins, a parasitoid of *Laodelphax striatella* (Fallén) (Delphacidae), that maternal body size differentially impacted the body sizes and survival rates (and longevity) of the progeny; larger females generated both male and female progeny, and smaller females generated only male progeny.

Furthermore, the sex proportion may depend on the host. Favaro et al. (2018) investigated the parasitisation of *Neodryinus typhlocybae* female on *Metcalfa pruinosa* (Say) and the influence of the host developmental stage on the sex ratio of the offspring. They observed that *N. typhlocybae* parasitised mostly the third, fourth and fifth host nymphal instars. From the third instar, only male progeny was generated; from the fourth instar, both male

and female progeny were generated, though the sex ratio remained male biased; and from the fifth instar, a higher percentage of female progeny was generated.

Sexual reproduction: Ovigyny, eggs and spermatozoa

Studies by Espinosa and Virla (2018) described for the first time the anatomy and histology of the ovaries and the reproductive maturation in a Dryinidae species (*G. bonaerensis*, Gonatopodinae). This species has the most typical ovaries of the hymenopteran species: meroistic type with three polytrophic ovarioles. It is an autogenic species where newly emerged females can lay eggs without previously having eaten. This can be explained because females have an average of 3.7 mature eggs at emergence. After feeding, the number of mature oocytes increases 3.8-fold during the first 48 h of life. Also, *Gonatopus flavifemur* hatches with mature eggs in its ovaries and can parasitise at a young age (Sahragard et al. 1991).

As was pointed out by Espinosa and Virla (2018), ‘ovigyny’ is an important physiological trait to consider in biological control because it influences parasitoid life history and ecology (Ellers et al. 2000), including host-parasitoid population dynamics (Kidd & Jervis 1989), anatomy of mouthparts and alimentary habits (Flanders 1950), types of egg and resorption capability (Jervis et al. 2001), female body size in relation to the dimension of the eggs (Ellers & Jervis 2003) and longevity (Jervis et al. 2001). Flanders (1950) designated the hymenopteran parasitoids as ‘proovigenic’ when females emerge with the full complement of eggs ready to lay and ‘synovigenic’ when females produce oocytes throughout their lives. Later, Jervis et al. (2001) formulated an ‘ovigyny index’ that ranged from 0 (extremely synovigenic) to 1 (strictly proovigenic) in order to characterise species that are intermediate in this regard. Furthermore, host-feeding is associated with synovigenic parasitoids (Jervis & Kidd 1986). In the Dryinidae, it could mean that those groups with developed chelae would be mostly synovigenic and the groups without chelae, Aphelopinae and Erwiniinae, would be proovigenic.

The species *G. bonaerensis* (Gonatopodinae) is a strong synovigenic species when parasitising its usual host, *Delphacodes sitarea* Remes Lenicov & Tesón (Delphacidae); however, when attacking the occasional and non-preferred host *Peregrinus maidis* (Ashmead) (Delphacidae), it is weakly synovigenic (Espinosa & Virla 2018).

Furthermore, Espinosa and Virla (2018) reported the possibility of egg resorption in *G. bonaerensis* because mature egg numbers in ovarioles decreased significantly in females that were deprived of hosts for more than 72 h. Conversely, according to Sahragard et al. (1991), no egg resorption was observed in *G. flavifemur* when parasitising the brown planthopper; mature eggs were

observed in the ovaries of females dissected at the end of life, even when a few hosts per day were available.

According to Kidd and Jervis (1991), generally, parasitoids that practise host-feeding produce ‘anhydropic’ eggs, that is, eggs rich in nutrients (as opposed to ‘hydroptic’ eggs, i.e., eggs poor in nutritional substances). If we apply this hypothesis of Kidd & Jervis to the Dryinidae, it could be inferred that those subfamilies that practise host-feeding have anhydropic eggs, and the Aphelopinae, which do not practise host-feeding, have hydroptic eggs instead.

As can be seen, knowledge about the ovigeny in Dryinidae is scarce and is based only on a few species of Gonatopodinae.

The external morphology of the eggs is described only in a few species from three subfamilies (Aphelopinae (Buyckx 1948), Dryininae (Abril Ramirez 1992) and Gonatopodinae). Fenton (1918) and Guglielmino and Virla (1998) both characterised the egg’s morphology in species of Gonatopodinae. The egg is oval or kidney shaped and can be light yellow, dark grey or dark brown. On the chorion, there is no sculpturing. Further fragmentary notes on the morphology of the egg were given by Clausen (1940), Raatikainen (1961), Barrett et al. (1965) and Jervis (1980). Guglielmino and Virla (1998) described how the chorion opens when the larvae I of *G. lunatus* emerge.

Eggs can be considered morphologically exterior, according to Olmi (1984, 1994). For the Gonatopodinae, more research needs to be done to determine if the egg is fully implanted into the host’s body or merely partially inserted into the intersegmental membrane; Olmi (1994) indicated that the egg is partially internal and partially exterior, as Guglielmino and Virla (1998) later stated for *G. lunatus*. They claimed that the posterior pole protrudes outside of the host body. Incubation of eggs is variable depending on the species and environmental factors such as temperature. In species of the genus *Gonatopus*, the egg lasts between 2 and 5 days (Virla 1992, 1995).

The spermatozoa of Dryinidae are poorly known; the only publication on the subject is that of Quicke et al. (1992), in which the spermatozoa of *Lonchodryinus ruficornis* (Dalman)(Anteoninae) (named as *Prenanteon basalis* (Dalman)) are described and illustrated. According to Kornhauser (1919), males of *Crovettia theliae* emerged from the cocoons in which they had overwintered with spermatogenesis already completed and sexual maturity attained. However, this observation should be validated.

Mating behaviour

Mating behaviour of dryinids is known only for a few species: *Aphelopus melaleucus* (Aphelopinae) (Jervis 1979), *Anteon brachycerum* (Dalman) (Jervis 1979) and three species of Gonatopodinae: *Gonatopus distinctus* Kieffer (as *Pseudogonatopus*) and *G. bicolor* (Haliday) (as *Dicondylus*) (Waloff 1974), and *G. chilensis* (Virla &

Espinosa 2019) (Figure 4a). Despite maintaining an experimental breeding of *Dryinus poecilopterae* (Richards) (Dryininae), Abril Ramirez (1992) was never able to observe the copula.

The courtship procedures in *A. melaleucus* are basic, according to Jervis (1979); the male contacts the female from behind with its antennae, seizes it up with its first two pairs of legs and then mounts it. The male reclines backwards during the copula and is pulled along the substrate by the female. After a few seconds, the two separate. Similar behaviours have been recorded for *A. brachycerum* in the field (Jervis 1979). In addition, Jervis (1979) collected 39 males and 9 females of *A. melaleucus* within seconds of beating with a net a hornbeam tree (*Carpinus betulus*, Betulaceae), and he attributed this to swarming behaviour.

In Gonatopodinae, copulation takes place fairly quickly from the time the two sexes meet, usually within half an hour. The male inserts from below its genitalia into that of the female, supported by its hind and median legs on the substrate flapping its wings and with the forelegs resting on the gaster of the female. During the copula, the female remains motionless or moves its antennae, sometimes performing cleaning movements on them with its mandibles. Females often move several centimetres with the male during copulation. After copula, females rest for several seconds and clean themselves. In general, males rest for more time with the antennae pointing forward (Virla & Espinosa 2019; Waloff 1974). In *G. chilensis*, copulation lasts between 8 and 40 s. Females were occasionally re-mated by the same male (Virla & Espinosa 2019).

There is no information on the mating system in dryinid species or on whether they are monandrous (single-partner mating at or soon after emergence) or polyandrous (multiple mating along the life) species, nor on mating frequencies, but monandry is considered common in the Hymenoptera (Eickwort & Ginsberg 1980).

Oviposition

It has been inferred that for the localisation of the host, the Dryinidae are oriented mainly by sight and by vibrational signals (Figure 5). In Dryinidae species attacking Fulgoromorpha (Olmi 1999), the antennae of the females hold peculiar and complex sensory structures named ‘antennal dorsal organs (ADOs)’ involved in the perception of vibratory stimuli. These sensorial organs are not present on male antennae and were well described by Riolo et al. (2016) for *Neodryinus typhlocybae*. According to Waloff (1974), most dryinid species were not able to distinguish between parasitised and non-parasitised hoppers if offered as hosts on different occasions.

Generally, the host is pursued or stalked, and after that, the female catches the hopper rapidly and accurately, grasping it with its chelate foretarsi (Figure 5b).



FIGURE 4 Different behaviours of the dryinid *Gonatopus chilensis* (Olmi). (a) Mating; (b, c) female devouring the gaster of the male immediately after copula (from Virila & Espinosa 2019, reproduced with permission from the copyright holder, © Acta Ethologica).

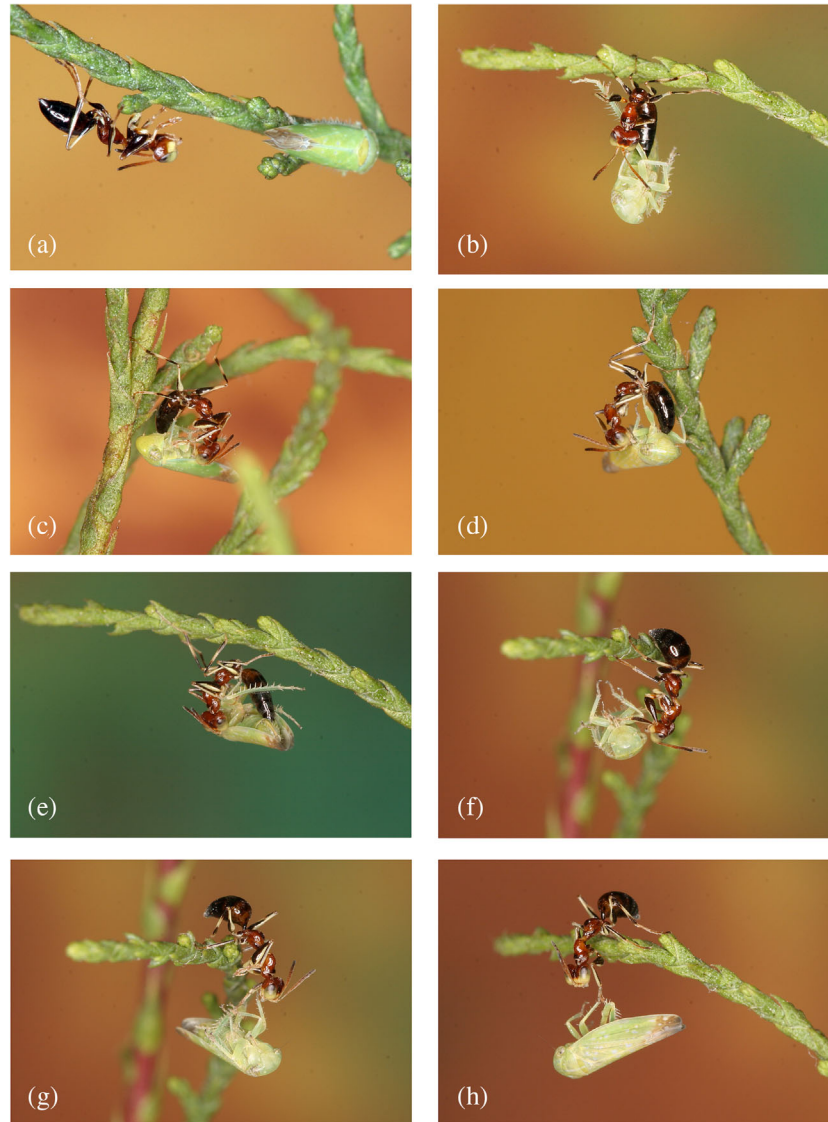


FIGURE 5 The parasitic behaviour of *Gonatopus albolineatus* Kieffer on *Opsius lethierryi* Wagner (Cicadellidae) during its parasitisation progression. Targeting the host (a), grabbing it by the chelae (b) and injecting the stinger into the host's prothorax to paralyse it (c, d), followed by the laying of the eggs (e). The female gently places the host, which is already parasitised, on the twig and rattles until it comes out of sedation (f–h).

Upon grasping the host, the female stings the host ventrally between the head and thorax, injecting a substance that leaves the host immobile. When the host is numb, the female repeatedly stings the ventral area of the thorax and abdomen, after which it searches with the

ovipositor for a suitable area of the host's body to lay the egg between two overlapping sclerites (Figure 5c,d). After oviposition, the female carefully deposits the host on the plant, touching it repeatedly to help it to recover and to return to its normal activities (Guglielmino et al. 2007).

Dryinid females may also hold the hopper carefully with their mandibles (Richards 1939; Virla 1995; Yamada & Kawamura 1999). Despite the Dryinidae being classified within the Aculeata, their ovipositor is used also for oviposition (Olmí & Virla 2006). In Dryinidae, oviposition lasts from a few seconds to about 2 min, as observed in *G. desantisi* (30–60 s) (Virla 1995) and in *Anteon pubicorne* (15–120 s) (Waloff 1974).

Because Aphelopinae females lack chelate foretarsi, they must catch and hold the hosts using only their mandibles and fore and middle legs (Jervis 1980; Olmí 1994). It was stated that *Aphelopus* species oviposit in any of the nymphal stages of their hosts (Jervis 1980). According to Olmí (1994), *Aphelopus* females sting the Typhlocybinae nymphs between two intersegmental membranes laying the egg in the haemocoel. The hosts and biology of the non-chelated Erwiniinae are unknown.

In Anteoninae, some species belonging to the genus *Anteon* usually lay the eggs in the intersegmental membranes, laterally in the thoracic region (see photographs in Guglielmino et al. 2017). In other *Anteon* species that parasitise *Macropsis* spp. (Cicadellidae), the egg is implanted ventrally between two abdominal sclerites (M. Olmí, personal communication, September 8, 2022). In *Deinodryinus*, the egg is inserted dorsally between the head and pronotum (see fig. 81A in Olmí et al. 2019). In Dryininae, the egg may be inserted between two sclerites of the thorax (see Plate XXIII in Olmí 1999: *Dryinus collaris* (L.)), abdomen (see Plate XXV in Olmí 1999 and fig. 1 in Guglielmino et al. 2015: *Dryinus tarraconensis* (L.)), or between the host's metathorax and abdomen below the metathoracic wing-pad. In *Dryinus poecilopterae*, the deposited egg appears as a small brown dot located between two abdominal sclerites of *Poekilloptera phalaenoides* (L.) (Flatidae) (Abril Ramirez 1992).

In the majority of the Gonatopodinae, the eggs are inserted into the connecting membrane between two overlapping abdominal or thoracic segments, usually laterally in the tergal portion (Guglielmino & Virla 1998; Virla 1995). Normally, the egg is not easily visible.

Based on oviposition behaviour, Yamada and Kawamura (1999) demonstrated how they could distinguish whether females of *Haplogonatopus atratus* (= *H. oratorius*) lay 'female' or 'male' eggs, based on the time it took the female to lay the eggs. Also, Yamada and Imai (2000) described that the mated females of *Echthrodelphax fairchildii* ceased moving their stings for 2–3 s before inserting female eggs and for less than 1.5 s when laying male eggs. Females may be transferring sperm from the spermatheca to an egg, resulting in an extended oviposition time. In the case of the unmated females, the behaviour is different, and it takes between 1 and 20 s.

Mora-Kepfer and Espinoza (2009) stated that dryinids ovipositing in a smaller host could have a negative effect on the developmental success of the progeny. Also, Uy and Espinoza (2018) studied the differential host handling behaviour between feeding and oviposition in

H. hernandezae and observed that the older hosts were more often chosen for consumption than the younger hosts and that the younger hosts were chosen more often for oviposition.

Pre-imaginal development and life cycle

The knowledge on the postembryonic development and the morphology of immature and mature larvae of the Dryinidae is very scarce. The first descriptions of the structure of the Dryinidae larvae were published by Mik (1882) and Giard (1889). Nowadays, the available data concern only a few species belonging to 5 (Aphelopinae, Anteoninae, Bocchinae, Dryininae and Gonatopodinae) out of 12 extant subfamilies.

Dryinidae have hypermetamorphic development with four or five larval instars (Figure 6). There are two types of larvae (immature and mature larvae), which differ in shape, physiology and feeding habits.

The immature larvae live generally as ectoparasites of juvenile instars or adults of Auchenorrhyncha with the anterior region of the head immersed into the host's coelom and the posterior one protruding from the intersegmental membranes of the host's body (except for *Crovettia* larvae, completely endoparasitic in all instars, and *Aphelopus*, endoparasitic only in the first larval instar). The position of the larvae is generally characteristic of a dryinid species (Waloff 1974) but may be a bit variable depending on the species and size of the hosts (Virla, personal observation) (Figure 7).

The discarded exuviae of previous larval instars cover the body of the larva forming a 'larval sac' named 'thylacium' (sensu Olmí 1994) protecting the larva's body (Guglielmino & Virla 1998; Perkins 1905; Ponomarenko 1975).

The shape of the immature larvae varies from cylindrical and elongate in *Mytrophorus formicaeformis* Ruthe (Guglielmino & Bückle 2010) or slightly bent ventrad in *Bocchus scobiolae* Nagy (Guglielmino et al. 2022) to strongly bent or rounded in Aphelopinae, Anteoninae, Dryininae and Gonatopodinae (Buyckx 1948; Guglielmino & Bückle 2003; Guglielmino et al. 2006, 2015, 2017; Guglielmino & Virla 1998; Virla & Mangione 2000; Xu et al. 2011).

The study of the postembryonic development of dryinids highlights a vast morphological diversity of the immature larvae among different subfamilies. On the other hand, we know very few about their feeding patterns. The immature larvae are firmly attached with their cephalic region to the intersegmental membrane of the host's body. In *Aphelopus*, when the first larva is pushed out of the coelom through the wound caused by the mother's ovipositor and gets stuck in the wound with the head inside and the rest of the body outside, a cuticular ring is formed around the head of the larva that attaches it to the host body and prevents it from being detached

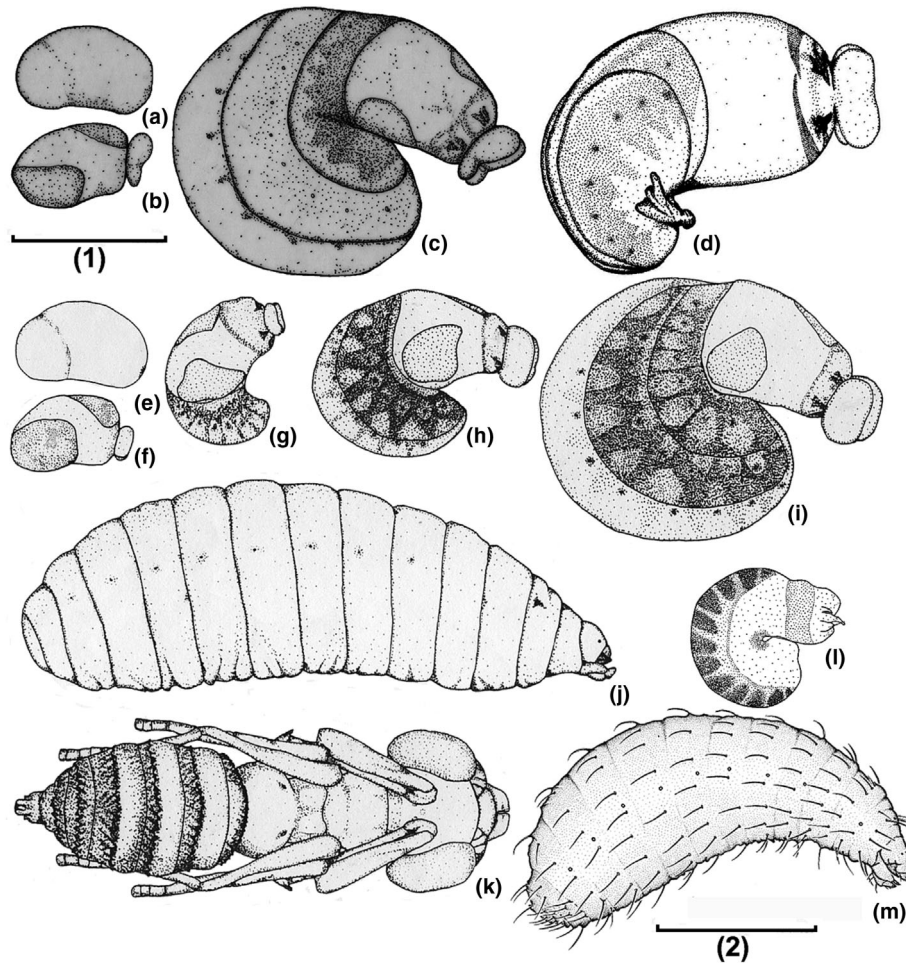


FIGURE 6 Some examples of pre-imaginal stages of Dryinidae. (a) Egg of *Gonatopus bonaerensis* Virla; (b) first immature larva of *G. bonaerensis*; (c) last immature larva of *G. bonaerensis*; (d) last immature larva of *Gonatopus chilensis* (Olmi); (e) egg of *Gonatopus lunatus* Klug; (f) larva I of *G. lunatus*; (g) larva II of *G. lunatus*; (h) larva III of *G. lunatus*; (i) larva IV of *G. lunatus*; (j) mature larva of *G. lunatus*; (k) pupa of *G. lunatus*; (l) last immature larva of *Anteon* spp.; (m) mature larva of *A. flavicorne* (Figures (a)–(c) adapted from Mangione & Virla 2004; Figure (d) adapted from Virla & Mangione 2000; Figures (e)–(k) modified from Guglielmino & Virla 1998; Figure (l) adapted from Ponomarenko 1975; Figure (m) modified from Guglielmino et al. 2017; © Magnolia Press, reproduced with permission from the copyright holder) (scale 1: 0.5 mm for Figures (a)–(i) and (l); scale 2: 1 mm for Figures (j), (k) and (m)).

from the host body (Olmi 1994). In addition, the larvae of some studied species of Gonatopodinae (e.g., *G. bartletti*) (Guglielmino et al. 2006) and Dryininae (e.g., *Dryinus poecilopterae*) (Abril Ramirez 1992) have a ventral process, located near the anterior end of the larva with the function of anchoring the parasitoid to the host (for examples of species holding this process, see Guglielmino & Virla 1998).

The frontal area of the cephalic region shows distinct, but still little sclerified whitish mouthparts. It is covered by a ‘membrane trophamniotique’ (sensu Buyckx 1948) in Aphelopinae or a ‘mask’ in Anteoninae (Guglielmino et al. 2017) and in a species of Bocchinae (*M. formicaeformis*) (Guglielmino & Bückle 2010). The oral region is characterised in some subfamilies by the presence of two vesicles (named oral or cephalic lobes according to different authors) of various shapes: ovoid, small and in contiguity with the underlying mandibles in

M. formicaeformis and *B. scobiolae* (Bocchinae) (Guglielmino & Bückle 2010; Guglielmino et al. 2022); sickle shaped and quite distant from each other in Dryininae (Guglielmino et al. 2015); and kidney shaped, well developed, touching each other at their base in Gonatopodinae (Guglielmino et al. 2015; Guglielmino & Virla 1998).

The oral vesicles are evaginations of the body wall, unrelated to the digestive apparatus, but some authors supposed their involvement in the feeding process (Carcupino et al. 1998; Ponomarenko 1975). The mechanism of feeding of Gonatopodinae larvae, as well as the putative role of the oral vesicles, was discussed by Virla and Mangione (2000). The immature larvae of the polyembryonic genus *Crovetia* (Aphelopinae) are an exception being totally endoparasitic, developing inside the host haemocoel and feeding through a trophamnion (Kornhauser 1919; Olmi 1994).



FIGURE 7 Position of the thylacium (= larval sac) in different species of Dryinidae. (a, b) Thylacium of *Aphelopus alebroides* Xu et al. on *Arboridia sinensis* Guglielmino et al. (Typhlocybinae); (c) nymph of Deltocephalinae attacked by *Gonatopus* sp.; (d) nymph of *Exitianus obscurinervis* Stål with the thylacium of *Gonatopus caraibicus* (Olmí); (e) *Anteon pilicornae* (Ogloblin) on the adult of the Macrostelina *Balclutha rosea* (Scott); (f) brachypterous female of *Delphacodes sitarea* (Delphacidae) affected by *Gonatopus bonaerensis*; (g) nymph of *Peregrinus maidis* (Ashmead) parasitised by *Haplogonatopus hernandezae* Olmí; (h) thylacium of *Gonatopus chilensis* (darker) and *Gonatopus bonaerensis* (brown) and with transversal bands on a nymph of *Metadelphax propinqua* (Fieber); (i) mature larva of *Gonatopus bonaerensis* emerging from the planthopper host nymph (Figures (a) and (b) from Xu et al. 2011, reproduced with permission from the copyright holder [JKES]).

Certain characteristics of the life history of the Aphelopinae are distinctive and have been discussed in depth by Buyckx (1948) and later by Olmí (1994). The egg is much more internal, and the first-stage larva, at least, is surrounded by a peculiar, hypertrophied mass of tissue (trophamnion). All food consumed by the parasite larva must pass through the trophamnion until the parasite larva of I instar reaches the II instar. The egg chorion dissolves, exposing the first instar larva to the host's body cavity. The larva's trophamnion, a membrane composed by cells of the embryo, allows respiratory and digestive exchanges. Because the tracheae are filled with liquid, respiration is cutaneous. Initially, the second instar larva remains motionless near the parasitoid ovipositor's wound. However, after the last nymphal moult of the Typhlocybinae host and under pressure from the host's alimentary canal, the *Aphelopus* larva becomes compressed against the host integument. As a result, it extrudes throughout the ovipositor wound from the host's body, so the 'larval sac or thylacium' (= larva and its exuviae) is visible on the exterior of the Typhlocybinae adult, between two overlapping sclerites; therefore, the entire posterior half of the larva's body is external, whereas the head is internal, consuming host's hemolymph inside the

haemocoel. The 'thylacium' of *Aphelopus* is cylindrical, with a rounded distal end and a significantly softer texture than those of other dryinids.

Crovettia theliae is the unique species of *Crovettia* (the other Aphelopinae genus), whose biology is known. According to Kornhauser (1919), this is a polyembryonic and endoparasitic species attacking treehoppers (Hemiptera: Membracidae). The *Crovettia* female stings the intersegmental membrane of the treehopper nymph and deposits an egg in the hemocoel. The dryinid embryo divides into 50 or more embryos, each of which develops as a larva with a trophamnion surrounding it. They spend their lives in the coelom of the host, feeding the hemolymph. *Crovettia* does not stop host metamorphosis: If *Crovettia* lays its egg in a first instar nymph, its mature larva leaves the host when the host reaches the fifth nymphal instar, but if the eggs are laid in fourth- or fifth-instar nymphs, the host is able to reach the adult state, and so the mature larvae abandon the body of the dead adult.

The mature larva of Dryinidae is hymenopteriform (sensu Clausen 1940 and Gauld & Bolton 1988). It is an eucephalous larva with developed mouthparts, apodous, sub-cylindrical, with well-developed head, 3 thoracic and 10 abdominal segments (Figure 6j,m). The head is



FIGURE 8 Cocoons of Dryinidae. (a) General view of a Gonatopodinae cocoon built on gamma grass (*Cynodon dactylon*) (from Olmi 1999; Plate XXVI); (b) *Gonatopus contortus* cocoon containing the pupa; (c) cocoon of *Bocchus scobiolae* covered with soil particles and the host's rest attached (*Caliscelis wallengreni* (Stål) (Fulgoromorpha: Caliscelidae)); (d) *Gonatopus chilensis* cocoon containing Encyrtidae hyperparasitoid pupae and faeces.

prognathous, well sclerotised, generally with its posterior part retracted partially under first thoracic segment. The antennae are very simple in structure, reduced to two small areas both with two small conical sensilla medially. Head capsule, clypeus and labrum have long slender bristles and sensory pits in variable number. For further details of the mature larva, see Buyckx (1948), Guglielmino et al. (2006, 2015, 2017, 2022) and Guglielmino and Bückle (2010).

The mature larva consumes the host's hemolymph and internal tissues and kills the host. Afterwards, it moves about freely for a short time, until it spins a silk cocoon for pupation. The host normally dies attached by its rostrum to the host plant. The mature larva is very active and can pupate on the host plant or in the soil. Aphelopinae, Anteoninae and Bocchinae build their cocoons in the soil covering it by soil particles, Dryininae and Gonatopodinae on the plants. The white cocoon is made of dense silk and a close-fitting inner lining (double wall) (Barrett et al. 1965; Fenton 1918; Lindberg 1950; Perkins 1905; Virla 1992, 1995, 2002) (Figure 8, and see beautiful photographs in Chireceanu et al. 2019). For the species building the cocoon on plants, the size of the cocoon varies according to the surface that serves as support. The mature larvae of *Gonatopus desantisi* spends 12–60 h to build the cocoon (Virla 1995). In other species, as *Neodryinus typhlocybae*, the mature larva generally builds the cocoon under the empty body of its host; in some cases, the larva incorporates also tufts of wax torn from the body of the dead host (Guglielmino & Bückle 2003).

The duration of the life cycle (from egg to adult emergence) was studied mostly under laboratory conditions. Gonatopodinae is the subfamily with the largest number of species studied, and the life cycle is variable. For *Gonatopus desantisi*, it ranged from 20.5 to 57.5 days according to the temperature (Virla 1995); in *G. bartletti*, it lasts a mean of 46.6 days (Rios-Reyes & Moya-Raygoza 2004), and in *G. lunatus*, 69–118 days in spring and 24–34 days in summer (Guglielmino & Virla 1998). In addition, in some species, such as *G. bonaerensis*, the duration of the life cycle is very similar to the development period of their hosts (Virla 2002). For the other subfamilies, data are scarce; among others, there are the contributions for Aphelopinae: *Aphelopus atratus* (Munroe 1991); *Anteon pubicornis* (Dalman) (mentioned as *Anteon lucidum*) (Anteoninae) (Waloff 1975); and the Dryininae: *Dryinus stantoni* (as *D. lycormae*) and *D. latus* (Yan et al. 2010; Yang 1994).

Superparasitism

In the Gonatopodinae, the species are essentially solitary although superparasitism (the presence of more than one egg of the same dryinid species on the same host) is common (Sahragard et al. 1991; Stiling et al. 1991; Waloff 1990).

According to Chua et al. (1984), superparasitism in *Gonatopus flavifemur* is rare in nature, but it is frequently observed in laboratory conditions. Virla (2002) reported for *G. bonaerensis* that ~1% of the adult hosts parasitised

in the field carried two larvae. In laboratory, this species is capable to superparasitise around 20.5% of the exposed hosts, ovipositing two or more eggs on them; however, the fate of those parasitoids' larvae was not recorded, and it is not yet known if the Gonatopodinae are strictly solitary parasitoids (Espinosa et al. 2019).

Abril Ramirez (1992) studied the biology of *D. poecilopterae* (Dryininae) and registered that superparasitism is common in laboratory; the female lays up to four eggs in the same host, but only one develops.

Superparasitism in solitary parasitoids could increase the fitness of the ovipositing female under certain conditions (Yamada 1988) but undoubtedly involves competition for resources between the two or more larvae. For solitary parasitoids, the competition is severe because only one individual can survive to adulthood, and second comers are usually disadvantaged in the competition. Therefore, several works have described the occurrence of infanticide in the dryinids *Haplogonatopus atratus* and *Echthrodolphax fairchildii* (Yamada & Ikawa 2003; Yamada & Kitashiro 2002; Yamada & Sugaura 2003). These authors registered the occurrence of conspecific superparasitism (in which the mothers of the first and second comers are different) and self-superparasitism (in which the mother of the first and second comers is the same) (Ito & Yamada 2005). An interesting analysis of these phenomena and their ecological significance can be found in Yamada and Ikawa (2003). Later, self-discrimination, conspecific discrimination and infanticide behaviours in *E. fairchildii* were investigated, finding that females can distinguish between self-superparasitism and conspecific superparasitism up to 0.75 h after the first egg is laid (self-superparasitism frequency < conspecific superparasitism frequency). In addition, it was observed that the females frequently laid female eggs when superparasitising (Ito & Yamada 2014, 2016).

Host response: Effect of venom and host paralysis and effect of parasitism on host morphology

So far as known, in Anteoninae, Bocchinae, Dryininae and Gonatopodinae, oviposition is preceded by the emission of a temporary paralysing substance.

When a host is parasitised in the adult stage by a Dryinidae, it usually does not show any significant alterations. On the other hand, parasitism of nymphal stages can have a variety of outcomes if the host's metamorphosis is not stopped by the Dryinidae (as in the case of *Crovettia* and *Aphelopus* species) or if the metamorphosis is stopped so the host does not reach adulthood (as in Anteoninae, Bocchinae, Dryininae and Gonatopodinae species) (Olmi 1999).

In the Aphelopinae, where the female parasitises only nymphal stages and do not stop the moulting process of its hosts, fundamental morphological, anatomical and

physiological changes were observed in the adults (depigmentation, males similar in appearance to females and/or the so-called 'parasitic castration' with internal morphological changes, especially in their genitalia, with degeneration of the ovaries in females, or of the vas deferens and the ejaculatory duct in males) (Buyckx 1948; Giard 1889; Olmi 1999).

In Anteoninae, Bocchinae, Dryininae and Gonatopodinae, no ecdysis has been seen when oviposition occurs in a host nymph (Lindberg 1950; Ponomarenko 1975; Virla 1992); these authors noted that the host can moult if the female dryinid lays the egg and the nymph's moulting process is underway; however, if the nymph has the dryinid larva (protruding outside), ecdysis is no longer possible. It is advantageous for the dryinid to interrupt the moulting process of the nymph, because ecdysis in the host would result in the loss of the exuvium to which the eggs or small larvae of the parasitoid are attached. This would result in the expulsion of the immature dryinid from its food source, or the host may die due to the entanglement of their exuviae in the presence of the developed dryinid larva (Virla 2003a). According to Olmi (1999), if the host nymph's development is stopped, two or more Gonatopodinae larvae growing on the same host can mature. In contrast, Kitamura (1988) studied the developmental period of each nymphal instar of the planthopper *Sogatella furcifera* parasitised by *Gonatopus apicalis* Perkins and found that the developmental rate between parasitised and non-parasitised hosts was different, but both are able to moult. Kitamura never explained what happened to the exuviae from each moult of the developing nymphs, which had to be 'trapped' with the dryinid's larvae.

The mechanism by which the host's development is slowed and/or blocked is unknown; it could be related to compounds injected by the female during oviposition and/or substances produced by the dryinid larvae as they develop. Virla (2003a) studied the moult inhibition by *Gonatopus chilensis* in the planthopper *Peregrinus maidis* and obtained evidence that the injected substance is at least one of the sources of the nymph development arrest, and it could be discarded that arresting development is due only to the action of the developing dryinid larva. Pillault (1951) suggested that the metamorphosis of *Dryinus tarraconensis* (Dryininae) hosts is stopped by a larval factor. He mentioned that the host could not develop if the parasitoid larva was alive, but it was able to recommence the development, moulting, when the dryinid larva died. Also, Subba Rao (1957) stated that *Dryinus pyrrillae* stopped the development of the hosts.

From the point of view of the type of parasitism, Dryinidae can be called 'koinobionts' because, according to Gauld and Bolton's (1988) definition, dryinid larvae allow the host to continue more or less normally (although often the moults of the young are prevented), contrasting in this with 'idiobiont' parasitoids that instead block the host in its developmental stage by paralysing it.

According to Olmi (1999), a parasitised adult host is unable to reproduce, but this should be further investigated. Also, the chemical nature of Dryinidae venom has not yet been studied.

Gynandromorphism

Gynander pincer wasps are rare. Only a few individuals belonging to Anteoninae, Gonatopodinae and Dryininae have been documented: *Anteon scapulare* (Haliday) in the Palaearctic region; *Deinodryinus rusticus* Olmi and *D. steineri* Olmi in the Afrotropical region; and *Gonatopus cavazzutii* Olmi, *G. desantisi* and *Dryinus* sp. in the Neotropical region (Olmi et al. 2019; Olmi, Onore & Guglielmino 2022; Olmi & Virla 2014; Richards 1948). All the described gynanders showed random (harlequin) patterns.

MUTUALISTIC RELATIONSHIPS, ANT MIMICRY AND INTERACTIONS WITH PLANT PATHOGENIC VIRUSES AND MOLLICUTES

Mutualism and mimicry in dryinids

The Auchenorrhyncha Cicadellidae (leafhoppers) and Membracidae (treehoppers) can establish mutualistic interactions with ants (Delabie 2001; Styrsky & Eubanks 2007). These interactions are widespread in Hemiptera, and most of the ant-tended species share several characteristics: nymphs and adults are gregarious; they feed on plant phloem; and they produce honeydew. In return for the received honeydew, ants protect the attended Hemiptera against predators and parasitoids.

Dryinid parasitoids should be kept away from Auchenorrhyncha species that establish ant mutualism, but there are several reports of pincer wasps attacking ant-tended hopper species. This is possible because some dryinid females are ant-like in general appearance, especially the apterous females of Gonatopodinae, allowing them to capture hosts that often form mutualistic associations with ants (Guglielmino 2002; Waloff & Jervis 1987). So far, all reported cases of Dryinidae attacking Auchenorrhyncha species in mutualism with ants correspond to Gonatopodinae and Anteoninae affecting leafhopper and planthopper species. Some Gonatopodinae species were discovered within the ant nest and are identical in colour and shape to the ant (Olmi 1984). Apparently, dryinids developed mimicry to avoid attacks and predation by ants (Fenton 1918). In corn plantations (Argentina), the planthopper *Peregrinus maidis* shows mutualism with the ants *Paratrechina silvestrii* Emery and *Solenopsis saevissima* F. Smith (Formicidae). Three species of Gonatopodinae have been collected in these communities: *Gonatopus chilensis*, *G. bonaerensis* and *Haplogonatopus hernandezae*, which not only mimic ants but also imitate their

behaviour (Cuezzo & Virla 2001). In addition, Fenton (1918) mentions that dryinid larvae are taken by the ants to the nest where they pupate.

In the case of Anteoninae, which are winged and have small chelae, Perkins (1905) observed *Anteon myrmecophilum* (Perkins) females parasitising leafhoppers frequently tended by ants and showing behaviour resembling that of ants, so that this species can be considered definitely myrmecophilous (Olmi 1994).

It was reported that the leafhopper *Dalbulus quinque-notatus* De Long & Nault is attended by several ant species, but *Brachymyrmex obscurior* Forel (Formicidae) is the most common (Larsen et al. 1991). Ants live in an obligatory mutualism with adults and nymphs of this leafhopper species at the base of gamma grass *Tripsacum* (Poaceae) wild habitats (Moya-Raygoza & Nault 2000). In this habitat, the Anteonine *Anteon ciudad* Olmi parasitises nymphs of *D. quinque-notatus* guarded by ants. Nymphs parasitised by *A. ciudad* are observed living among tending ants (Moya-Raygoza & Trujillo-Arriaga 1993). In the presence of *B. obscurior* ants, an average of 24% of *D. quinque-notatus* nymphs are parasitised (Moya-Raygoza 1995), but at low ant densities, levels of parasitism by *A. ciudad* increase (Moya-Raygoza & Larsen 2008).

Dryinidae interactions with Auchenorrhyncha hosts and plant pathogenic virus and mollicutes

As previously stated, Dryinidae larvae develop on/in nymphs and adults of Auchenorrhyncha. Many of these host species belong to planthoppers (Delphacidae) and leafhoppers (Cicadellidae) that can carry and transmit viruses and mollicutes (phytoplasmas and spiroplasmas), causing important diseases in several crops such as maize, barley, wheat, rice and oats (Nault 1994, 1997; Trivellone 2019; Trivellone & Dietrich 2021; Weintraub & Beanland 2006; Wilson & Weintraub 2007). These viruses and mollicutes are vectorised to plants via a persistent-propagative mechanism in which the pathogens replicate within the nymphs and adults of Auchenorrhyncha (Nault 1997). This means that once the virus or mollicute is acquired by the vectors, they remain infected all their lives, and if dryinids parasitise them, their larvae must grow and interact with the pathogen.

Increasing evidence indicates that viruses and mollicutes can influence host plant phenotypes and the behaviour of insect vectors to facilitate their spread. In the interaction between viruses, mollicutes and host plants, pathogens manipulate plant signals that in turn influence the orientation, feeding and dispersal behaviour of vectors. In this way, pathogens ensure that they can colonise other plants and thus spread the disease (Mauck et al. 2018). The 'adaptive host manipulation hypothesis' highlights the fitness benefits of

manipulation as a strategy and proposes that pathogens/parasites can evolve to control features of their host's phenotype and so maintain or improve their transmission rates (Poulin 2010). Interactions among viruses and mollicutes with their vectors, Delphacidae and Cicadellidae, have been broadly investigated. However, little is known about how plant pathogens and vectors interact with parasitoids (like dryinids) in nymphs and adults. Studies related to aphid vectors (Sternorrhyncha) found that infected insects carrying a plant pathogen experienced great vulnerability to the parasitoid *Aphidius colemani* (Dalman) (Hym.: Braconidae) (de Oliveira et al. 2014). In a study related to dryinid parasitoids, it was found that when the Gonatopodine *Gonatopus bartletti* and the *Spiroplasma kunkelii* coexisted within *Dalbulus maidis* (De Long & Wolcott) (Cicadellidae), the development of the dryinid was not affected by the spiriplasma (Moya-Raygoza et al. 2006).

POPULATION DYNAMICS AND VOLTINISM

Seasonal phenology, overwintering and diapause

The species found in temperate areas appear to have one to three generations every year, with the winter spent in the cocoon as mature larvae or prepupae. In tropical climates, there appear to be numerous overlapping generations without diapause; during the dry season, however, the activity of the dryinids is greatly reduced (Chandra 1980).

The metabolic activities of dryinids can suffer transient arrests, during which the insect blocks its development. The developmental stages involved in this phenomenon generally are those that take place inside the cocoon (mature larva, prepupa and pupa). According to Olmi (1994), the evidence shows that among the Dryinidae, there are species that have a true diapause (i.e., *Neodryinus typhlocybae* and *Aphelopus melaleucus*), whereas others only go through a state of quiescence. He provided several examples of species that have to go through a mandatory quiescence stage in order to develop successfully after being exposed to low temperatures. The diapause of adults is less frequent. Pruthi and Mani (1942), in Pakistan, found that *Dryinus pyrillae* performs two diapauses, one during summer, by adults, and the other in winter, by pupae in the cocoons; they argue that the two diapauses coincide with the low field densities of specimens of *Pyrilla perpusilla* (Walker) (Lophopidae).

Jervis (1980) stated that the *Aphelopus* species occurring in the woodlands of Wales display univoltinism (i.e., *A. serratus*) and others show bivoltinism with a tendency to enter into diapause early in the season. In Europe, *Gonatopus clavipes* (Thunberg) (= *G. sepsoides* Westwood) is bivoltine or trivoltine, and the mature larva

hibernates into the cocoon. Its generations are timed to coincide with those of its hosts (Cicadellidae) (Waloff 1974). *Anteon pubicorne* and *Lonchodryinus ruficornis* (mentioned as *Prenanteon basalis*) are bivoltine in England, and larvae overwinter in their cocoons (Waloff 1974). Some dryinids, for example, *Aphelopus serratus* Richards, overwinter as first larval instar (Jervis 1980). During the winter, *Crovetia theliae* is thought to be in the pupal stage (Kornhauser 1919).

Just as some species of leafhoppers, for example, *Alebra albostriella* (Fallén) and *Alebra wahlbergi* (Boheman), show different voltinism according to their area of distribution (univoltine in Greece and two to four generations in Italy) (Loukas & Drosopoulos 1986; Vidano & Arzone 1987a, 1987b), it is possible that a similar situation may occur in the Dryinidae.

Dryinid efficiency and functional response

In some cases, high rates of parasitism by dryinids in the field (40%–70%) have been reported (Barrett et al. 1965; Baspinar et al. 1994; Freytag 1985). According to Mora-Kepfer and Espinoza (2009), the behaviour of females of *H. hernandezae* as predators and parasitoids promotes a stable control of the planthopper *Tagosodes orizicolus* (Muir) in Costa Rica. However, some pincer wasp species are not thought to play a significant role in controlling leafhopper and planthopper populations that live in rice field in Asia (Chandra 1980), acidic grasslands in England (Waloff 1975, 1980) or Bermuda grass in Georgia (USA) (Buntin 1989).

The functional response (laboratory studies on the relationship between the rates of attack and the host density) was scarcely addressed. Chua et al. (1984) described a sigmoidal functional response (type III curve) of *Gonatopus flavifemur* (as *Pseudogonatopus*) against Asian rice planthoppers. This dryinid has a good search efficiency, but mutual interference was observed when two females were caged together.

Giordano et al. (2002), through field studies, found that the regulatory activity of dryinids on cicadellids in northern Italian forests is noteworthy and provides important perspectives in the applied field. They observed that even though it is not evident, dryinid activity is quite successful in keeping cicadellid populations below the damage threshold.

Many contributions suggest that some species of Gonatopodinae cause greater control of populations of their hosts by predation (i.e., host-feeding) than by parasitism (Jervis et al. 1996; Kidd & Jervis 1989; Olmi 2000a; Sahragard et al. 1991), for example, *Haplogonatopus atratus* (= *H. oratorius*) attacking *Laodelphax striatella* and *Sogatella furcifera* (Horvath) (Delphacidae) (Kitamura 1982), and *G. bartletti* on *Dalbulus maidis* (Rios-Reyes & Moya-Raygoza 2004). But Espinosa et al. (2019) observed that *G. bonaerensis* kills more planthoppers by

parasitism than by host-feeding when faced with its usual host, but in front of an occasional host, predation prevails. As a result, Espinosa et al. (2019) suggested that the studied hosts in the aforementioned papers may not have been optimal hosts (though they may have been the economically most important ones), but rather suboptimal or occasional hosts.

CO-OCCURRENCE OF DRYINIDAE WITH OTHER PARASITIDS

There are few community-level ecological studies describing the relationships between dryinids and other groups of parasitoids. Most of them include information about the seasonal occurrence and/or voltinism of the co-occurring species of parasitoids, like the contributions by Waloff (1974, 1975). Most of the information available on this topic refers to Auchenorrhyncha species associated with agroecosystems and anthropogenic systems, where several species of Dryinidae co-occur with other nymph and adult parasitoids such as Diptera Pipunculidae and Strepsiptera (Waloff & Jervis 1987). Stiling (1994) registered that diverse species of the three parasitoid groups could parasitise a single leafhopper species.

Jervis (1980) studied in South Wales woodlands a biocenosis composed of Typhlocybinae (Hemiptera: Cicadellidae) and a complex of hopper parasitoids: Dryinidae (*Aphelopus* spp.) and Pipunculidae (*Chalarus* spp.), as well as the dryinid hyperparasitoid *Ismarus dorsiger* Curtis (Hym.: Ismaridae). Moya-Raygoza et al. (2004) studied the populations of *Dalbulus maidis* attacked by the three groups of parasitoids in different maize fields of Mexico; however, they observed that, in each field, the leafhoppers were attacked only by species from one of the three groups of parasitoids and concluded that there is probably no competition between them. In tropical America, on maize, barley, sorghum and its surrounding vegetation, both the pipunculid *Eudorylas subopacus* (Loew) and the dryinid *G. bartletti* parasitised the leafhoppers *D. maidis* and *D. elimatus* mostly during the dry season rather than in the wet season (Moya-Raygoza 2007). In Asia, on rice fields, the communities of leafhoppers co-existed with the three parasitoid groups (Bambaradeniya et al. 2004; Chandra 1979).

Interactions between larvae of different parasitoids within a parasitised Auchenorrhyncha have been poorly investigated. Virla (1992) recorded one adult of the planthopper *Chionomus haywardi* (Muir) (as *Delphacodes haywardi*) affected by the presence of a larva of *G. chilensis* (Dryinidae) and a male of *Elenchus* sp. (Strepsiptera). The delphacid's external genitalia were completely altered. According to Ponomarenko (1971, 1975), if a host nymph, already parasitised by Pipunculidae and/or Strepsiptera, is attacked by a Dryinid, its development and that of the larvae of the other parasitoids are blocked.

DRYINIDAE NATURAL ENEMIES

Dryinid species are susceptible to a variety of natural enemies, parasitoids and predators, which can drastically reduce their populations and efficiency (Guglielmino 2002; Olmi 1984, 1999, 2000a). These authors stated that larvae could be predated by species of Cabronidae and Sphecidae (Hymenoptera); their cocoons by several insects, birds and small rodents; and the dryinid adults by ants. Tommasini et al. (1998), studying *Neodryinus typhlocybae* in northern Italy, registered that 48%–60% of the cocoons on the ground were preyed on during the winter.

All the known parasitoids of Dryinidae belong to different Hymenoptera families: Aphelinidae (affecting Gonatopodinae), Ceraphronidae (affecting Gonatopodinae), Chalcididae (affecting Dryininae and Gonatopodinae), Ismaridae (affecting Anteoninae and Aphelopinae), Ichneumonidae (affecting Gonatopodinae), Pteromalidae (affecting Gonatopodinae), Eulophidae (affecting Gonatopodinae, genus *Neodryinus*), Eupelmidae (affecting Gonatopodinae, genus *Neodryinus*), Torymidae (affecting Gonatopodinae, genus *Neodryinus*) and, mostly, Encyrtidae (affecting Anteoninae, Bocchinae, Dryininae and Gonatopodinae) (see Guglielmino 2002, Viggiani et al. 2002 and Guerrieri 2006 for details, and see the revisions at the regional level by Xu et al. 2013, Olmi & Virla 2014, Olmi & Xu 2015 and Olmi et al. 2019).

Regarding dryinid parasitoids, the most studied are the Encyrtidae. Their females usually oviposit into immature Dryinidae larvae contained in the thylacium, and their larvae develop inside the Dryinidae larval body until the host completes the construction of its cocoon. Subsequently, the encyrtid larvae eat the pincer wasp larva, pupate and then emerge from the cocoon (Olmi 1999) (Figure 8d). In general, more than one Encyrtidae specimen emerges from a single Dryinidae cocoon, except for the species *Cheiloneurus cupreicollis* Ashmead, which is solitary (Virla 2003b). Rarely, encyrtids oviposit into mature larvae, pupae or prepupae present in dryinid cocoons.

Parasitism rates caused by dryinid parasitoids can vary a lot, reaching sometimes 100% (Freytag 1987). For example, according to Chandra (1980), in the rice fields of the Philippines, rates of parasitism of 30%–50% were found. In Hawaii, authors recorded percentages of 24%–68% by *Ceraphron abnormis* Perkins (Ceraphronidae), devastating the populations of *Haplogonatopus vitiensis* Perkins (Swezey (1908) cited by Olmi (1999, 2000a)).

ECONOMIC IMPORTANCE AND USE AS BIOCONTROL AGENTS

Drynidae have a high potential as biological control agents of Auchenorrhyncha, which often are economically significant (Olmi 1999, 2000a). 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 and by parasitism. The example of *Gonatopus flavifemur* is useful in asserting the role and importance of dryinids in biological balances: The female can parasitise over 400 hosts and prey about 50 during its life (which lasts about 19 days) (Chua & Dyck 1982; Sahragard et al. 1991). As mentioned before, only adult *Aphelopus* (and possibly Erwiniinae) are not predaceous upon hosts.

The low natural incidence of parasitism (only valid for some agroecosystems) and the unavailability of mass-rearing technologies for most of the species, according to Chandra (1980), hindered the development of dryinids as biocontrol agents. The relevance of the family Dryinidae has been recognised for a long time, but only a few biological control programmes have been implemented. According to information by Olmi (1977, 1999, 2000b), Guglielmino (2002), Guglielmino et al. (2013) and recent research, they can be summarised as follows:

1. Hawaii (1906–1907), control of the Sugarcane Planthopper, *Perkinsiella saccharicida* Kirkaldy: introduction of *Pseudogonatopus hospes* R. Perkins (now junior synonym of *Gonatopus nigricans* (R. Perkins)) from China and *Haplogonatopus vitiensis* R. Perkins from the Fiji Islands. This experience failed, apparently, because in the subsequent years some hyperparasitoids were accidentally introduced into the islands, including *Cheiloneurus americanus* (R. Perkins) (Williams 1931).
2. New Zealand (1935), control of the Froggatt's Apple Leafhopper, *Typhlocyba froggatti* Baker (now junior synonym of *Edwardsiana crataegi* (Douglas)): introduction of *Aphelopus typhlocybae* Muesebeck (now junior synonym of *Aphelopus albopictus* Ashmead) from the United States.
3. Italy (1994), control of the flatid planthopper, *Metcalfa pruinosa*: introduction of *Neodryinus typhlocybae*. This project is continuing still in other European countries (Vétek et al. 2019). Recently, the species was introduced in Korea (Seo et al. 2018). This is the most successful project of biological control by dryinids.
4. Colombia, Costa Rica, Cuba (from 1999), control of the Rice Delphacid, *Tagosodes orizicolus*: introduction of *Haplogonatopus hernandezae*, in rice fields.
5. Nigeria: use of Dryinidae against *Cicadulina* spp., well-known pests of maize (M. Olmi, personal communication, September 8, 2022).

From an applied point of view, for biological control, the species of pincer wasps with sexual reproduction create many problems in breeding farms (mass production), so those species with thelytokous parthenogenesis are the best to use (Olmi 2000a).

Biological control of leafhoppers and planthoppers with dryinids is still infrequently used, despite the well-

known effectiveness of pincer wasps, primarily because of the lack of knowledge about this interesting family.

Dryinids can be a problem in some weed biological control programmes. This is the case of the programme in South Africa to control the water hyacinth, *Pontederia crassipes* (Martius) (Pontederiaceae), by the South American planthopper *Megamelus scutellaris* Berg. The native African dryinid *Echthrodelphax migratorius* Benoit is already having an impact on the biocontroller populations, which is detrimental to the programme's viability (Kraus et al. 2019).

FUTURE CHALLENGES IN THE STUDY OF PINCER WASPS' BIONOMICS

After a brief overview of the Dryinidae's bionomics, many topics still require in-depth study to gain a fuller knowledge of the fascinating world in which these insects live. Thus, the following traits need to be investigated in depth or even for the first time:

- Nutrition: It would be important to conduct field research on the various food sources used by dryinid adults, how these substances are exploited and how they influence their performance.
- Voltinism: This fact is not well recognised, and many works that do address it rely more on inferences than on scientific evidence. It should be looked at how the climate, host availability and density, refuges and so forth affect the number of annual generations.
- Dispersal: Understanding the mechanisms that govern the spatial distribution of adults and larvae would be intriguing. Regarding adults, we can distinguish: (1) Do winged adults most likely move by flying, or can they make migrations by exploiting wind or updrafts? Do wingless adults move only by walking or by exploiting phoresis with other insects or updrafts? (2) Larvae move via their hosts; if they are adults, they can always migrate by updrafts, but if they are nymphs, their ability to spread is limited. This will allow us to improve our understanding of the local or regional distribution of these wasps.
- Superparasitism: Apart from the gregarious species *Crovettia theliae*, all other taxa of Dryinidae are currently considered solitary parasitoids, although superparasitism has been observed in these insects as a not rare phenomenon. In dryinids, is superparasitism a common occurrence or a one-time occurrence brought on by extreme conditions? Therefore, it would be interesting to understand what factors (host density, age of the female etc.) induce a female to deposit one or more eggs in the same host, whether these factors represent a last chance for the female to leave its eggs under particular environmental conditions and what effects there are on the fate of this offspring. Information on superparasitism is largely unknown for almost all subfamilies.
- Effects of parasitisation on hosts: It would be interesting to understand the parasitisation strategy evolved by

dryinids (adults, larvae or both) to overcome host defence barriers and to slow or stop their development, as well as the paralysing substances that precede oviposition.

- Peculiar biology of the Dryinidae: The biology of the Dryinidae is so peculiar that it is not always possible to apply to them definitions such as endoparasitoid or ectoparasitoid, idiobiont and koinobiont. It would probably be more appropriate to create new definitions more suitable to the behaviours exhibited by these wasps.
- Mating behaviour: Only a few species in two subfamilies of dryinids have been studied for their mating behaviour (Aphelopinae and Gonatopodinae). The mechanisms that Dryinids employ to recall both sexes (pheromones?), the mating systems (monandrous or polyandrous), the frequency of mating during life and how this influences the performance of the species should be studied.
- Reproduction: Thelytoky as an ability to reproduce in particular situations of male shortage is either an alternative feature of sexual reproduction in Dryinidae or it is induced exclusively by the presence of endosymbiotic organisms such as *Wolbachia*.
- Sexual cannibalism: It should be important to ascertain whether sexual cannibalism is common among Dryinidae and, if so, what impact it has on female longevity, fecundity and fertility.
- Protection of offspring: Only two species of Gonatopodinae have had studies on the ability of females to identify hosts that have previously been parasitised by themselves or by other conspecifics. It would be highly intriguing to look into aspects that may affect how females choose their hosts for feeding and/or parasitism, as well as how females' past experiences may affect current rates of predation and parasitism.
- Oogenesis and eggs: The types of eggs (hydropic or anhydropic), as well as the oosorption phenomenon (particularly for parasitoids with anhydropic oocytes), have received little or no attention. Until now, the ovigeny of only a few Gonatopodinae species has been studied. The hypothesis that species lacking chelae and lacking host-feeding behaviours are proovigenic, whereas species with developed chelae and host-feeding habits are synovigenic, must be tested in other subfamilies as well.
- Postembryonic development and modality of immature larval feeding: Knowledge of the postembryonic development and morphology of immature and mature larvae of the Dryinidae is based on a small number of species from five subfamilies (Aphelopinae, Anteoninae, Bocchinae, Dryininae and Gonatopodinae), but it is still limited. Clarification is needed, in particular, about a number of features of larval feeding and the functions of the trophamniom and cephalic vesicles.
- Relationships with their hosts: Although it is one of the most frequently addressed aspects, it is necessary to improve the knowledge of the relationships among Auchenorrhyncha–Dryinidae and the evolutionary factors (chemical signals, host defences, parasitism strategies etc.) that underlie them.
- Relationships with ants: Studies elucidating the relationships between Auchenorrhyncha, ants and Dryinidae are not yet available (e.g., Membracidae, ants and *Crovetia* spp.). Future research is also required to fully understand how ants defend treehoppers and leafhoppers from Dryinidae. What factors (mechanical, visual and chemical signals) come into play?
- Relationships with plant pathogens: Plant–Auchenorrhyncha interactions are known to be altered when plant pathogens are present in vectors. Completely unknown are the effects that these pathogens may have on the eventual larvae of Dryinidae that parasitise the vectors.
- Auchenorrhyncha interactions with Dryinidae, Pipunculidae and Strepsiptera: It would be interesting to observe whether, in the absence of multiparasitism, the action of these different groups of parasitoids has a synergistic effect in controlling hopper populations. Additionally, it should be studied whether interspecific competition and multiparasitism affect the effectiveness of the control system.
- Natural enemies of Dryinidae: Up to now, the antagonists of the pincer wasps (particularly their predators) have received limited attention.

This knowledge enables us to explore the interesting world of the Dryinidae and, on the other hand, could be used to control the Auchenorrhyncha species, which are considered 'pests' and significantly damage a variety of crops worldwide.

CONCLUSIONS

The knowledge about the biology of pincer wasps is quite scarce and fragmentary. This absence of information hinders its use in biological control programmes. Gonatopodinae is the relatively best-known group, but there is a remarkable absence of information on the biological aspects of important subfamilies such as Dryininae and Anteoninae, though many of their species attack recognised crop pests. We lack knowledge about biological traits for the subfamilies Apodyrininae (hosts unknown), Apoaphelopinae (hosts unknown), Bocchinae (only known some hosts), Conganteoninae (hosts unknown), Erwiniinae (hosts unknown), Thaumatomyrininae (few hosts known), Plesiodyrininae (hosts unknown) and Transdryininae (hosts unknown).

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

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