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BIOLOGY AND PARASITES OF COLEOPHORA FRISCHELLA LINNAEUS (LEPIDOPTERA COLEOPHORIDAE)

by Jean VERBEKE (Brussels).

INTRODUCTION.

When starting research on *Coleophora* spp. (= *Eupista*), it was the intention of the author to study and rear the parasites of the two species *C. spissicornis* HAWORTH and *C. frischella* LINNAEUS.

The information received from different specialists of the Museums at Paris and Brussels shows that both species, although relatively rare, are largely distributed over the greatest part of Europe, accompanying practically everywhere their food plants.

M. E. JANMOULLE (Brussels) informed us that only six records were known for *C. spissicornis* in Belgium, the most successful capture being that of a few dozen specimens by the light trap method at Aye (Belgian Ardennes); the recorded dates range from 15.VI. to 4.VIII. For *C. frischella* only five records were known, and the species is considered as very scattered in the country; the dates range from 15.VI. to 15.VII.

In the well known « Catalogue des Lépidoptères » by L. LHOMME, we find a few data concerning both species, which are reproduced here :

C. spissicornis HAWORTH : « France, répandu, V-VII » recorded from 23 departments out of 83, ranging from the extreme north to the extreme south. Belgium : only three records. Further the author states : « Chenille sur *Trifolium arvense* LINNÉ, sur les têtes florales, dans un fourreau jaune brun, tubulaire, presque rectiligne, légèrement recourbé sur les bords, qui sont plus clairs que le fond. Hiverne et se métamorphose sur les arbres voisins ». This species has been observed as a pest of clovers in New Zealand (DUMBLETON, 1952).

C. frischella LINNAEUS : « France, répandu presque partout, V-VIII »; recorded from 26 departments, extending over the whole territory.

Belgium : only two records. Further he states : « Chenille sur *Melilotus arvensis* WALLR. (=*officinalis* G. G.), *M. alba* DESR., *M. altissima* THUIL. (= *macrorrhiza* G. G.), *Trifolium*, dans un fourreau cylindrique formé de l'enveloppe des graines, sur graines de Mélilots; VIII-X ».

As a result of this information prospection trips have been undertaken in Belgium and North-Eastern France, mainly in Alsace-Lorraine (departments of Meuse, Meurthe et Moselle, Moselle, Vosges, Haut-Rhin, e.a.), with the double purpose of finding localities most heavily infested with wild *Trifolium* and *Melilotus* plants and with the greatest population of *Coleophora* spp. These investigations have been made by means of net, aspirator and light traps; the food plants as well as the collected specimens have been carefully examined in the field and in the laboratory by means of a LEITZ binocular.

The results of our investigations were not entirely in agreement with the above information, for it was found that *C. spissicornis* was pratically absent from the region in 1951, in France as well as in Belgium, the light traps being used without any result at the same localities and on the same dates where on previous years half a score of specimens had been obtained.

On the contrary, *C. frischella* has been found in great numbers, in a few localities in the extreme South of Belgium and the above-mentioned part of France. It must be remarked that the food plants of the latter species occur commonly on artificial soils, cornfields, roadsides, etc., all rich in lime. Consequently, our efforts have been concentrated on the latter species, *C. frischella* LINNAEUS.

The present investigations have been made largely in the region of Virton, the collected material originating from Ethe and Virton (Belgian Luxembourg) and Montmédy (France, department Meuse). The identity of all the collected and studied specimens has been confirmed by Mr. E. JANMOULLE. We are also indebted to Mr E. JANMOULLE for having revised our manuscript and to Mr S. JACQUEMART for drawing figures 14 to 17.

Coleophora frischella LINNAEUS.

GEOGRAPHICAL DISTRIBUTION.

The geographical distribution of *C. frischella* seems to correspond with the climatic area situated between the yearly isotherms of 10° and 14° C.

In Western Europe this area includes South Britain, the Netherlands, part of Denmark, Belgium, Luxembourg, part of Germany, France, Switzerland and North Italy.

Captures have been mentioned with certainty from Britain, Belgium, Luxembourg, France (north to south), Sweden, Switzerland, Germany, etc. It is found at low and moderate altitudes, in maritime as well as in continental regions, extending from the mediterranean zone to far north.

ETHOLOGY.

Habits of the adult. — In nature, the adults are generally quiescent during the daytime, placing themselves vertically on a yellow flower or a leaf of *Melilotus*, with the antennae held in a characteristic porrect position. The wings are bronze-black, with metallic lustre. The adults frequently feed upon the flowers of *Melilotus;* in the laboratory feeding on a solution of peptone and sugar was also observed. Their activity in general but particulary their flight activity increases in the evening between 4 and 6 p.m. Flight is rapid and irregular but over short distances only, and is often interrupted by a long period of rest.

No swarming has been observed, but once copulation has been seen at evening and probably it takes place at this time of the day. This may be the case also for oviposition; however in the laboratory it occurred during the whole day.

The present species seems to prefer sunny slopes and other warm situations, although the adults protect themselves from intense sunshine and high temperatures.

Oviposition. — Oviposition generally takes place within or upon the flowers of *Melilotus*, mostly within the corolla, occasionally on a foliole or upon young, still entirely green, spikes of flowers. The egg is well concealed and deposited singly, however as many as seven may occur together in one mass and as many as twelve were found in one corolla. Normally two or three occur together (figure 15).

After a few days the egg becomes brownish at one end, indicating the development of the young larva. The incubation requires six days, at a temperature of approximately 30° C during the day and 15° C during the night.

Larval development. — The newly hatched first-instar larva, which averages 0,75 mm in length, is free-living within the flower of *Melilotus* during one or two days, feeding upon the soft parts of the latter and upon the immature pod. Later the larva attacks a larger pod, the interior of which is eaten away through a hole made in the shell; the larva then enters the pod and closes the entrance hole with silk. When the contents of the pod have been consumed, the larva nibbles an outlet hole and starts consuming another pod, the old empty pod remaining attached to the new one.

A certain number of pods are consumed in this way, each pod being fixed to the preceding one in a broken line. This constitutes the first type of portable case. It is usually composed of 5 or 6 pods when containing a more or less mature larva, but up to eight may be joined together. It is brown-green in color (figures 14 and 17).

Later, the mature larva leaves the old case and within a few hours makes another, larger and stronger one, for hibernating. It consists of one large pod with an opening at one end and a long woven part at the other, composed of three flaps meeting in the shape of a Y at the apex. This constitutes the second type of case (figure 16). It is brown in color and cylindrical in shape and is suspended singly on the pods of *Melilotus* (figure 17). It averages 6,0 to 7,5 mm in length. These cases are often found hibernating in the soil in clusters under stones, roots, etc.

The last-instar larva increases rapidly in length and diameter and becomes yellowish as a result of the development of the fat body. It averages 7,0 to 8,0 mm in length when full grown. The mature larva remains on the plant for a few days before entering the soil for hibernating (winter diapausis). The cases of parasitized and dead larvae remain on the plant for a longer period and may be easily collected in this way.

Life cycle. — The life cycle of *Coleophora frischella* is long, for its whole development occupies about one year. However its larval development is short, averaging 15 days from egg to mature larva. The latter enters into diapausis before the winter and pupation takes place in the spring without resumption of feeding. In the regions visited the adults emerge in June.

In the Moselle valley, the period of flight of the adults was at its maximum during the first half of July, mature females being found on July 3 and 4. At Virton (south Belgium), the maximum was in the second half of July, mainly between July 12 and 20, the whole period extending from the end of June to the end of July. Table I shows the occurrence of the adults during 1951 in the area extending from North-Western Belgium (Antwerp) to Northern and Middle Eastern France (Luxueil and Belfort).

In the laboratory, the first eggs have been deposited on July 13, but oviposition took place earlier in nature, being observed on July 8-10. In the laboratory oviposition was at its maximum between July 15 and 25.

In nature, the young first-instar larva appeared about July 15, being present until the end of the month, with maxima between July 22 and 27. In the laboratory, emergence of first-instar larvae began on July 20. The cases of type I, composed of two or three pods and containing first- and second-instar larvae, have been found during the last week of July at Virton and somewhat earlier at Montmédy. The first mature larvae bearing a case of type II were observed at the end of July and the beginning of August, being at a maximum at about August 15 and entering into diapausis between August 20 and 25.

There are four larval instars, the first of which presents very distinctive characters.

TABLE I.

Collecting localities, dates and frequency of adults of *Coleophora frischella* in Belgium, Luxembourg and France, during 1951.

Locality	Province or Department	Date	Number collected	Remarks
France :				
Montmédy...	Meuse	3-VII	5	
Mainville-Malmaison ...	Moselle (1)	3-VII	4	3 ♂♂, 6 ♀♀ ♀♀ mature
Mangonville	Meurthe-&-Moselle	4-VII	6	
Luxeuil	Hte Saône	4-VII	3	♀♀ mature
Belfort	Tre de Belfort	6-VII	1	
Mulhouse	Ht Rhin	10-VII	1	
Mangonville	Meurthe-&-Moselle	10-VII	9	
Hagondange	Moselle	11-VII	3	
Luxembourg (Grand-Duché) :				
Ettelbrück	—	15-VII	1	
Belgium :				
Berg	Brabant	29-VI	1	
Antwerp (left river) ...	Antwerp	30-VI	1	
Ciney	Namur	1-VII	1	
Jemelle	»	2-VII	8	
Aye	»	2-VII	3	
Virton	Luxembourg	3-VII	5	
»	»	11-VII	10	
Lamorteau	»	13-VII	33	ovipos. in
Ethe	»	14-VII	25	labor.
Virton-Ethe	»	16-VII	20	
Ethe	»	17-VII	12	
»	»	18-VII	40	
Virton	»	20-VII	37	mass. ovi-
Ethe	»	22-VII	12	position
Berg	Brabant	23-VII	6	
Melle	Flandre or.	25-VII	3	
Ethe	Luxembourg	27-VII	10	
»	»	28-VII	2	end of period of flight at Ethe

(1) In the Moselle valley, the period of flight of *Coleophora frischella* was over on 19-VII.

An equal number of male and female progeny has been observed, the sex ratio being 1 : 1. One female deposits in all approximately 50 eggs, of which 10 to 15 are mature at the beginning of the oviposition period.

The adults of most parasites appear in the second half of July and oviposit during the last week of the month and the beginning of August.

Morphology of adult and immature stages.

The genitalia of both male and female are shown in figures 1 to 5. For more details about these structures we refer to Pierce and Metcalfe (1935) and Toll (1952).

The egg is white in color and approximately spherical in shape, the chorion with an indistinct reticulate ornementation, the micropyle consisting of 6-7 radiating canals on each side (figures 6 and 7). It averages 0,44-0,58 mm in length and 0,28-0,35 mm in width.

The first-instar larva is characterized by the absence of hooks on the prolegs and averages 0,75 mm in length when newly hatched. The hooks appear in the second-instar larva, increasing in number until the last stage, which possesses 8-17 hooks on each of the four abdominal pairs and 12-20 on the anal pair.

THE PARASITES.

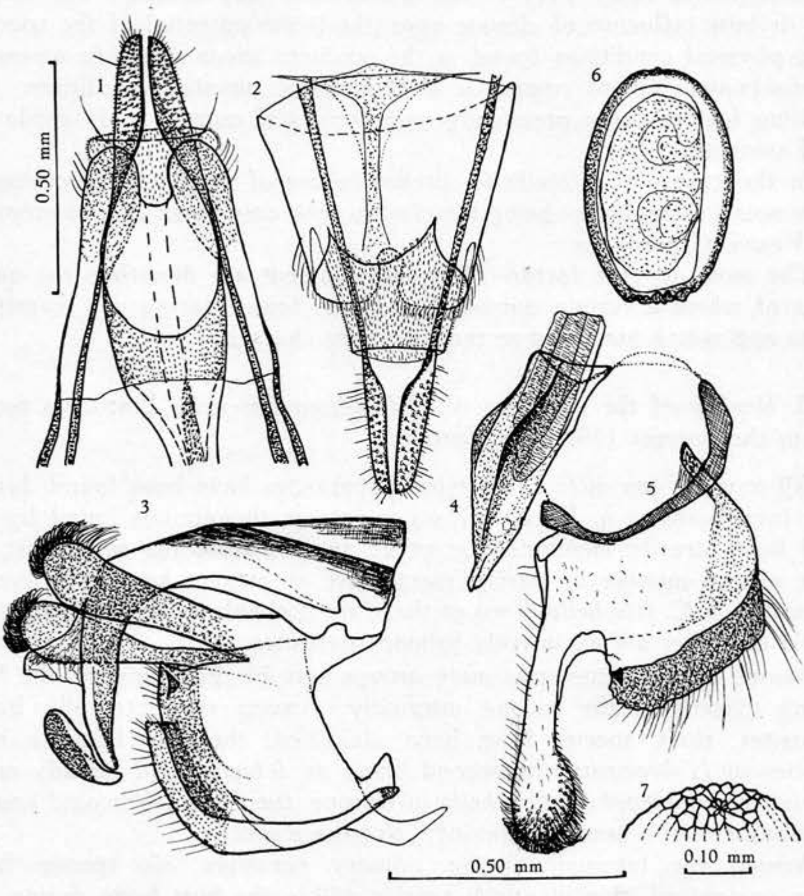
A. Factors limiting the frequency of *Coleophora frischella* Linnaeus.

When taking into account the large number of offspring produced in each generation, the number of generations per year in the different regions of Europe, the sex ratio and its general ability to survive under given physical conditions, there can be no doubt as to the high biotic potential of this species, and the fact of its low frequency in certain countries of Europe may be due to either physical and biological factors.

In the visited region which reaches from North-Western Belgium (Antwerp) to North-Eastern France as far as Nancy (Moselle valley), two main climatic areas have been distinguished as regards the abundance and the developmental velocity of *Coleophora frischella*.

The first main area is situated north of the Belgian Ardennes, the second south of these, occupying the extreme south of Belgium and part of France as previously indicated. The rather low frequency of *Coleophora frischella* in the northern area seems to be due in first instance to physical factors, particularly to temperature, which is too low to allow the full development of its biotic potential. However it must be stated that in two localities in this area (Antwerp and Berg near Brussels), the species was moreover heavily parasitized, and this biological factor must be considered in the reduction of its frequency.

In the second climatic area, the abundance increases, reaching from several hundred specimens on a few square meters to several thousand on well protected and warm situations such as the slopes at Montmédy. In the latter locality a great deal of the work on *Coleophora frischella*



Figures 1 - 7.

Coleophora frischella LINNAEUS.

Fig. 1. — Female genitalia, dorsal face.
Fig. 2. — Female genitalia, ventral face.
Fig. 3. — Male genitalia, lateral view.
Fig. 4. — Aedœagus of the male.
Fig. 5. — Clasper of the male genitalia.
Fig. 6. — Mature egg.
Fig. 7. — Micropyle, with radiating canals and reticulate structures on chorion.

has been done. Nevertheless as is the case in the northern area, only one generation develops each year, while more to the south, towards the Mediterranean coast, two or three generations may develop. This shows the definite influence of climate upon the biotic potential of the species. The physical conditions found in the southern areas seems to represent approximately or to approach the optimum physical conditions, the limiting factors being practically only biological ones, namely predators and parasites.

In the case of *C. frischella*, predators are of very little importance, only occasionally larvae being attacked in their case by such *Hymenoptera* as *Vespa*, *Crabro*, e.a.

The most adverse factors of its environment are doubtless the parasites of which a certain number have been found during our investigations and which are listed in the following chapter.

B. Review of the parasites of *Coleophora frischella* LINNAEUS found up to the present (1953) in Europe.

All together ten different species of parasites have been found during our investigations in Europe; 2 other species though not found by us, had been already mentioned by other authors from the same host, so that a total number of twelve species are at present known to live as parasites on *C. frischella*. Two of these are probably secondary parasites, while the other are exclusively primary parasites.

Among the parasites, two main groups may be distinguished, the first living externally, the second internally. Among the externally living parasites, three species have been identified, the first being a new species of *Habrocytus*, the second being an *Ichneumonid* already mentioned from *Coleophora frischella* in Europe, the third a *Braconid* known as a parasite of a great number of *Coleophora* species.

Among the internally living primary parasites, six species have been recognized, two of which remain within the host body during the summer and hibernating months, in the first-instar larval stage. All belong to the family *Ichneumonidae*.

1. External primary parasites : adult feeding upon the body fluids of the host larva; the latter killed before oviposition; egg and larva hymenopteriform.

   Habrocytus milleri DELUCCHI and VERBEKE (fam. *Pteromalidae*) : three generations; adult larva smooth.

   Ephialtes (Epiurus) brevicornis GRAVENHORST (fam. *Ichneumonidae)* : one generation; adult larva covered with minute tubercules and setae.

   Bracon (Glabrobracon) osculator NEES (fam. *Braconidae*) : two generations; adult larva covered with minute spines.

2. Internal primary parasites :
   a) First-instar larva of the caudate type, remaining within the host larva during the summer months and the hibernating period; one generation; egg hymenopteriform, chorion smooth, brown or white in color

   Pristomerus orbitalis HOLMGREEN : first-instar larva with long tail; egg brown; emergence period mainly June.
   Angitia majalis GRAVENHORST : first-instar larva with short tail; egg white; main emergence period : April-May; a few specimens emerged during the same season as oviposition, before winter (September-October).

   b) Larvae achieving their development and adults emerging in the same season as oviposition (immature stages unknown) :

   Omorgus (prope) *ensator* GRAVENHORST.
   Anilastus (prope) *caedator* GRAVENHORST.
   Meloboris rufiventris GRAVENHORST.
   Angitia majalis GRAVENHORST.
   Gelis palpator GRAVENHORST : in the litterature from Britain (MORLEY and RAIT SMITH, 1933).

3. Internal primary or secondary parasites :
   Hemiteles areator PANZER.
   Hemiteles palpator GRAVENHORST : in the litterature from Britain (THORPE, 1933).

REMARKS :

Dr HINZ of Hannover, who kindly determined the different species, has made some remarks about the value of his determinations, in view of the present status of systematics of *Ichneumonidae*, which are reproduced here :

« *Epiurus brevicornis* GRAVENHORST. Gehört zu dieser Gruppe, die aber noch nicht systematisch geklärt ist. Von meinen Vertretern dieser « Art », die aber auch nicht einheitlich sind, weichen Ihre Tiere deutlich ab. Bei der Schwierigkeit dieser Gruppe wage ich kein Urteil darüber, ob es sich um Wirtsrassen oder um verschiedene Arten handelt ».

« *Omorgus* prope *ensator* GRAVENHORST. Eine einwandfreie Determination ist auch hier nicht möglich. Ich besitze ein Weibchen von Göttingen, das ich mit einem (?) hierher gestellt habe. Es hat die gleiche Zeichnung, weicht aber durch einen etwas längeren Bohrer ab. »

« *Anilastus* prope *caedator* GRAVENHORST. Auch hier keine einwandfreie Determination möglich. »

« *Meloboris rufiventris* GRAVENHORST. Ein leiser Zweifel bleibt auch hier bestehen. Schade das kein Weibchen dabei ist. »

« *Angitia majalis* (?) GRAVENHORST. Die Art doch sehr fraglich, vielleicht hätte man besser « prope *majalis* » geschrieben. »

Later, Dr FERRIÈRE (Geneva) has confirmed this determinations.

TABLE II.

Localities, dates of emergence and frequency of the parasites of *C. frischella* L.; degree of parasitization.

Name	Collecting locality	Dates of emergence	Number of specimens			Percentage of parasites out of 3000 *Coleophora* larvae		
			♂	♀	total	spec.	gr. spec.	total
Habrocytus milleri DELUCCHI and VERBEKE	Montmédy Virton	See life cycle	—	—	180	6,0		
Ephialtes brevicornis GRAVENHORST	Montmédy	»	—	—	84	2,8	9,96	
Bracon osculator NEES	Virton Montmédy	»	—	—	35	1,16		
Omorgus ensator GRAVENHORST	Montmédy	10-15-IX-51 26-27-IX-51	8	3	11	—		
Anilastus caedator GRAVENHORST	Montmédy	10-26-IX-51	1	4	5	—		
Meloboris rufiventris GRAVENHORST	Montmédy	10-18-IX-51	1	—	1	—	0,7	77,26
Angitia majalis GRAVENHORST	Montmédy	10-18-IX-51	2	—	2	—		
Hemiteles areator PANZER	Virton	1-10-IX-51	1	1	2	—		
Pristomerus orbitalis HOLMGREEN	Virton Montmédy	mainly June (1) of the following year	—	—	±500	16,6		
Angitia majalis GRAVENHORST	»	mainly April-May (1) of the following year	—	—	±1500	50,0	66,6	

(1) Under the laboratory conditions.

C. Factors to be considered in the parasitization of *Coleophora frischella.*

Two main factors must be considered as intervening in the parasitization, namely multiple parasitization and hyperparasitization.

Multiple parasitization occurs as a result of the high ratio of parasites to host population, oviposition by the external parasites upon host individuals already parasitized by the internal parasites being unavoidable in at least some proportion. In the present case the external parasite destroys the internal parasite by bringing about the premature death of the host.

Only two cases of hyperparasitization have been observed, both species being *Hymenoptera,* the first living externally, the second internally.

The first concerns *Habrocytus milleri* DELUCCHI and VERBEKE, which was observed twice only as a hyperparasite on the larvae of another external parasite, namely *Bracon osculator* NEES. It must be remarked that probably it is secondary only accidentally, as a consequence of attacking a host within a case, where another external parasite was already present.

The second concerns two specimens of *Hemiteles areator* PANZER which have been obtained from the *Coleophora* rearings and of which it is known that they live as secondary internal parasites, probably in one of the other internal parasites (primaries), the adults of which emerged before the winter.

No traces of hyperparasitization are found in these internal parasites which follow the diapausis of the host.

The extent to which the primary parasites are themselves parasitized is in a large measure dependent on the habits of those species, particularly on the degree of their concealment while in the pupal stage and upon the length of the period spent in this stage. In this respect the parasites of *C. frischella* are in a favorable position since all of them spend their whole larval and pupal development within the entirely closed case in which the host lived.

D. Ethology and immature stages of the ectoparasites.

1. Habrocytus milleri DELUCCHI and VERBEKE.

The *Habrocytus* species parasitic upon *Coleophora frischella* in Europe, has been found to be a new species, related to *H. acutigena* THOMSON and has been described by V. DELUCCHI and J. VERBEKE (1954) as *H. milleri.*

The larva lives as an external parasite, generally solitary but occasionally a little gregarious, and its whole larval and pupal development takes place within the cylindrical case in which the host lived.

This species is quite different from *Habrocytus fasciatus* THOMSON, which has been obtained in France from different *Coleophora* species, and within which it lives as an internal parasite (SUIRE, 1927). A certain number of *Pteromalidae,* particularly *Habrocytus* spp. are recorded by

THOMPSON (1945) from several other *Coleophora* species of different parts of the world, mainly of Europe, Canada and U.S.A.

Habits of the adult :

In this species the time between the emergence of the adult and the beginning of oviposition is short, being in normal conditions from one up to a few days. However the females seem to require for egg production a certain amount of food other than grape juice. The latter was supplied in the breeding tubes in the laboratory and was sufficient only to maintain life for a time.

It has been stated that the body fluids of the host insect are largely used by the females. As the host larva is contained in a case direct feeding is impossible and for this reason the female makes a feeding tube which extends from the puncture on the host body up to the wall of the case. Several feeding tubes may be made upon a single larva.

Another particular feature of this species is that the eggs are not deposited until the host has been killed by the sting. Decay sets in very soon thereafter, the larva becoming brownish and liquifying. In this case the larvae may be considered to be really saprophagous in habit, rather than parastic. Larval development was possible in the laboratory upon exposed larvae outside the case.

The reduction in diameter of the egg, during its passage through the ovipositor is shown by a comparison of egg diameter with ovipositor width. The egg averages 0,15 mm in width, whereas the outside diameter of the ovipositor is approximately 1/3 of this, or 0,05 mm. In the mature females, six fully developed eggs ready to be deposited are found, three in each of the ovaries at the same time. In the laboratory oviposition was continued during three weeks or more.

Egg and larval development :

The egg is deposited upon or near the host in the case, but is not adherent as in another species parasitic upon *Coleophora frischella*. In most cases only two or three eggs are deposited upon one host larva, but up to eight were found. Under normal conditions the egg develops in 2 or 3 days.

In the present species, normally only one larva develops upon each host larva, however in a certain number of specimens two or three were observed to develop. When a larger number of eggs has been deposited upon one host larva, a certain number are killed as the larva first hatched probably destroys the remaining eggs. The larvae do not seem to attack one another.

Parasitization results in a change of the activities of the host larva : while healthy larvae move downwards to the soil for hibernation, parasitized individuals remains on the seed pods for a longer period. In the early period of development of the host larva its case (of type I) does not increase in size any more and changes in color. These specimens may easily be recognized at that time. Pupation takes place in the case in which the host was contained, but the pupa is not attached and no cocoon is spun.

Life cycle :

The life cycle of *H. milleri* is quite short, averaging approximately 15 days from egg to adult. The incubation of the egg requires 2 to 3 days, the larval stage 8 to 10, the pupal stage 3 to 5. *Habrocytus milleri* is able to produce several generations and at least three took place upon the single brood of *Coleophora frischella,* a fourth being obtained artificially in the laboratory.

This species passes the winter as adult since large numbers emerged during the months September and October 1951. Consequently the adult life may be very long. Possibly it hibernates also as mature larva and hibernation may then take place within the case of the host.

The adults of the first generation appeared towards the end of July and the beginning of August. Three main oviposition periods have been observed, the first at the beginning of August, chiefly from August 4 to 8, the second chiefly from August 15 to 20, with a maximum about August 17, the third from August 25 to 31, with a maximum about August 28 and being continued during the first days of September. In nature these three periods overlap more or less. From the adults of the third generation a fourth has been reared artificially in the laboratory. Oviposition of this took place about September 15 in glass tubes provided with a controllable and constant stream of humid air (relative humidity 80 to 90 %), at a temperature of about 22° C. The larval development has been completed in the same tubes.

The mature larvae of the first generation were found from August 7 onwards, being present in large numbers from August 13 to 18. The corresponding emergence period of adults extends from August 16 to 28, reaching a maximum between August 23 and 28. The adult larvae of the second generation were present in large numbers from August 24 to 31 with a maximum on 28-29, and the corresponding emergence of adults took place between August 26 and September 7, with a maximum on September 4. Larvae and pupae of the third generation were largely present from September 5 to 12. The emergences which took place in the laboratory extended from September 13 to 27, being very numerous on September 13-14 and 26-27.

There are at least three larval instars, but no important distinctive characters have been found between them. A pronounced preponderance of females has been observed.

Immature stages :

The egg is ovate in shape and white in color. At one end it is attenuate, tubular and slightly curved; its length averages 0,55 mm, its width 0,15 mm. The chorion with the exception of the poles, is covered with minute spines or spicules, 6 to 12 microns in length, giving the egg a grayish color.

The first-instar larva is hymenopteriform with 13 distinct body segments, the head a little enlarged with three pairs of sensory setae and the integument bare. The mature larva which is brownish in color, shows very pronounced intersegmental grooves dorsally on the abdomen (figure 10). The mandibles are simple, 35 to 40 microns in length, and the integument is smooth and glistening. Three pairs of setae on the head as in the first instar and one pair on each of the thoracic and abdominal segments, except for the last one. The latter is divided into two lobes and bears two pairs of setae. The tracheal system has nine pairs of spiracles occurring on the last two thoracic and the first seven abdominal segments. The antennae average 12 microns in length.

2. Ephialtes (Epiurus) brevicornis Gravenhorst.

Ephialtes (Epiurus) brevicornis Gravenhorst belongs to the family *Ichneumonidae*, subfamily *Pimplinae* and lives as an external solitary parasite on the larva of *Coleophora frischella*. The species has been mentioned already from Europe by Thorpe and from Britain by Morley and Rait Smith (1933). It has been studied recently by Stuart (1957).

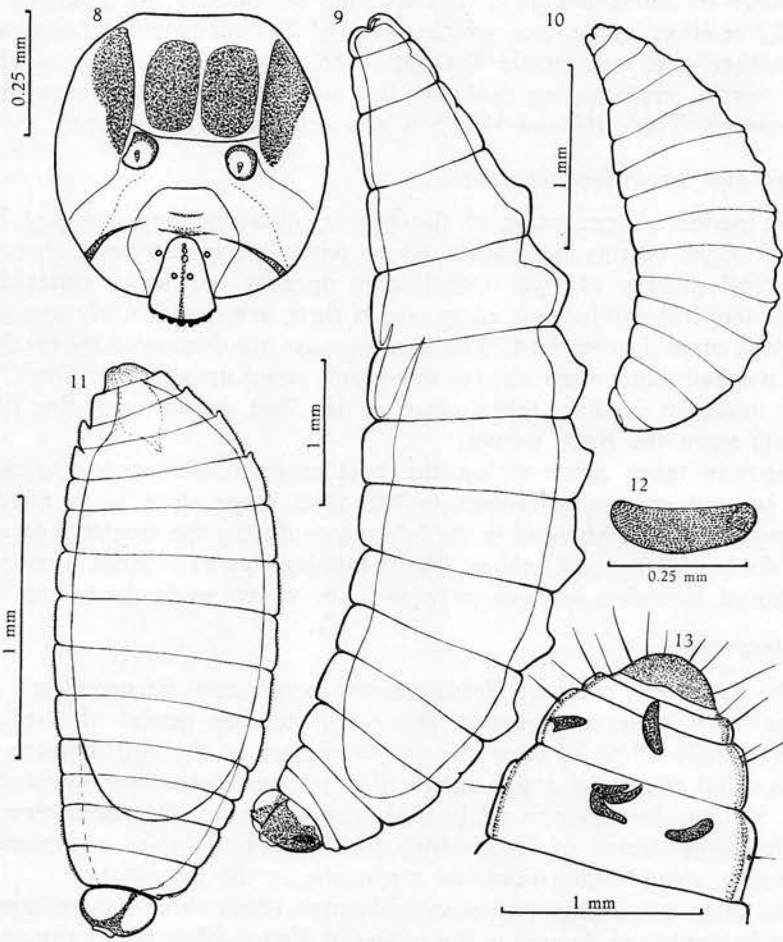
The egg is simple in shape and deposited within the case upon or near the host which is permanently paralyzed or killed by the sting of the parasite. The whole larval and pupal development takes place within the case in which the host lives and this type of external parasitization represents the least specialized and the most common one among the *Ichneumonidae*.

Habits of the adult :

In *Ephialtes brevicornis*, the pre-oviposition period is short, being from one to three days. The length of adult life, as it was observed in the laboratory, covers approximately three to four weeks. The species hibernates in the adult stage and it must be adapted for a long survival. The egg is placed upon any part of the body of the host or nearby in its case, and is slightly adherent.

The adult females feed intensively upon the body fluids and the tissues of the host larva, the entire body contents being sometimes consumed. For this purpose the punctures made with the ovipositor are often enlarged by the mandibles, an opening being bit away laterally in the larval case. This feeding seems to have no relation with oviposition. The latter was never observed on partially eaten larvae. Apparently this habit has developed into a distinctly predaceous habit independently of the reproductive activities, though very probably essential to oögenesis.

Moreover the host larva is permanently paralyzed or killed by the sting of the female at the time of oviposition. Since the stung larva becomes brown and liquifies, the female possibly injects a fungus disease, as a



Figures 8 - 13.

Parasites of *Coleophora frischella* LINNAEUS.

Fig. 8. — Head of mature larva of *Ephialtes brevicornis* GRAVENHORST.
Fig. 9. — Mature larva of *Ephialtes brevicornis* GRAVENHORST.
Fig. 10. — Mature larva of *Habrocytus milleri* DELUCCHI and VERBEKE.
Fig. 11. — Mature larva of *Bracon osculator* NEES.
Fig. 12. — Egg of *Pristomerus orbitalis* HOLMGREEN.
Fig. 13. — Extremity of abdomen of *C. frischella* larva with eggs of *Pristomerus orbitalis*.

mycelium has been found to develop in such larvae. In the laboratory we have observed one female consuming four larvae of *Coleophora frischella* in about ten days. During this period the same female has killed five other larvae upon which a total of 23 eggs have been deposited. In another case one female has deposited 40 to 50 eggs during about three weeks, representing probably the normal reproductive capacity of the species. Table III and IV show the activity of this species.

Egg and larval development :

The period of incubation of the egg is relatively long, ranging from 6 to 8 days; uterine incubation (even partial) has not been observed. The total number of eggs found upon or near one larva varies from one to ten, but within most cases one to three are found. Only one larva develops upon a given host. The surplus eggs are destroyed by the larva first hatched, since they always are found dried up and shrivelled. The most intensive feeding takes place in the last larval stage by direct feeding upon the body tissues.

Pupation takes place within the host case; a thin cocoon is made. The present species hibernates in the adult stage since large numbers of specimens have emerged in the laboratory during the month September and the beginning of October. The adult females of a large number of species of *Ephialtes* are known to pass the winter under bark, etc.

Life cycle :

The entire life cycle of *Ephialtes brevicornis* may be completed in a minimum of about one month, the actual feeding period of the larva covering only 15 to 20 days. As the incubation of the egg requires 6 to 8 days and the pupal stage about 10 days, one generation averages at least 31 days from egg to adult. Only one generation has been observed on the single brood of *Coleophora frischella* in Belgium and north of France, a second being obtained artificially in the laboratory.

The main oviposition period extends over about three weeks, starting at the beginning of August in the region of Virton-Montmédy, the second obtained artificially in the laboratory starting between September 10 and 15.

In nature, the first adults appeared at the beginning of August, being present during a great part of the month. Mature larvae have been observed from the end of August until middle September, being present in large numbers on August 31. The main emergence period, followed in the laboratory, extends over a long period ranging from August to October and reaching a maximum from September 13 to 20 and further from September 27 to October 3; some early emergences were obtained at Montmédy on August 23 and on September 5, 7 and 8.

In the laboratory a second generation has been reared from these adults in the same manner as described for *Habrocytus milleri*, and full larval development was also obtained. Though grape juice was supplied to the adults in the breeding tubes in the laboratory, no actual feeding was observed on it.

In the present species there is a slight preponderance of females, the sex ratio being approximately 3 to 2. There are five larval instars presenting very distinctive characters, as was observed and illustrated by A. M. STUART (1957).

Immature stages :

The egg of *Ephialtes brevicornis* is simple and elongate-ovate in shape, slightly attenuate at one end, whitish in color, without stalk or pedicel and with no sculpture of the chorion. It averages 1,4 mm in length, 0,30 mm in width.

The newly hatched first-instar larva which is whitish in color averages 1,0 - 1,10 mm in length. This larva attains about 2 mm in length before moulting. It is distinguished from the following instars by its bare integument, bearing only three small setae on each of the thoracic and abdominal segments. It is hymenopteriform and characterized by a large and heavily sclerotized head, slightly brownish in color.It shows 13 body segments of diminishing width. The tracheal system is vestigial.

During the next three instars, which are yellowish in color, the larva attains 3,0 to 3,5 mm in length and bears the same number of setae on each of the thoracic and abdominal segments as stated for the first-instar larva. It is characterized by the integument which is not bare but covered with minute spine-like tubercules or papillae of feeble density and which occur only on certain places of the ventral surface. In addition, each segment shows laterally, along its posterior margin a few band-like structures arranged in 4 to 6 series and acting apparently as prolegs. In these instars two white median longitudinal stripes on the head capsule, converging toward the base, become apparent. The tracheal system as in the final-instar larva.

The mature larva attains 5,0 to 5,5 mm in length and is slightly brownish in color. The head is yellowish with four large brown longitudinal stripes, the median ones being short and ovate, the lateral ones being long and slightly converging (figure 8). This instar is distinguished by the occurrence of 8 to 10 setae on each of the thoracic and abdominal segments and by the integument of the first eight abdominal segments which bears upon the entire surface numerous minute spot-like tubercules or papillae and shows the same lateral band-like structures described on the second-instar larva.

The two last abdominal segments show in general more band-like structures of feeble density which extend basally only, especially on the last segment. The latter is bare apically and divided into two lobes. The first and second thoracic segments bear 14 to 16 setae each, a little stronger than those of the third thoracic and the abdominal segments, which bear each 8 to 10 setae.

The body has 13 distinct segments without fleshy processes or appendages but with slight intersegmental ridges dorsally on the first seven abdominal segments and with two dorsal warts on the three thoracic segments and on the first, the 11th and the 12th abdominal segments (figure 9).

The tracheal system is characterized by the presence of 9 pairs of functional spiracles, the first situated between the first and the second thoracic segments, the following eight on each of the abdominal segments 1-8. In the fourth-instar a very small tenth spiracle is between the second and third thoracic segments.

In the mature larva the head bears two pairs of papillae and averages 0,64 mm in length, the mandibles, which are simple, 90 to 100 microns, with the sclerotized apical point 50 microns in length. The antennae average 25 to 30 microns in length.

Table III.

Showing the number of larvae eaten, the number of larvae killed and the number of eggs laid by one female of *Ephialtes brevicornis*, during 10-12 days in a breeding tube in the laboratory.

Larva & case n°	Larva			On the larvae killed before oviposition		
	not attacked	eaten	killed before oviposition	number of eggs	number of 3d instar larvae	number of 2d instar larvae
1	×	—	—	—	—	—
2	—	—	×	5	1	—
3	—	×	—	1	—	—
4	×	—	—	—	—	—
5	—	—	×	—	—	1
6	—	—	×	4	1	—
7	×	—	—	—	—	—
8	×	—	—	—	—	—
9	—	×	—	2	—	—
10	—	—	×	1	—	1
11	×	—	—	—	—	—
12	—	—	×	3	3	—
13	×	—	—	—	—	—
14	—	×	—	—	—	—
15	×	—	—	—	—	—
16	×	—	—	—	—	—
16	8	3	5	16	5	2
percentage	50 %	50 %		total : 23		

TABLE IV

Showing the result of the combined action of the attack of 11 ♀♀ of *Ephialtes brevicornis* and 23 ♀♀ of *Habrocytus milleri* upon 24 larvae of *C. frischella* within their case, in a breeding tube in the laboratory, during six days (from 28.IX to 3.X.).

Larva & case n°	Larva			number of eggs		number of 1st inst. larv.	
	not attacked	eaten	killed before oviposition	of *Habrocytus*	of *Ephialtes*	of *Habrocytus*	of *Ephialtes*
				on the larvae killed before oviposition			
1	×	—	—	—	—	—	—
2	—	—	×	3	3	—	—
3	—	—	×	2	—	—	—
4	—	×	—	—	—	—	—
5	×	—	—	—	—	—	—
6	—	×	—	—	—	—	—
7	—	—	×	1	3	—	—
8	—	×	—	—	—	—	—
9	—	×	—	—	—	—	—
10	×	—	—	—	—	—	—
11	—	—	×	—	—	—	1
12	—	—	×	8	—	—	1
13	—	×	—	—	—	—	—
14	×	—	—	—	—	—	—
15	—	×	—	—	—	—	—
16	—	—	×	—	—	—	1
17	—	—	×	2	—	—	—
18	—	—	×	—	1	—	—
19	—	—	×	2	1	1	—
20	×	—	—	—	—	—	—
21	×	—	—	—	—	—	—
22	—	—	×	2	—	—	—
23	—	—	×	2	—	—	—
24	—	—	×	2	—	—	—
24	6	6	12	24	8	1	3
percentage	25 %	75 %		total : 36			

3. Bracon (Glabrobracon) osculator NEES.

Bracon (Glabrobracon) osculator NEES belongs to the family *Braconidae*, and lives as a gregarious external parasite on the larva of *Coleophora frischella*. It has been mentioned already from Britain under the generic name *Microbracon*, by MORLEY and RAIT SMITH (1933), being reared from *Coleophora caespititiella* ZELLER (1) and *C. virgaureae* STAINT.

(1) recently corrected to *C. alticolella* ZELLER.

Generally two or three larvae live together in one case of *C. frischella* and this species is distinguished from the two preceding by the fact that the larva spins a cocoon for pupation in the case of the host. Development takes place in the summer months but during a shorter period being completed earlier than in the case of both other externally living species.

Habits of the adult :

Since this species has been obtained only in small numbers from the *Coleophora* larvae, it has not been possible to rear it in breeding tubes in the laboratory. It has been observed however that in the tubes the adults generally feed upon the grape juice which was supplied; although the adult female has been observed to feed also upon the body fluids of the host larva that it attacks; it apparently largely subsists on this latter feeding which seems to be essential for oviposition.

Moreover the parasitic larva feeds permanently upon a dead host larva since the latter is completely paralyzed and killed by the adult female before oviposition.

Larval development :

Two, or exceptionally three, larvae of *Bracon osculator* NEES develop at the same time upon one larva of *C. frischella*. Each larva spins an individual cocoon for pupation within the case of the host; two or three are situated together forming one mass. The cocoons are white in color on the inner surface. All specimens always emerge together (polyembryony).

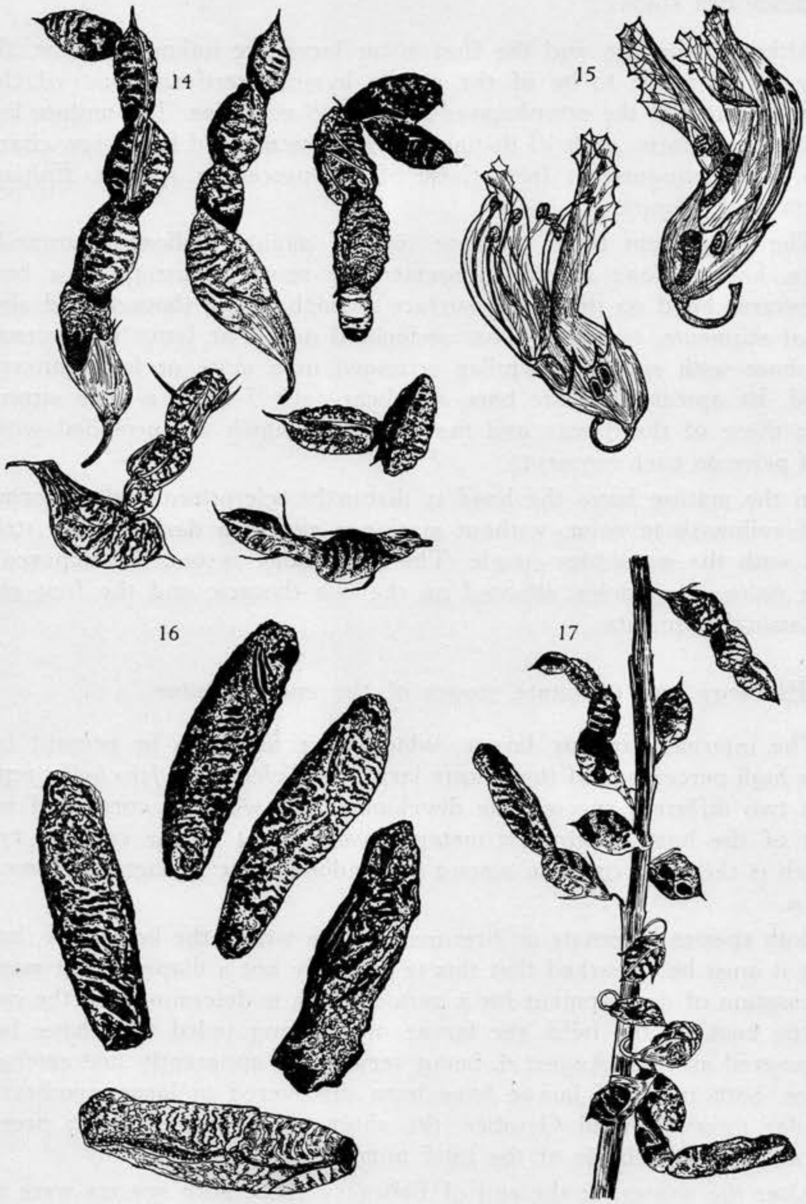
Life cycle :

The life cycle of *Bracon (Glabrobracon) osculator* is short; its development is not correlated with that of the host, and may be completed in about 18 days from egg to adult.

Two generations have been observed on the single brood of *Coleophora frischella*, the first extending from about August 4 to 22, the second giving mature larvae and pupae at about September 10 to 18. This species may have many generations each year, depending upon the availability of a suitable host.

Only one main emergence period has been observed ranging from August 20 to September 7, with a maximum on August 22, and this suggests the possibility of hibernation in the adult larval stage. However an isolated specimen emerged on September 20 and the species may therefore pass the winter in the adult stage as do the females of a large number of species.

In a few cases the mature larva has been found destroyed by a secondary parasite. *Bracon osculator* shows an unusually high preponderance of female progeny, the sex ratio being approximately 5 to 1. The mature larva attains 2,5 to 3,0 mm in length before pupation.



Figures 14 - 17.

Coleophora frischella LINNAEUS.

Fig. 14. — Larval cases of type I (× 6 env.).
Fig. 15. — Flowers of *Melilotus* sp. containing eggs and first-instar larvae (× 8 env.).
Fig. 16. — Larval cases of type II (× 6 env.).
Fig. 17. — Stem of *Melilotus* sp. bearing both types of larval cases (× 3 env.).

Immatures stages :

Although the egg and the first-instar larva are unknown to us, they may be supposed to be of the simple hymenopteriform type which is representative of the ectophagous forms of *Braconidae*. The mature larva is of normal form, with 13 distinct body segments and has a few characters that distinguish it from those of the preceding species, *Ephialtes brevicornis* (figure 11).

The integument bears a dense coat of minute, yellowish, spine-like hairs, half as long as the integumentary setae, occurring in a broad transverse band on the whole surface of each of the thoracic and abdominal segments, except the last abdominal one. The latter is covered at the base with spot-like papillae arranged in a more or less transverse band. Its apical lobes are bare and bear each 5 setae a little stronger than those of the thorax and the abdomen, which are provided with 3 or 4 pairs on each segment.

In the mature larva the head is distinctly sclerotized and uniformely pale yellowish in color, without markings except a dark median stripe, and with the mandibles simple. The respiratory system is composed of nine pairs of spiracles, situated on the last thoracic and the first eight abdominal segments.

E. Ethology and immature stages of the endoparasites.

The internal parasitic larvae, which were found to be present in a very high percentage of the mature larvae of *Coleophora frischella*, represent two different species, the development of which is correlated with that of the host. Their first-instar larvae belong to the caudate type, which is the most common among the endoparasitic species of *Hymenoptera*.

Both species hibernate as first-instar larva within the host body, however it must be remarked that this is probably not a diapause but merely a cessation of development for a period which is determined by the cycle of the host. In the field, the larvae of the long tailed type have been discovered as from August 4, being very small, apparently just emerged. Since, both types of larvae have been discovered in large numbers at regular intervals until October, the short tailed species being present for at least two thirds of the total number of specimens.

After the winter, at the end of February 1952, both species were still unchanged and practically not increased in size since August and September 1951.

On August 15, both species were already present in the above-mentioned proportion and in a percentage of 60 to 70 % at Virton and Montmédy, indicating that at this moment oviposition had ended. The development of the first-instar larvae ceased at about August 20 to 25, when the diapausis of *Coleophora* was starting.

4. Pristomerus orbitalis Holmgreen.

Characters of the egg and the first-instar larva; life cycle :

The egg, which is of the simple hymenopteriform type, is deposited internally, free in the body cavity of the living host larva and is often transported by the blood stream to the posterior part of the abdomen, where it lies dorsally in the fat body. It is cylindrical and curved in shape, the chorion smooth and without sculpture, but being brown in colour and shining, thus making it very conspicuous upon the yellowish colour of the fat body itself (figures 12 and 13). The egg is white when in the oviduct; apparently it becomes brownish after deposition within the host larva. It averages 0,26 to 0,27 mm in length and 50 - 60 microns in width.

The period of incubation is short. Apparently the female is not able to differentiate between parasitized and non-parasitized host individuals, since up to four eggs were found to be deposited into one host larva. However in most cases there is only one egg in each larva.

First-instar larva : the body is more or less cylindrical with 13 recognizable segments and the integument smooth and shining, without setae. Head narrow and long, one and a half times as long as broad at the base, bearing a minute pointed prominence basally on the ventral surface; mandibles falcate. The thoracic and abdominal segments about as long as broad; the tail very long and slender, about as long as the nine preceding abdominal segments, tapering to a sharp point at the end.

The abdomen with a dorsal arched surface between segments 11 and 12, situated above the anal vesicle which is largely separated from the intestine. No spiracles distinct.

This species hibernates probably as first-instar larva. The development starts during May; the long tail becomes shorter after each moult, attaining half of the length of the body after the first moult. This larval stage has been found from the end of May to the 25th of June. The exuviae were at the end of the abdomen. During June the larva rapidly reaches maturity. Pupation takes place within the case of the host. The first adult emerged on June 20, a few others between June 25 and 27, while the emergences were at a maximum between June 30 and July 10. The total emergence period, as observed in the laboratory, extends over about one month. In nature adults were found from June 22 to July 8. This species seems completely adapted to the cycle of the host.

The female does not feed upon the host larva. The ovaries are pointed and strongly developed, containing several hundred eggs. A large number of mature eggs were in the oviduct of a female examined 15 days after emergence and kept in a breeding tube in the laboratory.

5. Angitia majalis Gravenhorst.

Characters of the egg and the first-instar larva; life cycle :

Egg hymenopteriform, small, white and transparent, elongate, a little curved, deposited into the host larva. Oviposition has been obtained artificially in the laboratory in breeding tubes and the white egg has been found within the host larva. The ovaries contain 40-50 eggs. After 3 or 4 weeks (in the laboratory) about 15 to 20 of these are mature and pass into the uterus and the vagina, ready to be deposited.

First-instar larva : head broad and short, its length equalling its width at the base or at least two thirds of the latter, bearing a distinctly prominent bulb-like tubercule basally on the ventral surface; mandibles falcate. The length of each thoracic and abdominal segment averaging only one third to one quarter of their width. The tail short, averaging at most one third of the body length. Abdomen without projecting surface above the anal vesicle, which seems not to be separated from the intestine. No distinct spiracles.

This species mainly hibernates as first-instar larva. It develops during early spring (first half of April); mature larvae were already found on April 25. The development of both larva and pupa is rapid. The larva spins a thin transparent cocoon before pupation, within the case of the host. Emergences took place from April 20 to the beginning of June, with maximum from May 10 to 23. Thus an intermediary host seems necessary to complete the year cycle of this parasite. There are three larval instars. The head of the mature larva is white, without markings. The adult female does not feed upon the host larva.

* * *

Table V shows the most important measurements of the different body parts for two specimens of both endoparasitic larvae, indicating the most striking characteristics. However it must be remarked that they have only an approximative value because of the more or less curved attitude of the larvae, particularly of the anterior part of the body. The measurements have been made by means of an objective micrometer and the camera lucida on a Leitz microscope, and are figured in mm.

CONCLUSIONS UPON THE VALUE OF THE PARASITES.

When taking into consideration the distribution, the resistance to environment, the abundance and the effectiveness of the different parasites, there can be no doubt that for the natural control of *Coleophora frischella* the most valuable are the endoparasitic species completely adapted to the life cycle of the host and free of hyperparasites.

TABLE V.

Showing the most important measurements of the different body parts of the endoparasitic larvae.

Species	Head		Thorax & abdomen		Body length		Thorac. & abdomin. segments	
	length	width at base	length tail	length of rest	without tail	total	length	width
Pristomerus orbitalis ex. 1	0,10	0,05	0,74-0,78	0,85	0,96	1,70	—	—
Pristomerus orbitalis ex. 2	0,12	0,07-0,08	0,69-0,70	0,88	1,00	1,70	0,08-0,09	0,11-0,12
Angitia majalis ex. 1	0,15	0,15	0,30	0,55-0,65	0,75	0,95	0,05	0,16-0,17
Angitia majalis ex. 2	0,12-0,13	0,15	0,26	0,62-0,66	0,75	0,99	0,05	0,17-0,19

SUMMARY.

A brief account is given about the biology of the host, *Coleophora frischella* LINNAEUS. It has been stated that the egg is deposited within the corolla of the flower of *Melilotus*, and that the newly hatched larva is free living for a few days within the flower itself.

Later the larva carries, until the adult stage, a first type of case, which is then discarded, when a second type of case is made for hibernating and pupation. The species is single brooded in western and middle Europe and passes the winter as mature larva. The adult occurs in June and July, the larva mainly during August; the larval development is short.

The different factors limiting the development of *Coleophora frischella* are discussed and it is stated that parasites are the most important among them. Ten different species have been obtained in Europe, three being external parasites, representing about 10 % of parasites, the other seven living as internal parasites.

Of the latter group two species only are important, as they represent 60 - 70 % of parasites and pass the winter as first-instar larva within the host body. The remaining five do not follow the cycle of the host and are rather scarce.

The ethology and immature stages of the three external parasites, *Habrocytus milleri* DELUCCHI and VERBEKE, *Ephialtes (Epiurus) brevicornis* GRAVENHORST, *Bracon (Glabrobracon) osculator* NEES and the two main internal parasites, *Angitia majalis* GRAVENHORST and *Pristo-*

merus orbitalis HOLMGREEN, are explained. The principal characters and measurements of the different parasitic larvae are given, enabling them to be distinguished. Some factors influencing parasitization are discussed.

Among the ectoparasites one new species has been discovered, namely *Habrocytus milleri* DELUCCHI and VERBEKE; it has been described and figured elsewhere.

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