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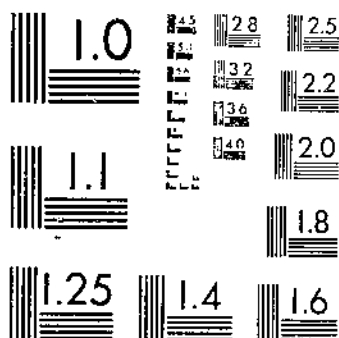
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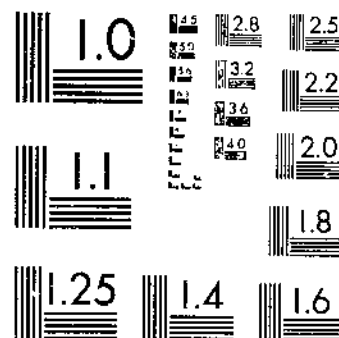
THE BIOLOGY AND MORPHOLOGY OF THE BRACONID CHELONUS ANNULIPES WESM: A. . .
VANCE, A. M.

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UNITED STATES DEPARTMENT OF AGRICULTURE
WASHINGTON, D. C.

THE BIOLOGY AND MORPHOLOGY OF THE BRACONID CHELONUS ANNULIPES WESM., A PARASITE OF THE EUROPEAN CORN BORER

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INTRODUCTION

Among the 30 or more known parasites of the European corn borer (*Pyrausta nubilalis* Hübn.) in Europe are found six species of Braconidae. Only one of these braconids, *Microbracon brevicornis* Wesm., is a true external parasite, living gregariously on the host larva. Its biology and anatomy have been treated by Genieys (3),² who considered it under the genus *Habrobracon*. Two others, *Macro-*

¹The present study of *C. annulipes* was begun in the summer of 1929 at the European parasite laboratory, Hyères, Var, France, and continued with various interruptions for a little over one year. The writer is very grateful for the constant interest of H. L. Parker, under whose guidance it has been a privilege to work, and for the helpful association of E. D. Smith, a fellow worker. He is indebted to C. Ferrière, of the British Museum, for his determination of the species, to Hugh Scott, of the same institution, for a translation of Thomson's Latin description, and to R. A. Cushman, of the taxonomic unit of the Bureau of Entomology, for the identification of all hyperparasites. He also expresses his appreciation to Esther Hart for her drawing of the adult, to B. E. Hodgson for his photograph of the cocoon, and to Theodore Malama for assistance in the rearing work.

²Italic numbers in parentheses refer to Literature Cited, p. 48.

centrus gifuensis Ashm. and *Apanteles thompsoni* Lyle, are also gregarious in habit, but live within the host. Parker (6) has published the results of his studies on the polyembryonic development, biology, and morphology of the former, and the writer (14) has published a bulletin on the latter. The braconids *Microgaster tibialis* Nees, *Chelonus annulipes* Wesm., and *Meteorus nigricollis* Thoms. occur as solitary internal parasites of the borer. The last-named species, however, is only occasionally found parasitic upon *Pyrausta* and is a negligible factor in the control of this host. Parker (7) has described its early stages and pointed out several interesting phases of its biology.

Chelonus annulipes, as a parasite of *Pyrausta nubilalis*, was first discovered by Parker in 1925, when three specimens were reared from cocoons collected in corn at Piacenza, Italy, in the south Padovian zone,* on July 29, and another cocoon was taken at Bergamo, in the north Padovian zone, on August 5. In 1926, 11 more specimens were reared from cocoons found near Bergamo. Thompson and Parker (12), who listed the parasite as *Chelonus* sp., stated that the species seemed to approach *C. carbonator* Marshall. It was their belief, based on the fact that the parasite cocoon normally bore the head capsule of the fourth-instar or fifth-instar host larva, that the eggs of this parasite were laid in some early stage of *P. nubilalis*, and they said in a footnote: "So far as is known all species of the group to which *Chelonus* belongs oviposit in the egg of the host."

No specimens of *Chelonus annulipes* were found during the collection of corn-borer parasites near Bergamo in 1927, and only a few cocoons were discovered in the same region in 1928. In the late summer of 1928 Parker made an extended search for this parasite in the "pump lands" of the Plavisian, Venetian, and south Padovian zones, and finally succeeded in locating a field of corn in the vicinity of St. Giorgio di Nogaro (Plavisian zone) in which parasitism by *C. annulipes* amounted to 9.9 per cent. In several other fields near by a lighter degree of parasitism by the same species was found, and a little later, at Piove di Sacco (Venetian zone), a few *Chelonus* cocoons were collected.

With such evidence in hand it was decided to inaugurate a drive for this parasite in the immediate region of St. Giorgio di Nogaro during the following summer. Accordingly the writer went there on July 20, 1929, and at once began field operations, which resulted in the collection and shipment in cold storage to the United States of 1,432 cocoons of *C. annulipes*.

A study of the biology of the parasite later brought out the fact that the species overwintered as a late first-stage larva within the body of the hibernating host larva, and that a more advantageous method of procuring the parasite in quantity was to collect large numbers of the dormant *Pyrausta* larvae and ship them direct to the United States, where the parasite would emerge in the spring. Such collections were made during the winter of 1929-30, and from these larvae 9,335 adults of *C. annulipes* were reared, bringing the total number of individuals shipped to 10,767.

* For a discussion of the zones the reader is referred to the section on geographical distribution.

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SYSTEMATIC POSITION AND IDENTIFICATION

Chelonus annulipes Wesm. is a braconid belonging to the subfamily Cheloninae.

According to both Dalla Torre (1) and Marshall (5, p. 366-383) the recognition of a genus known as *Chelonus* dates as far back as 1807, when the name was used by Jurine. Since that time various systematists have recorded and described many species of the genus. Nevertheless, the group has always been considered by students of taxonomy as difficult and extremely confused.

C. Ferriere, of the British Museum of Natural History, is responsible for the identification of this species from a study of several male and female specimens. His determination was based largely upon the description given by Thomson (13, p. 572-573). The species was previously listed as *C. inanitus* by Parker et al. (8).

PREVIOUS STUDY OF SPECIES OF CHELONUS

Notwithstanding the mention in systematic literature of a large number of species of the genus *Chelonus*, little biological or morphological work upon any of the group seems to have been undertaken. Various entomologists of different countries have at times listed certain species as parasitic upon particular insect pests and mentioned numerous points in their biology, but in most instances the references have been very brief.

In 1908 Silvestri (10, p. 154-157) made a short contribution on the two species *C. orientalis* Silv. and *C. elaeaphilus* Silv. as parasites of the olive moth, *Prays oleellus* Fab. In addition to descriptions of the adults, the eggs of the two species were described, and, in the case of *C. orientalis*, the external characters of the last-stage larva and the cocoon were given and the egg and last-stage larva illustrated. Brief notes upon the distribution, biology, and economic importance of these species were also included.

In 1912 the first detailed observations on the biology of any species of *Chelonus* were made by Pierce and Holloway (9) in their notes on *C. texanus* Cresson. These authors were the first to record oviposition by a member of the genus as taking place in the eggs of the host insect, and they discussed the occurrence, oviposition, and rearing of that species from both *Heliothis obsoleta* Fab. and *Laphygma frugiperda* S. and A.

Chelonus sonorensis Cam. has been mentioned by Van Zwaluwenburg (15) as the most important parasite of the moth borer *Chilo loftini* Dyar in western Mexico, where, in 1924, it parasitized about 23 per cent of the Chilo present in volunteer rice. Oviposition took place in the eggs of the host, and the parasite issued from the half-grown host larva to spin its cocoon. The life cycle from egg to adult under laboratory conditions was found to be 35 days.

Another species, *C. blackburni* Cameron, has been recorded by Willard (17) as a parasite of the pink bollworm, *Pectinophora gossypiella* Saund., in Hawaii, but few notes are given on its biology.

In his work on the fall army worm, *Laphygma frugiperda*, Luginbill (4) has listed *C. texanus* as one of the most important parasites of that insect, and has discussed, in several pages, its bi-

ology and seasonal history. He has also included good drawings of the adult, last-stage larva, pupa, and cocoon of that species.

Vickery (16) has also considered the importance of *O. texanus* as a parasite of the fall army worm and has treated several interesting points in its biology.

GEOGRAPHICAL DISTRIBUTION

O. annulipes, occurring as a parasite of *P. nubilalis*, has so far been found only in the northern part of Italy. The region of its known distribution (fig. 1) has, for the purpose of convenience, been divided into certain zones, the separation being based upon the geological divisions used by Thompson and Parker (12), and by Parker, Vance, Smith, and Gamkrelidze (8).

The geographical positions of the zones mentioned in this paper are briefly as follows:

The north Padovian zone, including the region of Bergamo, covers the plains of Lombardy and consists of that area in the northwestern part of Italy which is bounded on the west and north by the Alps and on the south by the Ligurian Apennines. On the east its border extends from the junction of the Trebbia and Po Rivers along the Po itself as far as the wide bend of the Adige River. Practically all this region is drained by the Po River and its tributaries.

The south Padovian zone, containing the region of Piacenza, in Emilia, may be considered as a triangular area lying south of a line drawn from the base of the Ligurian Alps along the Trebbia, the Po, and the easterly directed part of the Adige Rivers, bordered on the south by the Toscan Apennines, and spreading east to the shores of the Adriatic Sea.

The Venetian zone, consisting largely of the low country in the Venice and Padova regions, has a boundary which follows the Adige River from its mouth to the point where it reaches the foothills of the Trentin Alps and continues in a northeasterly direction along the base of the mountains to the Piave River, which it parallels to the Adriatic Sea, just north of the gulf of Venice.

The Plavisian zone, in the extreme northeastern corner of Italy, a region sometimes known as the Plains of Friuli, is a somewhat elliptical area whose northern half is hemmed in by the Alps and whose southern boundary follows the Piave River from the mountains to the sea and then goes along the coast toward Trieste. The city of Udine is situated in the north central part of this zone.

Throughout most of the plains of northern Italy, corn, wheat, oats, and field legumes are common crops, and garden vegetables, muskmelons, and watermelons, as well as various fruits and vines, are grown more or less generally. There exists, however, a certain diversity in the agriculture of the different zones just defined. In the north Padovian zone considerable rice is grown, and walnuts and hazelnuts are cultivated. The land in the south Padovian zone is devoted to a mixed type of agriculture. Quantities of tomatoes are grown around Piacenza and muskmelons and watermelons in the lowlands near Ferrara. Considerable hemp, tobacco, and sugar beets are grown from Ferrara south toward Bologna. Tobacco and sugar beets are also grown in the Venetian zone, but in the Plavisian

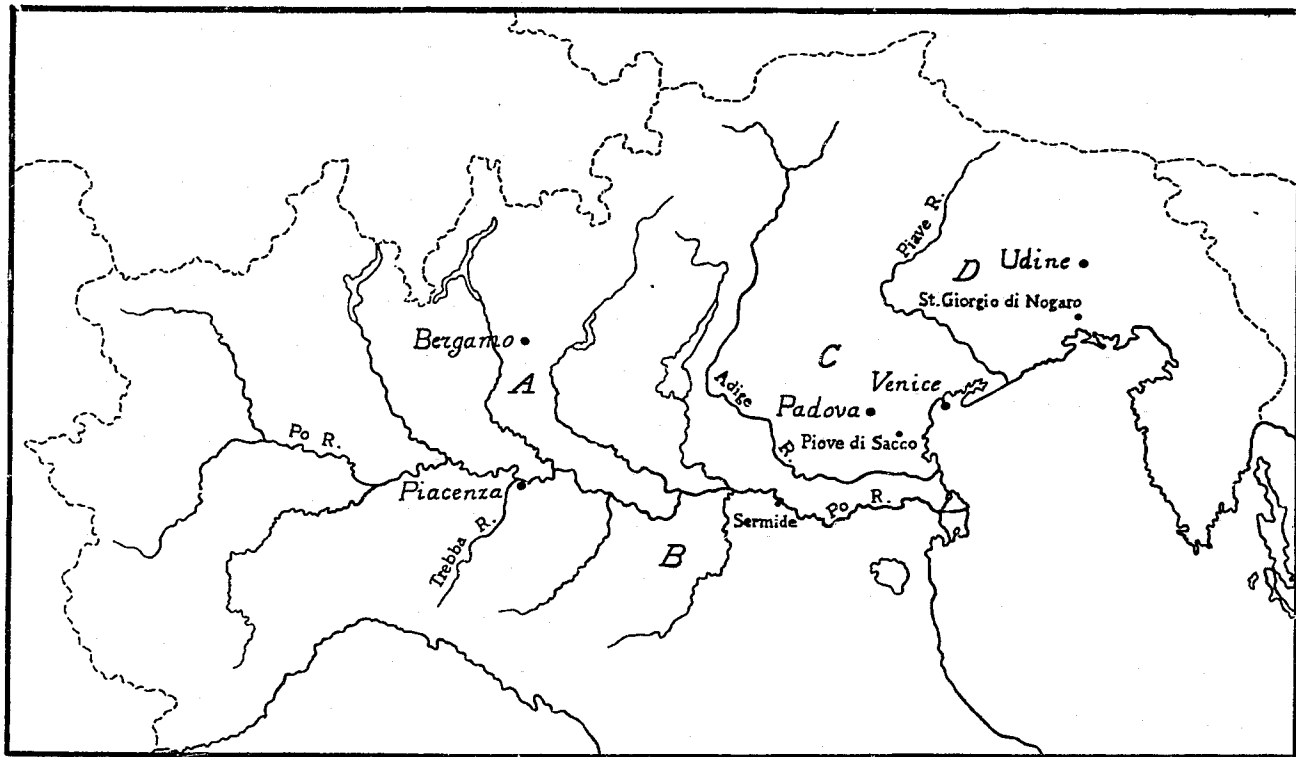


FIGURE 1.—Map of northern Italy showing zones where *Chelonus annulipes* has been found as a parasite of *Pyrausta nubilalis*: A, North Padovian; B, south Padovian; C, Venetian; D, Piavarian. Specimens of the parasite have been collected at all points on the map except at Padova and Venice

zone they are less extensively cultivated, and corn and cereals are prominent.

Chelonus annulipes has been taken in all of the four zones, and it is supposed that the species is present, to some extent at least, over this entire region of northern Italy. It is certain, however, that it is very unevenly distributed.

From present information it may be considered that *C. annulipes* is rare in the north Padovian zone, occurs only in small numbers in the south Padovian zone, is more numerous in the Venetian zone, and exists in greatest abundance in the Plavisian zone. Future studies may, of course, reveal a wider distribution and occurrence in other zones.

In the Plavisian zone heavy parasitism by *Chelonus* has so far been found only in a rather limited area around the town of St. Giorgio di Nogaro (18 miles south of Udine), and in the "pump lands" covering a radius of about 5 miles south, toward the lagoons along the coast. This area lies in a basin called the Laguna di Marano.

St. Giorgio di Nogaro, itself, is situated 23 feet above sea level, but the "pump lands" to the south, known in Italian as "bonifica," are reclaimed lands and lie below sea level. Normal precipitation, plus the natural seepage from higher water tables, supplies such land with sufficient moisture for agricultural operations. This, combined with a natural soil fertility, permits the production of excellent crops. The fields are intersected by a series of canals partly filled with water which is kept sufficiently low by powerful pumping stations that lift the excess to such a height that it can flow into the sea.

Corn of the flint type is one of the principal crops grown on these "pump lands." The plants are tall and strong and as a rule produce a good yield.

LIMITATION OF THE SPECIES

It is known that *Chelonus annulipes* is an important parasite of the corn borer at St. Giorgio di Nogaro, and that in other points of northern Italy, such as Piove di Sacco, Sermide, Piacenza, and Bergamo, it occurs only occasionally or in small numbers. It is also a determined fact that from thousands of *Pyrausta* larvae collected in various parts of France and central Europe, *C. annulipes* has never been reared. Yet Dalla Torre (1) cites the species from Belgium, Germany, Italy, Switzerland, and Hungary; Szépligeti (11, p. 234) describes it from Hungary; and De Gaulle (2, p. 73-88) lists it in his catalogue of the Hymenoptera of France.

This much is known of its general distribution and its more or less specific confinement to certain regions, but to ascribe any definite values to climatic or other factors, in their effect upon this parasite, without more extensive and precise investigations of both the parasite and its host and more data on their biological relationships, would be a speculative, if not hazardous, procedure.

From a study of temperature and precipitation in regions where *Chelonus* occurs in varied numbers, it has been learned, in one instance, that at St. Giorgio di Nogaro (Udine), where the species has

so far been found most plentiful, the monthly temperatures vary little from those prevailing at Bergamo, where the parasite is extremely rare, the former locality having a mean annual temperature of 55.4° F. and the latter, of 54.1°. The annual rainfall in the two places is practically the same—47 inches at St. Giorgio di Nogaro and 46.6 inches at Bergamo—but there is a certain variation in its monthly distribution. During the period January to March, inclusive, St. Giorgio di Nogaro receives a little more rain than does Bergamo; while from May to November, inclusive, only a slight variation occurs. For April, however, the rainfall at St. Giorgio di Nogaro is 2 inches less and in December 2 inches more than at Bergamo. Whether either of these monthly differences has any effect upon the survival of *Chelonus* is not known. It might be conjectured that the resumption of development of the partly grown first-stage larva—which probably takes place about April, after overwintering within its fourth-instar host—together with the general weakness of the host at the time, produces a susceptibility to a climatic fluctuation, such as excessive rainfall, that might make itself apparent in an eventual limitation of the abundance of the species. A further study of this question, considered in relation to the physiological effect of the parasite on its host, would be very interesting, and is certainly necessary before any conclusions can be drawn.

Humidity may be a contributory, and perhaps extremely important, factor in the successful existence of *Chelonus*, although the results of rearing experiments in the laboratory do not lend strength to the view. It is probably true, however, that the atmosphere covering the favored habitat of the St. Giorgio di Nogaro region—the “pump lands” lying near the sea and below its level, and interspersed with canals—is more humid than would be found in places situated farther inland or at higher altitudes, where the species exists in much smaller numbers.

ECONOMIC IMPORTANCE

The economic importance of *C. annulipes* as a parasite of the European corn borer in Italy is best illustrated by the figures given in Table 1. It is readily seen that the percentage of parasitism in all regions studied has been considerably higher in the first than in the second generation of host larvae. In 1929, at St. Giorgio di Nogaro, for instance, the average parasitism in the first generation was 16.9 per cent, while in the second generation it was only 3.5 per cent.

In the region of Bergamo, in the north Padovian zone, where nearly a million specimens of *P. nubilalis* and its parasites have come under observation during the 5-year period, 1925 to 1929, inclusive, *C. annulipes* has been practically negligible. It is also scarce in the vicinity of Sermide in the south Padovian zone.

On the other hand, in the environs of St. Giorgio di Nogaro, in the Plavisian zone, *Chelonus* must be considered one of the factors in the control of the corn borer. At Piove di Sacco, in the Venetian zone, it is also of economic importance. In Table 2 are given the results of a survey of parasitism in this latter region made during August, 1929, by an assistant. A total of 28 cornfields were visited,

and an average parasitism by *Chelonus* of 8 per cent was found for the region. In three fields the parasitism exceeded 20 per cent, and a maximum of 28.2 per cent was discovered in one field.

TABLE 1.—*Parasitism of larvae of Pyrausta nubilalis by Chelonus annulipes in northern Italy, 1925-1929*

Year	Locality	Zone	First generation			Second generation		
			Host specimens	Average parasitism	Maximum parasitism in single field	Host specimens	Average parasitism	Maximum parasitism in single lot ¹
1925	Piacenza	South Padovian	Number 13			Number	Per cent	Per cent
	Bergamo	North Padovian	11					
1926	do.	do.	192,703	0.01				
1927	do.	do.	172,261	0				
1928	do.	do.	312,153	.01				
	St. Giorgio di Nogaro	Plavistan	375	3.20	9.9	1,045	0.5	1.4
	Pieve di Sacco	Venetian				508	.1	.6
1929	Bergamo	North Padovian	225,267	.02				
	Sermide	South Padovian	162	.60	.6	1,888	.1	
	St. Giorgio di Nogaro	Plavistan	12,127	16.90	28.6	2,652	3.5	8.5
	Pieve di Sacco	Venetian	1,441	8.00	28.2	973	.1	

¹ Each lot contained from 250 to 300 larvae.

² First record.

TABLE 2.—*Field parasitism of larvae of Pyrausta nubilalis by first-generation Chelonus annulipes in the region of Pieve di Sacco, Italy, 1929*

Field No.	Date	Locality	Parasitism	Field No.	Date	Locality	Parasitism
			Per cent				Per cent
1	Aug. 1	Brugine	8.3	11	Aug. 5	Pieve di Sacco	17.5
2	Aug. 2	do.	8.8	12	Aug. 6	Arzarello	12.8
3	do.	Campolongo Maggiore	10.0	13	Aug. 7	Arzer Grande	7.1
4	do.	do.	15.3	14	do.	do.	8.3
5	Aug. 3	Pieve di Sacco	10.7	15	do.	do.	10.7
6	do.	do.	4.5	16	Aug. 8	Campagnola	28.2
7	Aug. 5	do.	2.9	17	do.	do.	25.0
8	do.	do.	8.3	18	do.	do.	23.5
9	do.	do.	7.7	19	Aug. 9	Correzzola ¹	2.2
10	do.	do.	4.5				

¹ In 9 other fields of this locality no parasitism by *C. annulipes* was found.

In 1929 parasitism by *Chelonus* in the first generation of the corn borer was not evenly distributed in the different cornfields examined in the vicinity of St. Giorgio di Nogaro. In certain fields the parasitism was very low while in others it exceeded 20 per cent. In five of the fields where *Chelonus* cocoons were most numerous the parasitism was as follows: 10, 18.8, 21.5, 21.8, and 28.6 per cent, with an average of 21.6 per cent. The maximum parasitism in any single field was 28.6 per cent.

Both the heaviest infestation by the corn borer and the highest parasitism of first-generation borers by *C. annulipes* were found in fields of early maturing corn which had reached the silking stage by the latter part of July. In the younger corn there appeared few hosts or parasites. Later, however, the slower maturing corn received the bulk of infestation by the second-generation borers which were attacked by the second brood of *Chelonus*.

In the above area the average infestation by the corn borer in six different fields examined equaled 22.7 per cent of the plants, with a maximum of 40 per cent in one field.

While the parasitism of the second generation, or overwintering host larvae, is numerically less than that found in the first generation, it is still a factor of importance. In Table 3 has been listed the degree of parasitism by *C. annulipes* in nine different lots of hibernating corn-borer larvae from which parasites were bred in the spring of 1930. A total of 2,652 borers were handled, and an average parasitism of 3.5 per cent was determined. The maximum for any single lot was 8.5 per cent.

TABLE 3.—Parasitism of larvae of *Pyrausta nubilalis*¹ by *Chelonus annulipes* of the second generation at St. Giorgio di Nogaro, Italy, 1929

Lot No.	Host specimens	Chelonus annulipes	Parasitism	Lot No.	Host specimens	Chelonus annulipes	Parasitism
	Number	Number	Per cent		Number	Number	Per cent
1.....	319	1	0.3	7.....	268	15	5.6
2.....	274	2	.7	8.....	280	16	5.7
3.....	291	5	1.7	9.....	306	26	8.5
4.....	283	5	1.8				
5.....	310	8	2.6	Total.....	2,652	93	3.5
6.....	312	15	4.8				

¹ The host larvae from which the above data were obtained were collected in the field during the winter months of 1929-30 and the parasites reared from them under controlled conditions in the laboratory.

HOST RELATIONS

The writer has bred *Chelonus annulipes* from *Pyrausta nubilalis* only. A few of the large round eggs of *Sesamia* sp. were several times placed before a female of *Chelonus*, but she refused to oviposit in them. Possibly this species of parasite would attack certain other Lepidoptera whose eggs are laid in masses similar to those of *Pyrausta*.

Pierce and Holloway (9), in their observations on *Chelonus texanus*, found that species to parasitize the solitary eggs of *Heliothis obsoleta* as well as those of *Laphygma frugiperda* deposited in large masses, and they have called attention to this host relationship. Vickery (16) has since added *Laphygma exigua* Hbn. and *Prodenia* sp. as hosts of *C. texanus*.

Only the olive moth, *Prays oleellus* Fab., was mentioned by Silvestri (10, p. 154-157) as host of *Chelonus orientalis* and *C. elaeaphilus*. Willard (17), in speaking of the parasitism of the pink bollworm (*Pectinophora gossypiella* Saund.) by *C. blackburni*, refers to the probability that the high percentage of parasitism by that species during a certain month was due to early development upon another host which permitted large numbers of the parasite to be in the field at an opportune time to attack the pink bollworm.

DESCRIPTION

ADULT

The adult (fig. 2) of *Chelonus annulipes* differs considerably in appearance from the other hymenopterous parasites of the European corn borer. It is a black, robust insect with smoky-colored wings and an abdomen covered by a single hard, dorsally convex sclerite, and little resembles the more wasplike forms of some of the braconids.

The following is a translation of the original description given to the species by Thomson (13, p. 572-573) and used by Doctor Ferriere in his determination:

O. annulipes: Black, with genae swollen and strigose, the frons subopaque and striate punctate, front tibiae and knees pale, hind tibiae broadly pale at the middle, postscutellum with a toothed and elevated carina, scutellum with its disk flat and almost smooth. Length, 6-7 mm.

* * * Best distinguished by its black tegulae, swollen genae, almost opaque and substrate punctate frons, by the apex of the abdomen not being shining and compressed, more rarely bimaculate, by the scutellum with disk flat and almost smooth, and by the female having the antennae about 24-jointed and shorter; very easily distinguishable from *O. rugigena* and *O. humilis* by the female having the antenna dilated and flattened above the middle, by the dentate-elevated carina on the postscutellum, and by the smaller body.

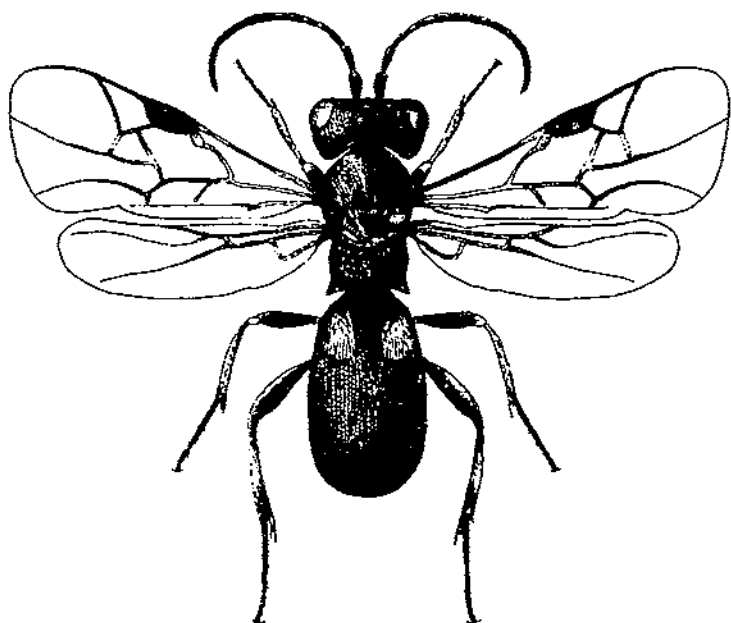


FIGURE 2.—*Chelonus annulipes*, adult female. $\times 8$

EGG

Length at oviposition, 0.2 mm.; greatest width, 0.04 mm.

The egg (fig. 3, A) of *C. annulipes*, immediately after deposition in a *Pyrausta* egg, is cylindrical, arcuate, of nearly equal diameter for its entire length, but slightly narrower at the caudal extremity. Both its cephalic and caudal ends are well rounded. It is translucent white in color and has a smooth glistening surface. As development proceeds the egg (fig. 3, B) becomes distended, and the cephalic end broadened.

FIRST-STAGE LARVA

MEASUREMENTS

At hatching: Length of larva, 0.2 mm.; width of head, 0.075 mm.; width of first thoracic segment, 0.047 mm.; width of first abdominal segment, 0.032 mm.; length of mandible, 0.038 mm.

At age of 10 days: Length of larva 0.72 mm.; width of first thoracic segment, 0.197 mm.; width of first abdominal segment, 0.144 mm.; width of head and length of mandible same as on hatching.

EXTERNAL ANATOMY

The newly hatched larva (fig. 4, A) of *C. annulipes*, found still partly surrounded by clinging masses of the serosal cells, has a translucent white body of eight more or less distinct segments. The head (*h*), in proportion to the other segments, is very large. It is rather square, slightly narrower at the posterior than at the anterior portion, except at the extreme front where the labrum and its processes form a slight projection. Though but slightly more than half as wide as the head, the first thoracic segment is only a little broader than the segments which follow. The anal segment, longer in itself than the other abdominal segments combined and in reality the fusion of several divisions, is further lengthened into a blunt appendage (*aap*) which is inclined ventrally.

A varying number of short translucent spines, pointing in a posterior direction, are arranged in two or three irregular rows across the dorsal surface of the second and third thoracic and the first four abdominal segments. On the last abdominal segment the spines are placed farther toward the front.

The differentiation of the larval segments seems to be a gradual process, and accordingly the later first-stage larva (fig. 4, B) varies from the newly hatched larva just described. The larva, when 10 days old, has changed considerably in its external appearance. The head (*h*) has remained the same size, while the body segments have enlarged. A peculiar aspect of this late first-stage larva is the relatively large segment back of the head which is at least three times as long as either of the following two segments. However, the writer has never been able to observe any further division of this segment and has taken it to represent the usual first thoracic segment.

In addition to the head, now relatively small in proportion to the body segments, there are three thoracic and six abdominal segments. The last of these segments is approximately four times as long as any of the other abdominal segments and bears on its dorsal surface a round raised area which represents an early phase in the evagination of the anal vesicle (*av*). The dorsal spines on the second and third thoracic and the six abdominal segments, in contrast to the increased size of the larva, are almost inconspicuous.

The mouth parts (fig. 4, C) at the front of the head are situated somewhat ventrally. Viewed from beneath, the labium (*lb*) appears to curve inward from the region near the base of the mandibles (*md*) and at the middle to form a rather square lip which covers a chitinous structure of similar shape lying within the mouth opening and behind which the points of the two mandibles approach. Near the

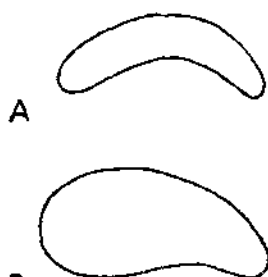


FIGURE 3.—Egg of *Chelonus annulipes*: A, Immediately after deposition in host egg; B, 2 days old and ready to hatch

middle of the lower lip, where it starts to form its squared portion, are located two labial setae.

The anteriorly rounded labrum (*lbr*) is pushed out beyond the curve of the mandibles, and possesses at its outer edge two widely separated processes (*lbrp*), which may be thrust forward from, or drawn in toward, the mouth opening. Each process divides at the

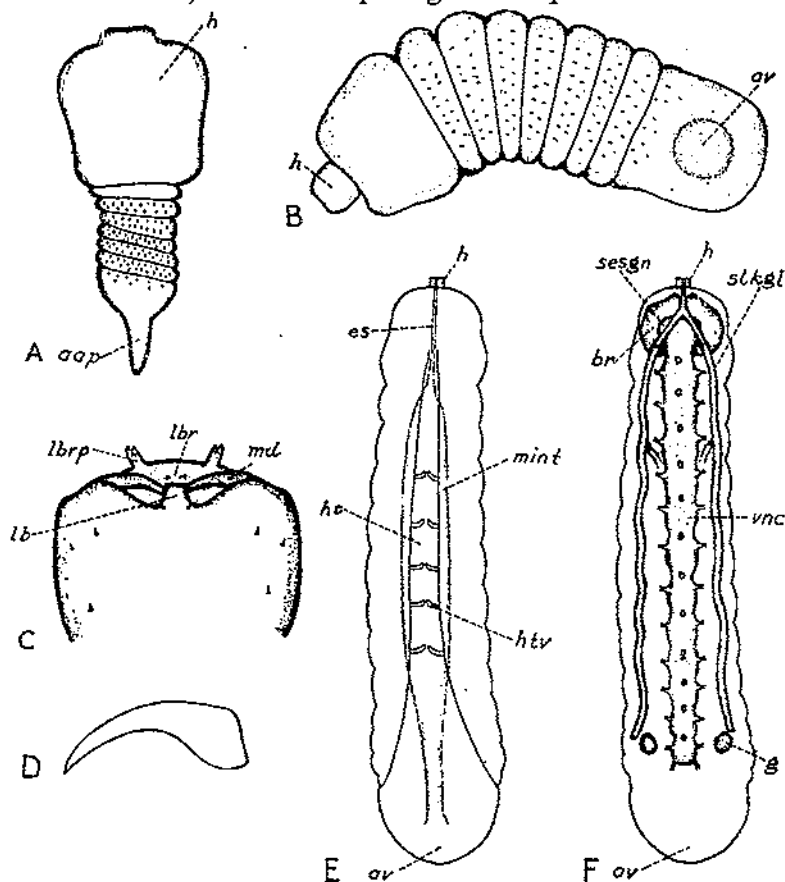


FIGURE 4.—*Chelonus annulipes*, first-stage larva: A, Dorsal view of newly hatched larva; B, dorsal view of larva 10 days old; C, ventral view of head; D, mandible; E, internal anatomy of larva viewed dorsally; F, internal anatomy of larva viewed ventrally. *aap*, Anal appendage; *av*, anal vesicle; *br*, brain; *es*, esophagus; *g*, gonad; *h*, head; *ht*, heart; *htv*, heart valve; *lb*, labium; *lbr*, labrum; *lbrp*, labial process; *md*, mandible; *mint*, mid-intestine; *sesgn*, subesophageal ganglion; *slkg*, silk gland; *vnc*, ventral nerve cord

extremity into three short blunt points. Near the lower edge of the upper lip appear two (and sometimes three) minute peglike structures which are probably sensorial in nature.

The mandibles (fig. 4, D) are dark brown in color, smooth, sharply pointed, decidedly curved on their inner edge, and well chitinated, especially toward their tips. Three small regularly arranged and widely separated spines occur ventrally, on each half of the head proper.

INTERNAL ANATOMY

The degree of development of the various organs differs with the age of the larva. The following description applies to a larva about 10 days old:

The digestive tract consists of a slender esophagus (fig. 4, E, *es*) leading from the mouth to the enlarged mid-intestine (*mint*) in the posterior region of the first thoracic segment. The tube forming the mid-intestine is not greatly distended and narrows slightly in the last four abdominal segments toward its culmination on the interior dorsal wall of the anal vesicle (*av*), which is considered the evaginated hind-intestine.

The heart (*ht*), leading from the anal vesicle, gradually narrows toward the anterior extremity of the first thoracic segment. Five valves (*htv*), located in the first five abdominal segments, control the forward flow of blood, which enters from the posterior opening and probably also from tiny ostia situated laterally along the heart in close proximity to the valves.

The nervous system is composed of a brain (fig. 4, F, *br*) and subesophageal ganglion (*sesgn*) filling most of the first thoracic segment, and a nerve cord (*vnc*) of 12 thick ganglia, each separated from the others by two closely placed heavy cords. In each of the occupied segments two lateral cords are given off from each of the main ganglia and nerves branch posteriorly from the last two.

In the forward part of the first thoracic segment the two lateral silk glands (*slkg*) branch from the short common duct leading from the base of the mouth and extend posteriorly. Each gland becomes bifurcated in the third thoracic segment, and the two branches continue to the vicinity of the seventh abdominal segment. The gonads (*g*) appear as round or somewhat pear-shaped bodies lying in the region of the seventh and eighth abdominal segments.

SECOND-STAGE LARVA

MEASUREMENTS AND EXTERNAL ANATOMY

Length near end of stage, 3 mm.; width, 0.5 mm.

The larva (fig. 5) of this stage is characterized by a rather straight and uniformly roundish body destitute of spines, a thick-walled and bluntly pointed anal vesicle (*av*) which is often indented dorsally, and a round-shaped head (*h*) possessing a very thinly chitinized armature. The body is creamy in color and consists of the head, three thoracic, and nine abdominal segments, not counting the anal vesicle. On the venter of each of the three thoracic segments occurs a pair of leg buds, and laterally on the second and third thoracic segments are two pairs of rudimentary wings. The histoblasts of the external genital appendages are located on the ventral surface of the eighth and ninth abdominal segments in the female, and on the ninth in the male larva.

The mouth parts appear as several raised areas on the forward part of the head and are very lightly chitinized. No strong mandibles are present, as in the first and last stages. On the labrum, however, appear to be located two pairs of small sensorial structures, and the round markings of the antennal rudiments are visible on the upper part of the head.

Usually the head cast and old skin of the first-stage larval molt are to be found on one of the last abdominal segments of the second-stage larva.

INTERNAL ANATOMY

The internal anatomy of this larva differs little essentially from that of the first-stage larva. All organs have increased in size, and the two silk glands, bifurcating in the third thoracic segment and lying very close to the body wall, have become more convoluted. The appearance of the gonads and heart is little different from that in the first-stage larva.

A large part of the head is occupied by the brain, and the nerve ganglia are located along the ventral floor of the body cavity. The tracheal system, although still closed, seems to be filled with air and has 10 principal branches in addition to the cephalic and caudal extremities. The two longitudinal trunks are united by a short dorsal transverse commissure in the first thoracic segment.

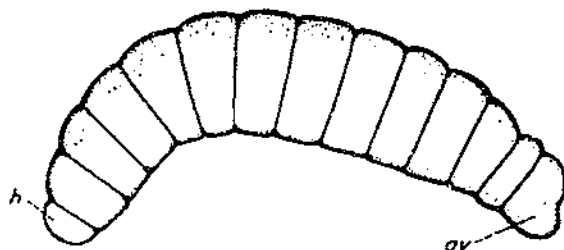


FIGURE 5.—*Chelonus annulipes*, second-stage larva: *h*, Head; *av*, anal vesicle

Urate cells are closely associated with the lateral fat lobes of the second to seventh abdominal

segments; in the seventh there are only a few of these excretory cells. Fat cells seem to be present in all segments of the body except the head and the last abdominal segment.

LAST-STAGE LARVA

MEASUREMENTS

After external feeding: Length, 7.5 mm.; width, 2 mm.; length of mandible, 0.214 mm.; diameter of third thoracic spiracle, 0.034 mm.; average length of large dorsal spines, 0.081 mm.

EXTERNAL ANATOMY

The last-stage larva (fig. 6, A), upon issuance from the host, is cylindrical, widening gently in diameter from the head (*h*) toward the abdominal segments and then becoming somewhat smaller at the rounded caudal extremity, where the anus (*a*) is located. The body is creamy or yellowish in color, and has a glistening appearance. Microscopical examination shows the skin to be thickly covered with tiny blunt spines. Fourteen segments are present. The last two abdominal are somewhat transparent and contain only the ramifications of the tracheae, a few scattered fat cells, and the hind intestine with the anus.

A number of tiny translucent spines are distributed, dorsally and laterally, over the various thoracic and abdominal segments (with the exception of the anal segment), and dorsally on each

of the abdominal segments two to six, inclusive, are located a few long and brown chitinized spines. On each of these five segments the large chitinized spines occur in two short transverse rows, one on each side of the dorsal heart line but slightly laterad.

The exact number of such spines in any group or on any segment is not constant for the same or for different larvae. The following example of their abundance and distribution is typical:

Second abdominal segment, 4 on left and 3 on right side of heart line, or a total of 7.

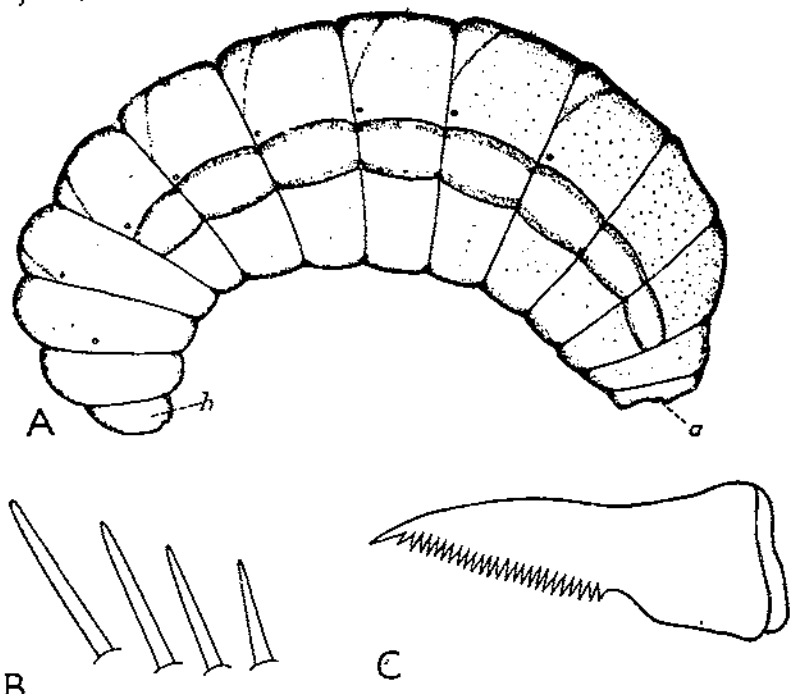


FIGURE 6.—*Chelonus annulipes*, last-stage larva: A, Lateral view; B, set of dorsal spines; C, mandible. a, Anus; h, head

Third abdominal segment, 1 on left and 3 on right side of heart line, or a total of 4.

Fourth abdominal segment, 3 on left and 4 on right side of heart line, or a total of 7.

Fifth abdominal segment, 3 on left and 2 on right side of heart line, or a total of 5.

Sixth abdominal segment, 1 on left and 1 on right side of heart line, or a total of 2.

Total of 15 spines on each side of heart, or 30 in all.

These spines (fig. 6, B) are not all of the same size, and usually there is a gradation downward in their length from the median line laterad.

From the well-developed tracheal system spiracles open near the anterior margin (laterad and slightly dorsad) of the second thoracic and first six abdominal segments. In the third thoracic segment the tracheal termination is only a mitten-shaped stub, located internally.

The arrangement of the integumentary muscles is responsible for decided lateral lobes on the first eight abdominal segments.

The chitinated head capsule or epicranium covers the superior and lateral portions of the head. This part is set off from the softer buccal region by the epicranial suture (fig. 7, A, *epsu*) which is arched over the mouth and labrum, curves slightly downward on each side, and is continued laterad, coincident with the superior maxillary suture (fig. 7, B, *smassu*) under the upper fold of the maxilla, and then along the side of the head to connect with the tentorial crosspiece (*ten*) which continues internally a little below the pharynx (*phx*). A short arm of the epicranium serves for the articulation of the mandible (*md*). A thickening, called the inferior maxillary suture (*imassu*), partly defines the lower edge of the maxilla, while a short chitinous bar extends from the superior to inferior maxillary sutures. Another part of the supporting structure of the head forms a somewhat elliptical border about the labium and is termed the labial suture (*lbsu*). Two rather large round markings near the top of the head, seeming to be slightly depressed toward their centers, represent the antennal rudiments. (Fig. 7, A, B, *ant*.)

The mouth (fig. 7, A, B, *mtk*) is bordered above by the labrum (fig. 7, A, *lbr*) on which are situated six very short regularly arranged spinous sensorial organs, while deeper within the opening on the very under edge of the labrum seem to be four very minute structures, possibly also sensorial in function.

Each maxilla (*mx*) possesses an oval 2-knobbed palpus (*mæp*) with one seta (*mæse*) above and another below it. Laterally to each of the maxillae stands a group of about six spines.

The labium (*lb*), very slightly raised above the surrounding chitinous support, carries on its lower half a considerable number of setae (*lbse*) and two widely separated palpi (*lhp*). These palpi are slightly elevated, rather oval in shape, and seem to terminate in three circular knobs. Near the upper part of the lower lip is found the slitlike opening of the common duct of the silk glands (*slkdo*). The area of the opening is a little raised, and from its upper edge the labium slopes into the mouth opening. The surface of the cuticle in this region is divided into many small polygonal areas. Below the labium a considerable number of spines are irregularly arranged.

From under the maxillae the points of the two mandibles (*md*) appear in the mouth opening. Each mandible (figs. 6, C; 7, A; 7, B) has a broad rounded base which articulates in the curved apophyses of the arms which extend laterad along the ventral margin of the epicranium, and tapers to a sharp distal point. It is hollow (at least in its basal portion), well chitinated, brown in color, and possesses along its inner edge a row of about 25 long sawlike teeth.

The appearance of the larva at this stage, after it has finished external feeding, is more plump, the lateral lobes are more swollen, and there is also a difference in coloration due to the contents of the peritropic membrane, which now varies from a light to a dark brown. With the external feeding the larger urate cells become more apparent. They are found only in the second to eighth abdominal segments, where they occur laterally in close association

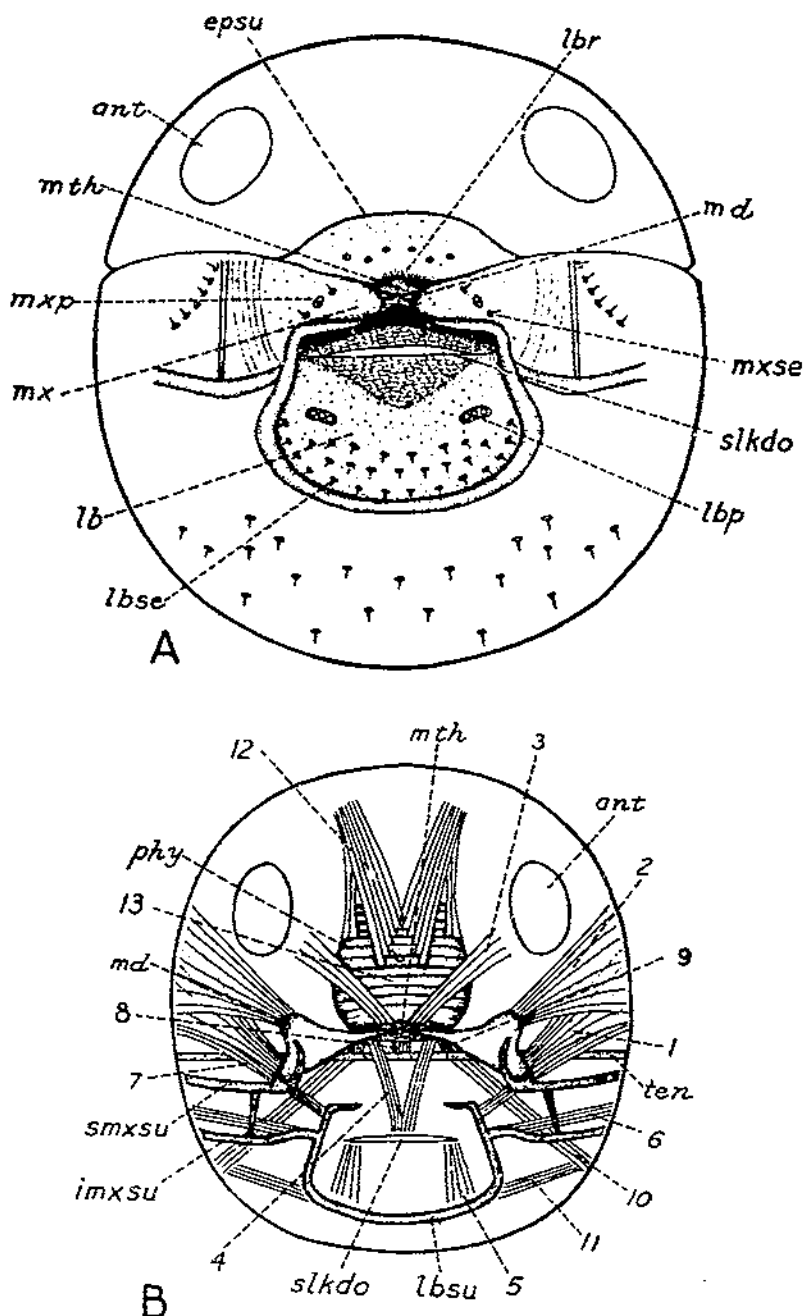


FIGURE 7.—*Chelonus annulipes*, last-stage larva; A, Front view of head; B, front view of head musculature. *ant*, Antennal rudiment; *epsu*, epicranial suture; *imxsu*, inferior maxillary suture; *lb*, labium; *lbp*, labial palpus; *lbr*, labrum; *lbse*, labial seta; *lbsu*, labial suture; *md*, mandible; *mth*, mouth; *mx*, maxilla; *mxp*, maxillary palpus; *mxse*, maxillary seta; *phy*, pharynx; *slkdo*, external opening of common duct of silk glands; *smxsu*, superior maxillary suture; *ten*, tentorial crosspiece; 1-13, various sets of muscles described in the text

with the fat cells. Fat bodies are noticeable in all but the head; only a few scattered cells occur, however, in the last abdominal or anal segment.

INTERNAL ANATOMY

After its issuance from the host, the larva (fig. 8, A) has a mouth (*mtb*), opening into a slender pharynx (*phy*), which is surrounded by muscular layers considerably thickened dorsally. This leads to the esophagus (*es*), which possesses a valve (*esv*) in the first thoracic segment. The digestive tract is then somewhat abruptly enlarged to form the mid-intestine (*mint*), which is much distended with the contents of the peritrophic membrane and closed at its posterior extremity. The hind-intestine (*hnt*) consists of a flattened bulb, which lies against the posterior extremity of the mid-intestine and continues by a narrowing tube toward the anal opening (*a*). The writer, in the course of numerous dissections, has never been able to find any signs of the Malpighian tubes usually present in most larvae of hymenopterous parasites, and is firmly convinced that no such tubes occur in *C. annulipes*. Proceeding from the upper part of the hind-intestine, however, are a number of short outgrowths which are considered to be the rudiments of the Malpighian tubes (*mal*) occurring in the adult insect.

The heart in this stage is wider and larger, but the valves can not be distinguished as in the two preceding stages.

The brain (fig. 8, A, *br*), rather oval in shape, is followed by the subesophageal ganglion (*esgn*) and 11 ganglia (*vnc*), lying in a chain along the ventral floor of the larva's body. The thoracic ganglia (fig. 8, B, *ngt*) are slightly larger than those of the abdominal segments (*nga*), and all are joined by pairs of rather thin longitudinal connectives.

The silk glands (fig. 8, A, *slkgl*) differ from those of the second-stage larva only in increased size and a more convoluted character. In the ninth abdominal segment, near the termination of the nerve cord, occur the rudimentary testes and histoblasts of the external genital appendages (*hbg*) of the male larva. In the case of the female larva the ovaries lie in the seventh abdominal and the histoblasts of the genitalia in the eighth and ninth abdominal segments.

The tracheal system (fig. 8, C) of this stage, functioning through a series of seven open spiracles (*sp*), consists of a longitudinal trunk from which 11 short lateral branches proceed dorsally and a similar number lead in a ventral direction, the two ends of which ramify in the cephalic and caudal extremities of the larva. All branches ramify, and in the first thoracic segment the two longitudinal trunks on either side of the body are joined by a dorsal commissure (*acom*).

In Figure 9, A, is shown a longitudinal section of the head and first two thoracic segments, and in Figure 9, B, a similar cut of the last three abdominal segments. Most of the structures have already been discussed. The group arrangement of the fat cells (fig. 9, A, *fc*), the form of the esophageal valve (*esv*), the location of the cells (*scpm*) which probably secrete the peritrophic membrane, and the attachment of the dorsal pharyngeal muscles (*phymt*), are illustrated. Figure 9, C, shows enlarged urate (*uc*) and fat (*fc*) cells and two oenocytes (*oen*), all from a last-stage larva.

The arrangement of the integumentary muscles of *Chelonus* is less complex than that of certain other parasitic larvae, and the fine fibers are not found grouped into bundles. In general the muscles of the thoracic and abdominal segments (fig. 10) may be classified as follows:

Ventral longitudinal muscles (*vlml*) occur on each side of the ventral nerve cord as a flat band of fibrous strands crossing the three thoracic and first nine abdominal segments. In the first thoracic

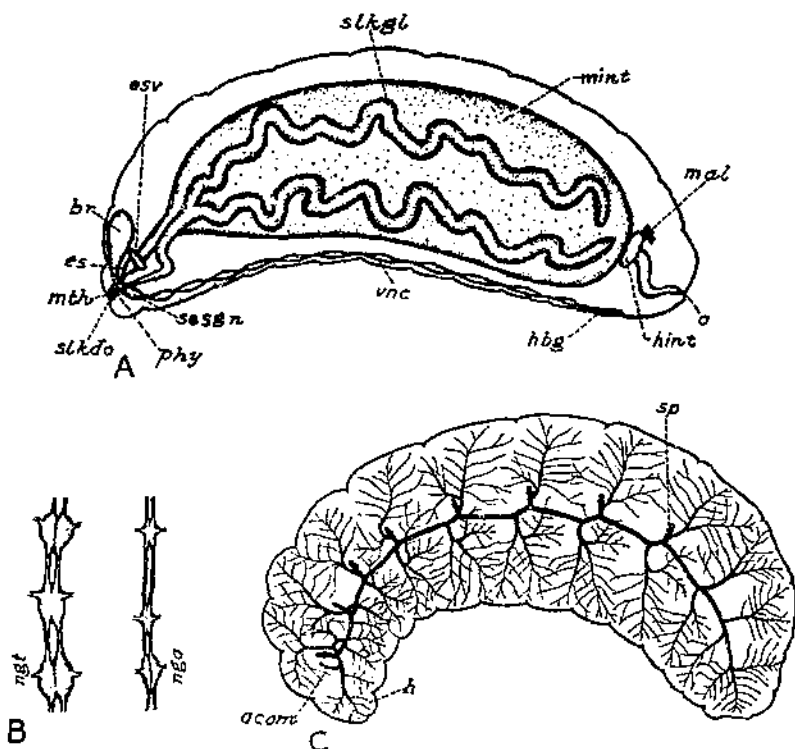


FIGURE 8.—*Chelonus annulipes*, last-stage larva: A, Internal anatomy viewed laterally; B, nerve ganglia of three thoracic and sixth, seventh, and eighth abdominal segments; C, lateral view of tracheal system. *a*, Anus; *acom*, anterior commissure; *br*, brain; *es*, esophagus; *esv*, esophageal valve; *h*, head; *hbg*, histoblasts of external genital appendages of male; *hint*, hind-intestine; *mal*, supposed rudiments of Malpighian tubes of adult; *mint*, mid-intestine; *mth*, mouth; *nga*, nerve ganglia of sixth, seventh, and eighth abdominal segments; *ngt*, nerve ganglia of three thoracic segments; *phy*, pharynx; *segn*, subesophageal ganglion; *slkdo*, external opening of common duct of silk glands; *slkgl*, silk gland; *sp*, spiracle; *vnc*, ventral nerve cord.

segment the band is subdivided, and a few of its fibers near the upper edge form a set extending forward and mediad to the anterior margin of the segment.

Dorsal longitudinal muscles (*dlml*) are also present in the three thoracic and first nine abdominal segments and form a band, about equal in width to that of the ventral longitudinal muscles, along the upper part of each lateral half of the body. The fibers in the first thoracic segment occur in two groups. The upper group crosses the entire segment, and the lower, of about the same width, is

attached about two-thirds of the way toward the front of the segment.

Ventral oblique muscles (*voml*) occur in narrow bands, one of which is attached at a point near the lower anterior edge of the ventral longitudinal muscles in the first thoracic segment and crosses diagonally mediad to the upper posterior corner of that set in the same segment. This type of muscle is found similarly located in the second and third thoracic and the first abdominal segments.

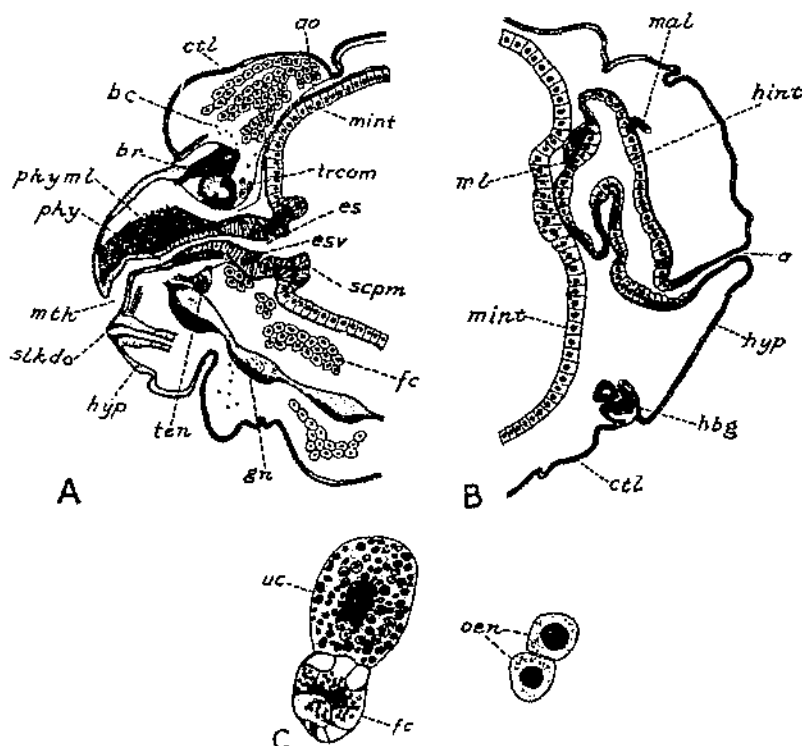


FIGURE 9.—*Ohelonus annulipes*, last-stage larva; A, Longitudinal section of head and first two thoracic segments; B, longitudinal section of eighth, ninth, and tenth abdominal segments; C, cells. *a*, Anus; *ao*, aorta; *bc*, blood cells; *br*, brain; *ctL*, cuticle; *es*, esophagus; *esv*, esophageal valve; *fc*, fat cells; *g*, ganglion; *hbg*, histoblasts of external opening of genital appendages of male; *hint*, hind-intestine; *hyp*, hypodermis; *mal*, Malpighian tubes of adult; *mint*, mid-intestine; *ml*, muscles; *mth*, mouth; *oen*, oenocytes; *phy*, pharynx; *phymL*, pharyngeal muscles; *scpm*, secreting cells of peritrophic membrane; *slkdo*, external opening of common duct of silk glands; *ten*, tentorial crosspiece; *trcom*, tracheal commissure; *uc*, urate cell

Lateral oblique muscles (*loml*) are bands of about the same width as those of the ventral oblique muscles and occur in the second and third thoracic and first five abdominal segments. Each set is attached to the body wall at a point adjacent to the upper anterior edge of the ventral longitudinal band and runs dorsad and caudad to the lower posterior corner of the dorsal longitudinal muscles in each occupied segment. In the second and third thoracic and first abdominal segments these muscles appear as continuations of the ventral oblique sets.

Dorsoventral muscles (*dvmI*) include two types. The first comprises very thin bands which run from the dorsal longitudinal to the ventral longitudinal muscles near the posterior segmental lines of the three thoracic and the first seven abdominal segments. The second consists of shorter muscle groups occurring near the middle, or slightly forward, of each lateral half of the second and third thoracic and first eight abdominal segments and attached at either end a short distance from the longitudinal muscles of the dorsal and ventral sets. In the last two thoracic segments the muscles of the latter set consist of only one or two large fibers, while in the abdominal segments the bands are much wider, becoming a little narrower in their upper attachment.

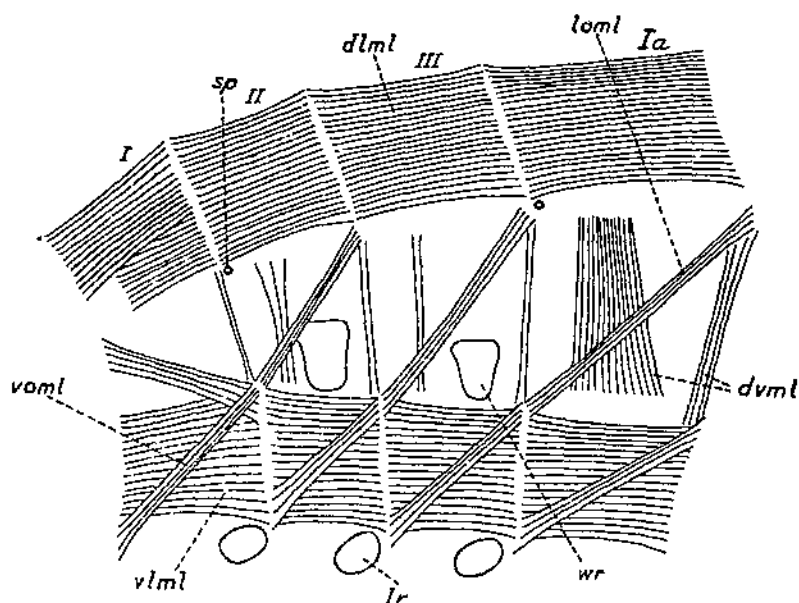


FIGURE 10.—*Chelonus annulipes*, last-stage larva: Integumentary muscles of three thoracic (I-III) and first abdominal (Ia) segments. *dlml*, Dorsal longitudinal muscles; *dvmI*, dorsoventral muscles; *lomI*, lateral oblique muscles; *lr*, rudiments of leg; *sp*, spiracle; *vlml*, ventral longitudinal muscles; *vomI*, ventral oblique muscles; *wr*, rudiments of wing

The muscles of the head region are shown in Figure 7, B. The largest muscles found in the head of a *Chelonus* larva are those of the mandibles (*md*) and consist of two sets, the extensors (1), attached near the outer base of the mandibles and spreading toward the lateral wall of the head, and the flexors (2), originating at the inner base of the mandibles and extending laterad in a fanlike form. The sets are about the same size.

Two sets of muscles (3), arising near the antennal rudiments (*ant*), approach each other on the lower margin of the labrum. The labium is equipped with two sets (4), which are attached somewhat apart near the lower edge of the mouth (*mtb*) and extend ventrally to converge in the region of the common silk duct opening (*slkdo*). A pair of muscles (5), located more ventrally in the labial region, probably functions in connection with the silk duct opening.

Two sets of rather narrow muscles (6, 7) are found in each of the maxillary regions. Both of these continue laterad, and the upper one also extends dorsad toward the base of the mandibular muscles.

From the middle of the internal crosspiece of the tentorium (*ten*) at the back of the head, a short and rather wide muscle (8) is attached somewhat forward to the under wall of the esophagus. A little to each side, another set of short muscles (9) also unites the under part of the esophagus with this crosspiece, and near the point of attachment to the bar, two long muscles (10) are affixed and extend out in a laterad and cephalad direction. On either side of the labium, near its lower edge, a set of muscles (11) proceeds laterad to the body wall. A number of upright muscles (12) extend from the upper wall of the cranium to points of attachment among the circular muscle fibers (13) which surround the pharynx.

PUPA

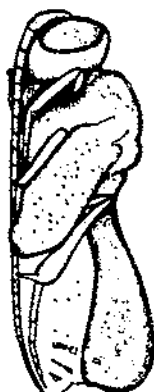


FIGURE 11.—
Pupa of
Chelonus
annulipes

Length, 4.75 mm.; width, 2 mm.

The pupa (fig. 11) of *Chelonus annulipes* is of the free or exarate type, exhibits no movement, and in general appearance is comparatively short and robust.

Its color, during the first five or six days, or for about half of the pupal stage, is pale yellow. The eyes and ocelli early appear as light-brown areas which gradually darken as development progresses. During the latter half of the stage the body darkens by degrees. The antennae, head, thorax, and heavily chitinized dorsal portion of the abdomen finally become jet black, the legs also darken, and the wings become smoky colored. The somewhat protruded ventral part of the abdomen is the only region remaining pale yellow in color, and it is somewhat darkened by a number of broken transverse black markings. A more detailed discussion of pupal development and the exterior changes which take place is to be found in the section on pupation.

Luginbill (4) has published a ventral view of the pupa of *C. lewanus*.

COCOON

Length, 8 mm.; greatest width, 3 mm.

The cocoon (plate 1) of this species is thin and almost papery in appearance. It is cylindriciform, roughly oval in shape, with the ends sometimes rather squared, and is somewhat thickened at the middle by a considerable number of circular threads which give it the appearance of being girdled by a narrow white band. It is constructed of glistening white threads loosely spun exteriorly but more tightly woven toward the interior and is attached by the outer threads either to the walls of the host tunnel or, as is more often the case, to the silken web made by the host larva during the latter part of its life. Through the cocoon the pupa in its different stages of development is dimly visible, and the cast meconium is seen pushed against the caudal extremity.

Generally the head and dried skin of the host larva are included in the outside web work, where they are attached at various points on the cocoon. In an examination of 54 cocoons from the field, the host head capsule and skin were found fastened to the cephalic end of 17 cocoons, to the caudal extremity of 25 more, and near the middle of 12 others.

BIOLOGY

METHODS OF REARING

The writer did not attempt to develop, to any degree, a method suitable for large-quantity production of this parasite; his aim was to rear only sufficient numbers to permit a study of the biology and morphology of the species.

Each male or female adult of *Chelonus*, upon emergence, was confined in a small glass-globe cage. This cage had a diameter of about 3 inches at the middle, and an opening of 2 inches diameter at each end. The top opening was provided with a removable tin cover, while the bottom was set upon a piece of strong white cloth tightly stretched across a 5-inch square wooden frame about an inch in height. The arrangement of the cage on the cloth frame permitted a constant interchange of air with the outside atmosphere and at the same time provided a suitable base to which the cage could be attached. A strong rubber band stretched over the top of the cage cover and around the wooden base united all so firmly that the cage with its base could be moved about without danger of overturning.

On the bottom of each cage, i. e., on the cloth frame, was placed a small 1-inch square of paraffined cardboard on which lay a half lump of dry sugar. Food in this form proved very convenient, and the parasites fed readily upon it. Water was applied with a pipette to the sides of the cage, usually only once a day.

Both honey-water and sugar-water solutions were found to be acceptable foods of the parasite. These foods were less convenient, however, for two reasons: They required constant changing; and there was always danger of the adults becoming stuck in the syrup.

In the writer's experiments, the male and female of *Chelonus annulipes* seemed to copulate most readily in the end of a 4-inch glass vial held toward a source of strong light. Mating in a globe cage was secured several times and at least once in a square box cage. None of the methods used proved certain, however, and many attempts to secure mating resulted in failure.

Oviposition was obtained by placing a mass of *Pyrausta* eggs on the floor of the female's cage. As a rule, the mass was attached to a small square of dock or corn leaf which, in turn, was glued to a piece of paper to prevent curling up. After the host eggs had been left exposed for a sufficient period, usually about 24 hours, the mass was removed and placed in a small glass-covered tin box with a few leaves of green dock. The borer larvae, on hatching, were allowed to feed on green dock leaves until they had reached the fourth instar. Each larva was then isolated in a 3-inch glass vial plugged with cotton and given more substantial food. When available, small pieces of green cornstalk were used as food for these older larvae; at other times portions of green fennel plant or

string beans served as nourishment. *Chelonus* cocoons spun in the glass vials⁴ were left in the vials and placed in controlled temperatures for pupation and adult emergence.

The host larvae were kept at a constant temperature of either 68° or 77° F. The latter temperature was decidedly more favorable for the development of both host and parasite. Some parasitized larvae were also kept in an outdoor insectary during March, April, May, and June at Hyères, France. Under these last conditions, however, development of both the *Pyrausta* and *Chelonus* larvae was greatly retarded by cool and changeable weather.

OVIPOSITION

The female of *Chelonus* deposits her eggs within those of *Pyrausta nubilalis*. The eggs are laid singly, and as a rule only one is placed within an egg of the borer. At times, however, especially when an insufficient supply of host eggs is provided, a female will deposit a larger quota per egg. On one occasion 22 *Chelonus* eggs were dissected out of a mass containing only 5 eggs of the borer. Many later dissections of single *Pyrausta* eggs or newly hatched larvae have shown that more than one parasite egg was deposited in each. As many as 5 *Chelonus* eggs have been removed from one small host larva, and 2, 3, and 4 eggs per host egg have been observed at different times.

It is thought that the presence of several *Chelonus* eggs in a single *Pyrausta* egg means the death of all but one of them. It may be, however, that the eggs sometimes hatch while only one of the resulting larvae survive. This, of course, is often the case among internal-feeding hymenopterous parasite larvae. Never, during the course of great numbers of dissections, has more than one larva of *Chelonus* in any stage been observed.

Neither a preoviposition period nor mating is essential to egg laying. Upon emergence from the cocoon the female has within her ovaries a number of well-developed eggs which she will deposit at once if provided with host material.

It requires but a few minutes for a female of *Chelonus annulipes* in a small cage to locate a *Pyrausta* egg mass. Running about the cage, when she approaches within an inch or two of the egg mass she immediately senses its presence. This seems to excite her, and she waves her antennae rapidly about, drawing nearer to the eggs. The antennae are lowered, and with the tips flattened against the leaf surface they are pushed forward until they encounter the egg mass. The female then brushes the flattened tips of her antennae over the surface of the eggs, draws her body directly forward a short distance until her unsheathed ovipositor finds the spot just sensed by her antennae, and inserts her ovipositor vertically into one of the eggs.

During the actual laying of an egg the female stands over the host egg mass, her entire body quite motionless, the antennae extended straight out before her or bent slightly downward. The

⁴ Glass vials open at both ends and plugged with two cotton stoppers would be preferable to the ordinary vial open at only one end. It would then be easy, when a *Chelonus* larva is spinning its cocoon in the proximity of a cotton plug, to remove the cotton from the opposite end and take out the remaining vegetable matter (which quickly decays) without in any way disturbing the parasite larva.



Cocoon of *Chelonix ananipes*

first movements following the deposition of an egg are a withdrawal of the ovipositor and a slight vibration of the antennae, after which the female turns around or goes to the other side of the egg mass before repeating the process. This proceeding may go on for some time, until seemingly every egg in the mass has been parasitized or the female has deposited all of the mature eggs which her ovaries contained.

The characteristic feeling of the surface of the eggs with the antennae and the moving forward of the body just prior to oviposition have been mentioned by Pierce and Holloway (9) in speaking of the parasitizing of egg masses of *Laphygma frugiperda* by *Chelonus texanus*, and Luginbill (4) has similarly described the oviposition of the same species in eggs of *Laphygma*.

The time required for the deposition of an egg by *Chelonus annulipes* varies, but in the case of a regularly ovipositing female it lasts usually from 15 to 30 seconds. The process often consumes several minutes, however. One female on her first day of oviposition was observed to deposit 16 eggs, spending an average of 1 minute and 40 seconds at each deposition. A maximum of 4 minutes and 30 seconds was required for one deposition, and a minimum of only 20 seconds for another. One day later this same female averaged 15 seconds per egg. On another occasion she oviposited ten times, using an average of 28 seconds for each egg, while she required only 10 seconds for depositing each of 6 other eggs.

Pierce and Holloway (9) observed that "less than a minute" was required for *C. texanus* to oviposit within an egg of *Laphygma frugiperda*. A few seconds to one-half minute or more is given by Luginbill (4) as the length of time that the ovipositor of the same species of *Chelonus* is retained within a *Laphygma* egg, and Vickery (16) gives four seconds for the oviposition of the same species and host. Luginbill speaks of 1 female of *C. texanus* ovipositing 13 times in 35 minutes at a temperature of 72° F., and of another individual ovipositing eight times in 1 minute and subsequently five times in a like period of time, and records that on 2 occasions the act of oviposition required only about 5 seconds.

The writer is of the opinion that the first ovipositions of a female of *C. annulipes* are sometimes of slightly longer duration than are those which follow when the insect is regularly depositing her normal quota of eggs.

The female of this species will oviposit in *Pyrausta* eggs of all ages, from fresh to mature. Apparently the age of the host egg does not influence the choice of the female nor the development of the parasite. *Chelonus* have been reared to the adult stage from eggs deposited in host masses which varied in age from a few hours to five days.

Table 4 presents the data obtained in a study of the oviposition of a *Chelonus* female in host eggs of several different ages. A number of corn borer egg masses, each differing in the maturity of the embryo which it contained, were exposed at the same time and for a 24-hour period to a female parasite. The eggs from each mass were then carefully dissected and the parasite eggs counted. The data so secured, together with other information obtained, seem quantitatively sufficient to warrant the conclusions drawn in the above

paragraph. The distribution of the eggs was, of course, somewhat dependent on chance, as the female would usually utilize those host eggs which she first encountered and might deposit a considerable number of her eggs before searching for other host material.

TABLE 4.—Oviposition of one female *Chelonus annulipes* in *Pyrausta* eggs of different ages, 1930

Date	Age of <i>Pyrausta</i> eggs								Total	
	Fresh		1 day old		2 days old		3 days old		Host eggs exposed	Parasite eggs deposited
	Host eggs exposed	Parasite eggs deposited	Host eggs exposed	Parasite eggs deposited	Host eggs exposed	Parasite eggs deposited	Host eggs exposed	Parasite eggs deposited		
	Number	Number	Number	Number	Number	Number	Number	Number	Number	Number
Apr. 5.....	11	6	12	10	19	15			42	31
Apr. 6.....			14	6	19	16	39	28	63	50
Apr. 7.....	14	7	11	11	19	13	11	13	46	44
Apr. 8.....	11	1	15	11	18	20			44	32
Apr. 9.....	23	10	15	3			21	8	62	21
Apr. 10.....	11	16	21	10	21	7			53	27
Apr. 11.....	7	6	12	2	22	0	15	4	58	12
Total.....	77	40	100	53	109	71	80	53	366	217

The studies summarized in Table 5 tend to prove that the larval and pupal development of the parasite is not decidedly influenced by the age of the host egg in which the female oviposits. There was found little variation from the averages of a larval period of 23.2 days, a pupal period of 9.3 days, or a total larval-pupal period of 32.5 days in parasites resulting from oviposition in host eggs of different ages.

TABLE 5.—Effect of age of *Pyrausta* egg masses upon length of larval and pupal periods of *Chelonus annulipes* at 77° F.

Pyrausta eggs	Larval period		Pupal period		Average length of combined larval and pupal period
	Individuals	Average length	Individuals	Average length	
	Number	Days	Number	Days	Days
Fresh.....	8	26.5	5	7.2	33.
1 day old.....	6	23.0	3	8.3	31.3
2 days old.....	8	20.0	4	8.0	28.0
3 days old.....	8	25.4	2	11.5	36.9
4 days old.....	33	22.3	16	10.4	32.7
5 days old.....	3	21.7	3	10.3	32.0
Total or average.....	66	23.2	33	9.3	32.5

Observations made during the experiment just cited further confirm the conclusion drawn therefrom. Frequently the female was watched as she deposited a number of her eggs in an egg mass of a certain age and then passed to a second mass, or several others, more or less mature, and there continued her oviposition as before. An ovipositing female was even pushed with a brush from one egg mass to another of different age without interfering with the process of egg laying.

It has sometimes seemed to the writer that there existed a slight aversion on the part of the female to eggs which were within a few hours of hatching. It may be that the movements of the larvae within such eggs are distasteful to her. Females showed no inclination to oviposit in the newly hatched corn-borer larvae.

In an attempt to learn the egg-laying capacity of *Chelonus annulipes* an unmated female was confined in a small glass cage, kept at a room temperature of about 75° F., and supplied with a new mass of corn-borer eggs every 24 hours. The host eggs ranged in age from one to three days, and at the end of each day they were dissected for a count of the parasite eggs. As shown in Table 6 this female lived 25 days and deposited a total of 655 eggs in 22 days, or an average of 29.8 eggs per day. Her maximum daily oviposition was 65, and her minimum eight. After death her ovaries were dissected, and 156 well-developed eggs were found. Thus this female produced 811 eggs, and it was noted that her ovaries were still in excellent condition and oögenesis was going on at a normal rate.

TABLE 6.—Daily oviposition of unmated female¹ of *Chelonus annulipes* at room temperature, 1930

Date	Number of eggs	Date	Number of eggs	Date	Number of eggs
June 7.....	22	June 15.....	28	June 23.....	49
June 8.....	21	June 16.....	19	June 24.....	29
June 9.....	16	June 17.....	29	June 25.....	41
June 10.....	22	June 18.....	36	June 26.....	31
June 11.....	21	June 19.....	20	June 27.....	8
June 12.....	9	June 20.....	52	June 28.....	62
June 13.....	40	June 21.....	26		
June 14.....	19	June 22.....	65	Total.....	655

Average per day..... 29.8

¹ Emerged June 6; died July 1. No eggs oviposited during last 3 days of life.

The oviposition of four mated females of *Chelonus* on certain days is given in Table 7. The most striking point illustrated is the enormous number of eggs (165) deposited by female 3 on April 24. This parasite had not been supplied with host eggs during the previous nine days and the indication is that a considerable number of her eggs had matured within the ovaries and were ready for deposition at the first opportunity. On April 8 female 1 laid a total of 89 eggs.

TABLE 7.—Intermittent¹ oviposition of four mated females of *Chelonus annulipes*, 1930

Date	Eggs deposited by—			
	Female 1, emerged Mar. 17	Female 2, emerged Mar. 17	Female 3, emerged Mar. 28	Female 4, emerged Apr. 7
	Number	Number	Number	Number
Apr. 6.....		39	53	
Apr. 8.....		50	38	
Apr. 7.....	28	44	54	
Apr. 8.....	89	35		56
Apr. 9.....		21		
Apr. 10.....		25		20
Apr. 11.....		12		14
Apr. 15.....			35	
Apr. 24.....			165	

¹ On those days showing no oviposition host eggs were not exposed to the females.

Four other mated females, kept under laboratory conditions and provided with host eggs at intervals, deposited 231, 343, 393, and 273 eggs during life periods of 27, 72, 39, and 65 days, respectively. In no instance were the females in a position to oviposit continually, and all eggs exposed were not dissected. The figures only demonstrate that from 200 to 300 eggs may easily be deposited by a female whose capacity for egg deposition probably is twice as great, and whose life may be prolonged more than two months.

One *Chelonus* female was confined in a cage and supplied with host eggs daily from March 6 to 21. In Table 8 the results obtained are summarized. In all a total of 1,807 host eggs were exposed to parasitism, and a hatch of 63 per cent was obtained. Certain of the parasitized larvae which hatched were reared until the *Chelonus* issued, whereas others were dissected and the presence of the parasite noted. With such a procedure 12.4 per cent of the original *Pyrausta* larvae were definitely established as parasitized. This female lived 65 days.

TABLE 8.—Data on daily oviposition of one female¹ *Chelonus annulipes* in eggs of *Pyrausta nubilalis*, 1930

Date	Host eggs exposed	Age of host eggs	Host larvae hatched	<i>Chelonus</i> larvae issued from host larvae	<i>Chelonus</i> eggs and larvae dissected from host larvae	Total <i>Chelonus</i> produced	Parasitism of host larvae
	Number	Days	Number	Number	Number	Number	Per cent
Mar. 6.....	23	5	23	4	6	10	43.5
Do.....	174	4	134	25	6	31	23.1
Mar. 7.....	87	4	54	3	4	7	12.9
Mar. 8.....	87	4	54	4	0	4	7.4
Mar. 9.....	146	4	123	9	5	14	11.4
Mar. 10.....	119	2	68	7	3	10	11.4
Mar. 11.....	77	3	47	9	0	9	19.1
Mar. 12.....	92	1	40	0	2	2	5.0
Mar. 13.....	103	1	79	6	3	9	11.4
Mar. 14.....	116	3	46	1	8	9	19.6
Mar. 15.....	122	3	65	12	1	13	20.0
Mar. 16.....	98	3	56	13	0	13	23.2
Mar. 17.....	174	4	138	0	5	5	3.7
Mar. 18.....	63	5	24	2	1	3	12.5
Mar. 19.....	93	2	43	0	0	0	0
Mar. 20.....	110	2	68	0	0	0	0
Mar. 21.....	123	2	58	1	1	2	3.4
Total.....	1,807	* 1,138	96	45	141	12.4

¹ This female was mated, but the fact that all of her progeny reared to the adult stage were males strongly indicates that fertilization did not occur.

* Equals 63 per cent of the total number.

The material to which host eggs are attached does not influence the female in her impulse to deposit eggs. Females were observed to oviposit with equal readiness in unattached eggs or masses of eggs on leaves of dock or corn, or on paper.

It was also learned that the position of the host eggs does not affect oviposition by the parasite. Oviposition was effected equally as well in eggs placed horizontally on the bottom of a cage, upside down on the inner surface of the cage top, or hanging in a vertical position in the middle of the cage. All *Pyrausta* eggs in the field.

so far as their position on the leaves of the corn plants is concerned, may therefore be considered subject to parasitism by *Chelonus*.^{*}

LARVAL DEVELOPMENT

With *C. annulipes*, as with other hymenopterous parasites whose larvae feed internally, it is difficult to follow closely the larval development. Many daily dissections of parasitized host larvae of various ages are necessary, and in addition the individual differences in the size of each parasite larva as influenced by the variations in their host environment enter to complicate the problem. However, from a considerable number of dissections, coupled with a study of the parasite larvae in relation to body size, head width, molted skin, etc., a general idea of the advancement of the larva may be obtained.

Dissections of 46 *Pyrausta* larvae of different ages containing *Chelonus* parasites kept at a constant temperature of 77° F. showed the length of the larval stages to be approximately as follows: First stage, 15 days; second stage, 3 days; last stage (internal), 1 day; last stage (external), 1 day; total, 20 days.

It is true, of course, that a considerable individual variation occurs in the length of the stages, and the above figures are no doubt somewhat low for the development of first-generation parasite larvae in the field during June and early July, when the cool nights would tend to slow up growth. Probably the average length of larval life in the region of St. Giorgio di Nogaro in the first generation is between 20 and 30 days, those larvae developing latest making the most rapid growth in the more intense heat of midsummer.

The *Chelonus* larva of the second generation spends nearly nine months of the year in an advanced condition of the first-stage larva within the hibernating host. In both generations the last two stages seem to be of comparatively short duration.

In a study of the total larval period (all stages) in host larvae kept at a constant temperature of 77° F., data on 82 individuals showed the average larval period to be 23.2 days, with a maximum of 34 days and a minimum of 15 days.

In one lot, at this temperature, from which 66 *Chelonus* larvae issued, the average length of time elapsing between the deposition of the parasite egg and issuance of the larva from the host was 22 days. Pupation of 50 unparasitized host larvae reared at the same time, counting from the time that the eggs were exposed to oviposition by *Chelonus* until the pupae were formed, required an average of 28.8 days. In other words the *Chelonus* larvae left their hosts on an average 6.8 days earlier than the latter normally pupated.

Similar information on larvae reared at a temperature of 68° F. is more limited. This is due to the difficulty of rearing *Chelonus* at the lower temperature. At 68° the host itself grew more slowly, and to an even greater degree the development of the parasite was

^{*} It occurs to the writer, however, that under actual field conditions the female *Chelonus*, in an effort to escape the intense heat of the sun's rays, may remain much of the time on the shady under surface of the corn leaves and probably oviposits more in egg masses which are found on that part of the plant. Oviposition, under such circumstances would, for the most part, take place with the female parasite clinging to an under surface or in a partly vertical position. Should such be the case these conditions would be favorable to the propagation of the species, as most of the corn-borer eggs themselves are attached to the under surface of the corn leaves.

retarded. Mortality among both parasitized and unparasitized corn borers was also fairly high. In fact, out of a total of at least 150 *Pyrausta* larvae from eggs exposed to the parasite, less than 10 per cent survived at the end of two months, and last-stage *Chelonus* issued from only two of the surviving larvae. From time to time various host larvae were dissected, with results as given in Table 9. Some of the *Chelonus* larvae, more than 2 months old, had not advanced beyond the late first stage. Of the 2 full-grown larvae which issued, 1 had lived 35 and the other 51 days within the host.

TABLE 9.—Rate of development of larvae of *Chelonus annulipes* within host larvae kept at 68° F.

Parasite larvae observed	Age of parasite larvae when observed	Stage of parasite larvae when observed	Parasite larvae observed	Age of parasite larvae when observed	Stage of parasite larvae when observed
Number	Days		Number	Days	
1	14	Late first.	2	37	Late first.
1	15	Do.	1	42	Do.
1	17	Do.	1	51	Last, just issued from host.
1	19	Do.	1	58	Late first.
5	31	Do.	1	59	Do.
1	35	Last, just issued from host.	1	62	Do.
1	36	Late first.			

In rearing work it was found that *Pyrausta* larvae parasitized by *Chelonus*, after a certain amount of feeding on either string beans or fennel plant, usually left their food and surrounded themselves with a light web work of threads, soon became plump and more or less curved dorsoventrally, and developed an appearance similar to that of an undersized prepupa. Within 24 to 48 hours *Chelonus* larvae issued from such borers. The host larvae did not invariably leave their food before spinning up, and a few *Chelonus* issued from borers still in the tunnels of the plant upon which they were feeding. The excessive moisture present in the vegetable matter was no doubt responsible for the crawling out of the host larvae after the stimulus for further feeding had ceased.

In addition over 100 young *Pyrausta* larvae which had been exposed to parasitism by *Chelonus* during the egg stage, were isolated in vials and subjected to the temperature of an outdoor insectary at Hyères, France, during the period April 2 to June 30, 1930. Many of the nights during the above period were uncommonly cool and the daily temperature was often lowered by cloudiness and frequent rains. Under these conditions the growth of both parasite and host was slow, and (as indicated in Table 10) 70 days elapsed before a *Chelonus* larva issued from one of the hosts. Even after 88 days two of the parasite larvae were still in the late first stage.

ISSUANCE AND EXTERNAL FEEDING OF LAST-STAGE LARVA

Soon after its molt into the last stage, the larva of *Chelonus annulipes* (with the anal vesicle now withdrawn into the body cavity where it forms the hind intestine) makes with its mandibles an opening in the host integument and pushes its head and body segments through.

TABLE 10.—Rate of development of larvae of *Chelonus annulipes* within host larvae kept in outdoor insectary between April 2 and June 30, 1930, at Hyères, France

Parasite larvae observed	Age of parasite larvae when observed	Stage of parasite larvae when observed	Parasite larvae observed	Age of parasite larvae when observed	Stage of parasite larvae when observed
Number	Days		Number	Days	
1	53	Late first.	1	76	Last, just issued from host.
3	57	Do.	2	77	Do.
3	68	Late first, 1; second, 2.	1	79	Do.
1	70	Last, just issued from host.	2	88	Late first.
1	74	Do.			

Within the body cavity of the corn borer, the *Chelonus* larva has been lying with its head oriented cephalad of the host, and, just prior to issuance, at least, has had the ventral part of its body against the dorsal wall of the host larva.

According to the writer's observations it issues from the dorsal side of the host, and usually in the region of the first to third abdominal segments. The exact point of exit is apparently dependent upon the relation between the length of the parasite larva and that of the host larva. In 15 observations, issuance in 9 cases was from the region of the first or second abdominal segment and in the other 6 from a point near the third abdominal segment.

The parasite larva works its body out rather quickly. This is accomplished by a squirming motion assisted by a bending of the exposed segments back toward the posterior end of the host, thus forming a sort of fulcrum at the point of exit. All but the last one or two of the abdominal segments are withdrawn; these remain within the host until external feeding has been completed. However, the larva is able to continue its feeding if the anal segments are entirely freed.

As soon as most of the body segments are outside, the parasite makes an incision with its mandibles at some point near the caudal extremity of the host and begins its external feeding. Such feeding generally continues for about 24 hours, although it is sometimes finished sooner. The larva feeds in a curled position until the host has been entirely exhausted and nothing remains but the chitinous head parts and the empty skin. During the feeding the mouth parts are frequently withdrawn and fresh incisions made at other points of the host's body.

In one instance divergence from the usual method of issuance was noted. In this case the parasite larva came out on the dorsal side in the region of the sixth abdominal segment of the host larva, and finally was observed entirely free, feeding at the exit hole. It seems that this *Chelonus* larva issued so near the posterior end of the *Pyrausta* larva that on bending its body caudad of the host, it found no food. In an attempt to move in some other direction toward a source of food, its anal segments became dislodged, and the open exit hole provided an immediate feeding point.

Practically all of the blood and internal organs of the *Pyrausta* larva are devoured, and within the peritrophic membrane of a *Chelonus* larva that has just finished its external feeding are to be

found rather large pieces of the host tracheae, parts of the severed nerve ganglia, fat, blood cells, and other parts of the internal organs.

The effect upon the parasite larva of this external feeding is quite noticeable in the more rounded and plump contour of the body and a darkening of the contents of the peritrophic membrane from a pale-yellowish to a rather dark-brown color, which affects the general coloration of the larva.

SPINNING OF COCOON

The cocoon (plate 1) is constructed of slender white threads secreted by the silk glands of the last-stage larva, and pressed out through the external opening of the common silk duct located on the upper border of the labium. The spinning process is begun very soon after the completion of the external feeding of the last-stage larva, and the construction of the cocoon requires from 12 to 24 hours.

During the spinning the head of the parasite is moved back and forth and up and down, and the threads, at first attached to the surrounding medium, are gradually woven into a cocoon. The silk is stretched in various directions, and in its viscous state is attached at different points by the pressure of the mouth of the larva, after which it dries and hardens. Within the framework so designed spinning is continued, and more threads are added until the structure is so thick that one is able to see the larva only by transmitted light. The head capsule and cuticle of the last-stage host larva are more or less incased in the outer web work of the cocoon.

Without having fed externally upon the host larva, the last-stage larva of *Chelonus* appears unable to construct a cocoon. In one instance the newly issued larva was removed from the host before it had the opportunity to feed externally, and was placed in a cotton cell, where it lived for over a week. This larva apparently had the impulse to spin, and a considerable quantity of thread was pushed out of the opening of the silk duct. All of the thread, however, was amassed in a sort of ball in the head region of the larva; the parasite seemed incapable of moving its body to attach the thread in the formation of a cocoon.

If a *Chelonus* larva, after it has completed its external feeding, is disturbed in any way, it is unable to construct a cocoon. This has been observed numbers of times. Such larvae, when deliberately removed from their normal position in the silken web of the host and placed in a cotton cell, would spin a few threads but were never known actually to construct a cocoon. A similar reaction took place in the case of larvae which were moved about in vials at the time that they were ready to spin. Those larvae which were unable to spin their cocoons were never known to pupate normally.

Vickery (16) has observed that *Chelonus texanus* will not complete its cocoon unless the larva is inclosed in a cell. That species, however, sometimes pupated within an incompleated cocoon.

PUPATION

The pupa of *Chelonus annulipes* lies largely in the posterior two-thirds of the cocoon, with the tip of its abdomen more or less sub-

ed in the semiliquid larval meconium which is pushed against inside wall of the cocoon at its caudal extremity. It is the writer's opinion that the water content of the larval meconium is responsible for a degree of humidity within the cocoon which is beneficial to the pupa.

The pupal period actually starts upon completion of the last larval molt, which takes place from 12 to 24 hours after the casting of the larval meconium. For some hours previous the insect has been in the intermediate state of prepupa. With a parasite like *Chelonus*, however, it is not easy to determine by observation of the cocoon just when the prepupal stage has terminated and the last larval molt occurred. One is able, however, through the semitransparency of the cocoon, to see the cast meconium, and it is this point which for practical purposes has been taken to indicate the beginning of the pupal period. The time of actual emergence of the adult from the cocoon has been designated as the end of the pupal period, although, strictly speaking, the transformation from pupa to adult has actually taken place a short time before the exit of the parasite.

The lengths of the pupal period at several controlled temperatures, as given in Table 11, were determined from a study of 76 individuals upon which daily observations were taken.

TABLE 11.—Length of pupal period of *Chelonus annulipes* at various temperatures

Temperature	Pupae	Length of pupal period ¹		
		Average	Maximum	Minimum
° F.	Number	Days	Days	Days
64	10	23.0	28	21
68	20	20.4	24	16
77	46	9.5	14	5

¹ The pupal period is considered as the length of time between the casting of the larval meconium and the emergence of the adult from the cocoon.

The effect of temperature upon the development of the pupa is quite evident. The average lengths of the pupal stage at constant temperatures of 64° and 68° F. were 23 and 20.4 days, respectively, both periods being more than twice as long as the 9.5 days required at 77°. Maximum and minimum temperatures varied accordingly.

A low temperature of 46° F. serves to retard pupal development, and it has been strongly indicated that a too long exposure to such cold results in a high mortality. During the summer of 1929, 48 *Chelonus* cocoons containing prepupae or early pupae, collected in Italy and brought direct to Hyères, France, in cold storage, were placed in a refrigerator at a constant temperature of 46°. Examination of these cocoons one month and a half later showed that within 33 of them the pupae had become black and were well developed, while in 12 others they were still yellow and in an early stage. Three of the latter individuals had died as larvae without pupating. Twelve of the late-stage pupae were placed at a temperature of 77°, and two adults emerged a few days later.

At another time five individuals of *Chelonus*, as soon as they pupated, were exposed to a temperature of 46° F. Upon removal from this temperature one month and a half later the pupae with the cocoons appeared yellow and still in a comparatively early stage. They were placed at 77°, and two male adults emerged 7 days later. It may, then, be stated that the pupal period in a few cases, at least, lasted for approximately a month and a half, at 46° F. but that the total emergence under such conditions was poor. Many more quantitative experiments than the writer has been able to undertake are essential for the determination of the exact length of time that *Chelonus* pupae may be subjected to a low retarding temperature, and still allow a satisfactory emergence of adults when the cocoons are exposed to a higher temperature.

Daily observations were made on a number of *Chelonus* pupae removed from their cocoons after the completion of spinning and kept continually at a temperature of 77° F. The average rate of development was determined as follows:

First day. Meconium cast and parasite remains as prepupa for 12 to 24 hours. The prepupa is pale yellow in color, with the eyes showing a light brown. Best described as the stretched-out last-stage larva. It is quite motionless.

Second day. Skin of last-stage larva has been shed. Pupa light yellow in color. Brown eyes and ocelli can be seen.

Third day. Little change except a darkening of the brown of the eyes and ocelli. Differentiation of the pupal segmentation and a general darkening of the yellow of the body.

Fourth day. Further darkening of eyes and ocelli, and of body in general.

Fifth day. First thoracic segment darkening to a black color. Mandible tips light brown.

Sixth day. Head and all of thorax black. Mandible tips dark brown. Wings, antennae, and legs still white.

Seventh day. Abdominal sclerites also black. Upper part of legs darkening. Drop of dark yellow fluid excreted in anal end of pupal skin.

Eighth day. Pupa all black except soft light yellow abdomen.

Ninth day. Adult issues from pupal skin and casts pellets and pupal meconium.

It is also of interest, as well as of certain practical value, to be able to estimate the development of the pupae of *C. annulipes* from an examination of the cocoons. This may be accomplished by viewing the color of the pupa through its cocoon. In Table 12 are listed the writer's observations on 14 cocoons kept at a constant temperature of 77° F. and examined daily during the entire pupal period. On an average, the pupa of *C. annulipes* appeared pale yellow in color for five or six days after the casting of the larval meconium. In three instances the pupa remained in this condition for a maximum of seven days, while in two cases it became black on the fourth day.

It was found that from the day when the pupa appeared black, an average of 6.7 days elapsed before the emergence of the adult insect from its pupal skin. This period, in the case of one individual, required a maximum of eight days and in another a minimum of only five days. Seven days were needed in each of six of the observations.

emergence.—Approximation of pupal development within the cocoon of *Chelonus annulipes* at a constant temperature of 77° F.

Individual No.	Period from casting of larval meconium until pupa appears black through cocoon	Length of period from time pupa appears black through cocoon until emergence of adult	Total length of period from casting of larval meconium to emergence of adult
	Day	Days	Days
1.....	Fifth.....	7	12
2.....	Fourth.....	5	9
3.....	Fifth.....	6	11
4.....	Seventh.....		
5.....	do.....		
6.....	Sixth.....	7	13
7.....	do.....	8	14
8.....	do.....	6	12
9.....	Fourth.....	7	11
10.....	Fifth.....	7	12
11.....	Sixth.....	7	13
12.....	do.....		
13.....	Seventh.....	7	14
14.....	Fifth.....		
Average.....	Fifth-sixth.....	6.7	12.1
Maximum.....	Seventh.....	8	14
Minimum.....	Fourth.....	5	9

It should be borne in mind, however, that the writer's figures are based only on cocoons kept at a constant temperature of 77° F. Higher or lower temperatures would tend to shorten or lengthen the pupal period, and consequently affect the appearance of the pupa.

Nevertheless, daily observations on pupae under definite conditions will give some idea of development. For instance, yellow pupae indicate an early stage, and black pupae show an advancement which will soon result in adult emergence. When the antennae and legs of the adult are seen to be free from the pupal skin and slight movements of the insect are taking place, it is certain that the pupal skin is nearly or entirely shed and that the adult will emerge soon. Shortly before emergence the adult usually moves somewhat forward in the cocoon and voids a number of small spiral pellets of excretory material and a small pupal meconium containing, for the most part, the broken-down mid-intestine of the last-stage larva.

EMERGENCE OF ADULT

When ready to emerge, the adult *Chelonus* tears with its mandibles an irregular opening near the anterior end of the cocoon through which it forces the body. Behind, in the other extremity of the cocoon, it leaves the molted skin and the cast meconium of the last larval stage. The adult after its exit from the cocoon is quite dry and at once moves about in a lively manner.

The following observation of the emergence of a male *Chelonus* made under the binocular microscope is typical of the procedure:

Through the somewhat transparent texture of the thin, white cocoon can be discerned the black adult with its abdomen pulled slightly away from the cast meconium and its head not far from the anterior end of the cocoon wall. The antennae and legs have been freed from the body and frequent movements of these appendages occur. The legs are more or less doubled under the body

and the insect pushes itself forward on its "knees" (joints of the femur and tibia) until its head rests close against the wall of the cocoon.

At this time, just 25 minutes after the start of the observation, the adult manifests more activity and moves its head about in several directions while its legs, which are now more stretched out, push the body strongly forward. Within five minutes the two chitinous mandibles have begun to move and the actual cutting of the exit hole has commenced. The mandibles go back and forth, tearing away the threads of the cocoon and after two minutes they have pierced the texture and pushed themselves outside. The tearing process continues until the insect, still pushing forward on its "knees," is able to thrust the head through. The head is again drawn inside of the cocoon, however, and a little more tearing with the mandibles is carried on for about a minute before the entire insect emerges. The actual tearing process of the mandibles has lasted exactly seven minutes.

In experiments in which three lots of cocoons were kept at a temperature of 77° F., the emergence of *Chelonus* adults was found to be 51.5, 60.8, and 65.5 per cent, respectively.

OCCASIONAL ABNORMALITY IN ADULT

It has been observed that at times the abdomen of a freshly emerged adult of either sex is somewhat swollen, protruding slightly beyond the chitinous exoskeleton, and in certain lots this condition has been extremely prevalent. The proper interpretation of this unusual condition would be an interesting study. The limited observations of the writer lead him to believe that the factor responsible for such abnormal swelling of the abdomen is an inability of the insect to expel a sufficient amount of excretory material accumulated in the body during the larval and pupal stages.

Normally, near the time when the pupa within the cocoon becomes black, a drop of dark-yellow fluid is excreted from the anus. A few days later the adult breaks through the pupal skin and lies free within the cocoon for some hours before tearing its way out. During this latter period the parasite expels, in the form of a long spiral or series of small spiral filaments, a considerable amount of a pasty material, rather fine in texture and pale yellow in color. As many as 50 of these filaments have been counted within a cocoon from which the adult had just emerged.

At other times adults emerge with distended abdomens and, after making their exit, cast pellets for a few hours. Sometimes part of the material has already been voided within the cocoon. In either case such parasites soon appear as normal as those which emerge after casting all of the excretory material inside of the cocoon.

Finally there are those individuals with decidedly extruded abdomens, that have cast little or nothing inside the cocoon and are unable to void anything after their freedom. In these, the distention of the abdomen persists, the individuals are weak, and death soon results.

PROPORTION OF SEXES

Under normal field conditions, in both the first and second generations of *C. annulipes*, as they occur in northern Italy, the proportion of the male and female sexes is probably about equal. An examination of 58 individuals which emerged from first-generation material collected in the field at St. Giorgio di Nogaro in July, 1929, showed the presence of 28 males and 30 females. Out of a lot of 53 individuals of the second generation of 1929 which issued from host larvae

collected during the late fall in the same locality, 27 were of the male and 26 of the female sex.

D. W. Jones, of the United States Entomological Laboratory, Arlington, Mass., has also found that the males and females bred from similar material occurred in a 50-50 ratio.

COPULATION

The copulation of individuals of this species of *Chelonus* may be secured under ordinary laboratory conditions. Although mating has been obtained several times by placing the male and female in a small box cage exposed to strong light, this method as a rule has given poor and inconsistent results. Often the male was quite attentive while the female would refuse all attentions.

The most satisfactory means of procuring fertilized females, so far found by the writer, is to place the two insects of opposite sexes in a 4-inch glass vial and allow them to approach each other in the closed end, which is held toward a source of strong daylight in a well-heated room. Under such circumstances the male becomes excited and pursues the female with antennae vibrating and wings whirring. Almost immediately he climbs upon her back and makes contact of the genital organs. The male then loses all hold of the female except that of the genital parts and lies more or less on his back while the female pulls away from him. The act of copulation lasts from 30 to 40 seconds, after which the two insects separate.

Certain females, even under the conditions described above, positively refuse to mate and prevent all attempts of the male to mount by a raising of their wings and a rapid retreat. Such refusal on the part of the female has been observed when she was placed with males of different ages and on various days.

The male often shows great interest in the female and attempts copulation as he pursues her with antennae waving and wings vibrating rapidly whenever he comes within her immediate vicinity. In certain instances, however, the male appears quite disinterested. It has been observed that a male will mate with more than one female and with only a few minutes' interval between the copulations, and that the female will sometimes permit a second mating.

K. Bartlett, of the United States Entomological Laboratory, Arlington, Mass., in working with large numbers of *Chelonus*, has observed mating at temperatures ranging from 62° to 88° F., with the largest proportion taking place from 75° to 80°. He has found that, although mating might occur at any time of day, the females were most susceptible in strong sunlight, and that to obtain a large number of matings at one time it was best to have present a preponderance of males over females in a 4-to-1 ratio. It is his belief that females which are three days old mate most readily.

PARTHENOGENESIS AND NONFERTILIZATION

The unfertilized female of *Chelonus annulipes* will oviposit readily, and her eggs will develop normally. In all known instances, however, the progeny from such parthenogenetic reproduction were males.

In the case of the mated female on which data have been given in Table 8, there was found an indication that apparently normal copu-

lation sometimes results in nonfertilization. This female emerged on the afternoon of March 5, and on the following morning a male 23 days old was placed with her. No interest was manifested on the part of either sex, and the male was removed. A younger male (only 6 days old) was then supplied, and after a few minutes copulation ensued. From the *Pyrausta* parasitized by this female during the following days, 49 adults of *C. annulipes* were reared, all of which were males. Although this is only an isolated case, it opens up a subject of considerable interest and one worthy of study.

REACTIONS OF ADULT

The adults of this species, being somewhat positively phototropic, are comparatively easy to handle in the laboratory. If, however, an individual is allowed to escape in a room some distance from lighted windows, it will pursue a zigzag course of flight toward the light and will come to rest several times on its way, sometimes in places that are somewhat shady or hidden. The tendency, though, is to approach the source of light. When isolated in a small globe cage, *Chelonus* shows little tendency to remain in that part nearest the light, but will walk or fly about in all directions and will often be found resting on the glass walls, at the bottom, or on the underside of the top of the cage.

The activity of the adult is largely dependent upon the temperature. At a steady cold of 46° F. the insect remains quiet a large part of the time. When subjected to constant temperatures of 64° and 68°, activity is increased, and at a temperature fluctuating around 68° a reasonable amount of activity is maintained. Under the last condition the parasite spends considerable time at rest, but moves about in search of food and water, or lingers over an egg mass depositing eggs. At a temperature above 68° it walks and flies about the cage much more rapidly than at the lower temperatures.

Like many other insects, the adult of *C. annulipes*, when suddenly disturbed, will "play dead." For example, when shaken from the top of the cage in which it is confined, the parasite will often land on its back or side with its antennae extended or bent back under the body, and will lie still as if dead. This motionless attitude is often maintained for several minutes, and in one instance the writer observed a female that remained perfectly still on her back for a period of nine minutes.

LONGEVITY OF ADULT

Normal individuals of *C. annulipes* are hardy insects and in optimum environment live for some time. In an effort to learn something of the relative length of life of the species, 90 freshly emerged adults at different times were subjected to various conditions of food, water, and temperature. Each individual, confined in a separate cage of the type already described, was given careful attention and observed daily until its death.

Table 13 presents the data resulting from such observations. The following remarks are explanatory of the tabulation. The temperatures of 46°, 64°, 68°, and 77° F. were electrically controlled and practically constant. The outdoor insectary used during February to May at Hyères, France, provided a rather cool temperature with normal daily fluctuations. Room temperature was that of the lab-

oratory where the average during the day was about 68°, becoming somewhat colder during the nights in the late winter and early spring months when the experiments were in progress. Food, in all cases, consisted of a half lump of dry loaf sugar placed on the cage bottom, and water was provided once daily in the form of drops on the inside of the glass walls of the cage.

TABLE 13.—Records of longevity of adults of *Chelonus annulipes* kept under different temperature and food conditions

Temperature	Length of life—									
	With no food or water		With food only		With water only		With food and water			
	Individ- uals	Aver- age	Individ- uals	Aver- age	Individ- uals	Aver- age	Individuals	Average for males	Average for fe- males	
° F.	Days	Days	Days	Days	Days	Days	Days	Days	Days	
46	7, 11, 13, 16	11.8	10, 11	10.5	14, 30, 33	25.7	15, 43	29.0		
64	2, 7, 10, 11	7.6	10, 12, 14	12.0	3, 10, 14	9.0	40, 51, 69	53.3		
68	5, 7, 9, 9	7.6	8, 9	8.5	5, 8	6.5	28, 37, 43, 69, 72	36.0	70.5	
77	3, 3, 3, 3, 5	3.4	4, 5	4.5	3, 4	3.5	9, 11, 130, 63	27.7	30.0	
Outdoor insectary	3, 6, 7, 8	6.0	10, 11, 13	11.3	10, 13, 14	12.3	59, 68	63.5		
Room	4, 7	5.5	6, 6, 8, 10	7.5	5, 6, 9	6.7	12, 14, 20, 22, 25, 29, 32, 39, 40, 41, 42, 43, 45, 46, 49, 65, 105, 172, 184	32.9	65.0	
Total male in- dividuals, number	23		16		16		27			
Average longev- ity for males, days		6.9		9.2		11.3		36.9		
Total female in- dividuals, number							8			
Average longev- ity for females, days									62.0	

¹ Females; all others are males.

The majority of the adults handled were males, and data were obtained on only eight females, all of which received both food and water. The life of these females kept at 68° F., at 77°, and at room temperature, varied from 30 to 84 days. The latter figure, attained at room temperature, was the maximum longevity for either sex under any given condition.

It is probably true in the case of this parasite, as in that of many others, that the longevity of the female exceeds that of the male insect (when both receive nourishment), and the data would seem to confirm this. In two instances the average longevity of the female was practically twice that of the male. For example, at 68° F. the average length of life of 3 males was 36 and that of 2 females 70.5 days, and at room temperature the average longevity of 32.9 days for 14 males, as compared with that of 65 days for 5 females. At 77° one female lived 30 days, whereas the average life of three males at the same temperature was 27.7 days. The maximum length of life for a male (at 64° with food and water) was 69 days.

Both food and water appear to be necessary for the prolongation of life longer than two weeks. With food alone or with water alone the longevity was somewhat greater than when neither was provided. Individual differences in this respect were not great, however, except in the cases of two individuals at the low temperature of 46° F. which lived 30 and 33 days, respectively, when water alone was supplied them.

Temperature did not play as important a part in relation to adult longevity as might have been expected. Perhaps the most noticeable evidence of its effect was in the shortening of the life of individuals kept at a temperature of 77° F., without food or water or with but one of the two substances, and less appreciably under the same circumstances at 68°. On the whole a temperature of 46° for a very long period of time acts rather unfavorably on *Chelonus* adults, and the other extreme of 77° is not conducive, in all cases, to prolongation of life. Room temperature which, at the time, fluctuated around 68° was very favorable to the parasites when they were given nourishment.

EFFECT OF PARASITE ON HOST

Pyrausta eggs parasitized by *Chelonus* hatch normally with those of the same mass which have not received any eggs of the parasite, and both parasitized and unparasitized larvae seem to develop at approximately the same rate until about the time they have reached the fourth instar. At this point the host larvae containing parasites are somewhat lighter in color (pale yellowish), smaller in size, (averaging 6 millimeters less in length and 1 millimeter less in width), and in general less robust than normal larvae of the same instar.

If the host larvae are of the first or summer generation, or are being reared under controlled laboratory conditions, those which are unparasitized continue their development into the fifth or last instar and pupate normally. On the other hand, those host larvae of the same generation which contain *Chelonus* are so retarded in growth that the parasites issue before the corn borers have entered the last stage.

In the case of the second or fall generation of host and parasite, the unparasitized larvae of *Pyrausta* molt to the fifth instar, but the borers infested by *Chelonus* remain in the fourth and do not equal in size the normal host larvae. These small parasitized larvae hibernate, and during the winter months it is easy to separate them, on the basis of size alone, from the normal overwintering borers. The results obtained from the separation of 87 "small" larvae out of a total of 1,166 overwintering host larvae from the field are given in Table 14. A total of 69 (or 79.3 per cent) of these isolated "small" larvae proved to be parasitized by *Chelonus*.

This possibility of isolating the small borers which are parasitized by *C. annulipes* from the others has a certain practical value, as during the packing of the borers for shipment the *Chelonus*-bearing larvae can be segregated in several boxes and receive special attention.

The reason for the smaller size of *Pyrausta* larvae containing *Chelonus* is not known. Whatever the causative factor, it undoubtedly exerts its influence during the early first stage of the parasite. Other host larvae from the same region may be parasitized by either

the ichneumonid *Inareolata punctoria* Rom. or the tachinid *Masicera senilis* Meig., but the presence of these parasites, except in rare instances, does not affect the size of the host larvae in any such way as does *Chelonus*.

TABLE 14.—Isolation, on the basis of size, of *Pyrausta nubilalis* larvae parasitized by *Chelonus annulipes* in 1930

Date	Lot No.	Total host larvae	Small host larvae isolated	Small host larvae from which <i>Chelonus annulipes</i> issued	Normal host larvae left	Normal host larvae from which <i>Chelonus annulipes</i> issued	Parasitism
		Number	Number	Number	Number	Number	Per cent
Feb. 27.....	1	306	28	25	278	2	8.6
Do.....	2	248	19	13	249	2	5.8
May 5.....	3	312	20	15	292	0	4.8
May 16.....	4	280	20	16	260	0	5.7
Total.....		1,166	87	69	1,079	3	6.2
Percentage of total.....			7.5	79.3	92.5	0.3	

¹ Of the total number of *Chelonus* secured from these 4 lots, 95.8 per cent issued from the isolated small larvae and 4.2 per cent from the normal larvae left in the main lot.

The general activity of a *Pyrausta* larva parasitized by *Chelonus*, even for a short time after it has reached its maximum growth as a small larva, does not appear to differ from that of the normal unparasitized host. This may be due to the fact that until that time the parasite larva has been in its first stage. Growth has been rather slow, and the feeding of the parasite larva has probably not been sufficient to noticeably weaken the host. The increased consumption of food by the larger and faster growing second-stage and third-stage *Chelonus* larvae reduces the vitality of the host, however, and during the later part of the parasite's internal existence the host larva moves about sluggishly. It then incloses itself within a light cocoon as if preparing for pupation. Within this cocoon the host larva appears rather plump, the body lies motionless and curved somewhat dorsoventrally, and it has much the appearance of the prepupal state. In about 24 hours after such a condition has been reached the parasite larva issues and begins its external feeding.

The host larva, immediately after the *Chelonus* has issued and even before external feeding has commenced, is to all appearances in a lifeless state, and its body is shrunken and flabby. This is true in spite of the fact that the parasite larva has not yet devoured any of the vital organs of the borer.

The result of the external feeding of the parasite larva is the consumption of the entire contents of the host's body until nothing remains but the cuticle and the chitinized head parts.

FORCED ISSUANCE OF PARASITE LARVA FROM HOST

The method of supplying contact moisture to the overwintering host larvae by frequent soakings in order to force pupation has an equally favorable effect upon the late first-stage larvae of *Chelonus* within the borers in causing them to renew development and issue.

In Table 15 are shown the effects of soaking of the host larvae upon issuance of the parasite larvae at temperatures of 68° and 77° F. At the former temperature, between May 16 and June 14, it required an average of 24.6 days to get the parasite larvae to issue from the host, the minimum period being 22 days. At 77° F. between February 25 and March 26, an average of 17.6 days was necessary to cause the last-stage parasite larvae to issue. One *Chelonus* issued in a minimum of six days. At the same temperature, but later in the spring, between May 5 and 30, *Chelonus* larvae whose hosts were subjected to contact moisture issued in an average of 12.8 days. This shorter period among host larvae exposed to moisture later in the season coincides with the fact that it is generally easiest to break up the hibernation of borers which have been a long time in a dormant state.

TABLE 15.—Time required for larvae of *Chelonus annulipes* to complete development within and issue from overwintering larvae of *Pyrausta nubilalis* when the latter are isolated, supplied with contact moisture, and kept at constant temperatures of 68° and 77° F., 1930

Length of time after isolation and soaking	Chelonus larvae issuing from host larvae			Length of time after isolation and soaking	Chelonus larvae issuing from host larvae		
	At 68° F.		At 77° F.		At 68° F.		At 77° F.
	May 16 to June 14	Feb. 25 to Mar. 26	May 5 to 30		May 16 to June 14	Feb. 25 to Mar. 26	May 5 to 30
	Number	Number	Number		Number	Number	Number
6 days.....				21 days.....		2	
7 days.....				22 days.....	3	3	
8 days.....				23 days.....		1	
9 days.....				24 days.....		1	
10 days.....				25 days.....	2	1	1
11 days.....				26 days.....			
12 days.....		3	6	27 days.....	1		
13 days.....		1	1	28 days.....			
14 days.....			3	29 days.....	1		
15 days.....			2	30 days.....		1	
16 days.....		2	1	Total.....	7	34	24
17 days.....		5	1	Average number of days.....	24.6	17.6	12.8
18 days.....		3					
19 days.....							
20 days.....		4	2				

SEASONAL HISTORY

In the Italian regions under consideration *Chelonus annulipes*, like its host, passes through two full generations annually. (Fig. 12.) After a hibernation period lasting approximately from the middle of September until early May, spent as a late first-stage larva within the body cavity of the host, development is resumed, and from the middle to latter part of May the last-stage *Chelonus* larva issues, feeds externally upon the host, and spins its cocoon.

Data on the development of 97 individuals of the overwintering second generation of *C. annulipes* in the spring of 1930 are presented in Table 16. According to these observations the first larva of the second stage appeared on May 15, the first last-stage larva on May 17, the first pupa (or cocoon) on May 27, and the first empty cocoon on May 29. During a part of the period from May 1 to June 12,

Chelonus parasites in all three larval stages and as pupae were found in the field. From May 27 to May 31 this was especially true. Spring pupation of the host, amounting to 2.3 per cent on May 1, reached 70.4 per cent at the end of the month.

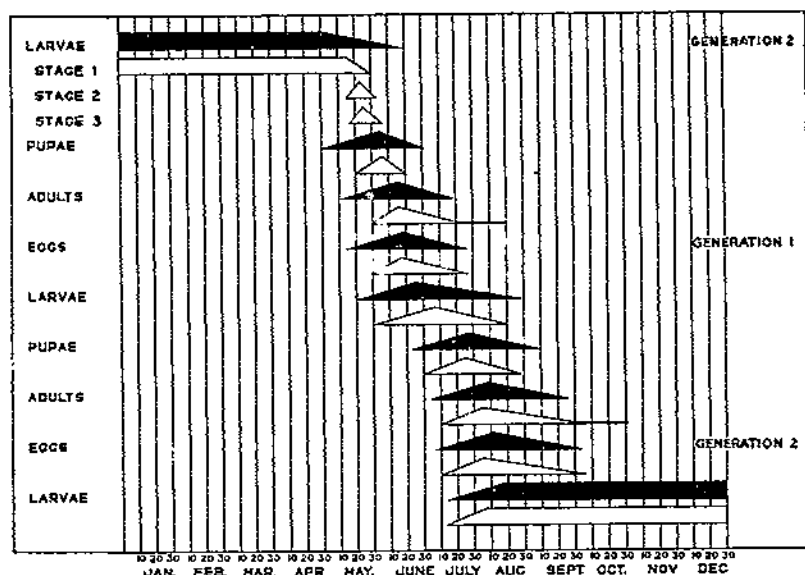


FIGURE 12.—Approximate relation between the seasonal history of *Chelonus annulipes* and its host *Pyrausta nubilalis*, determined from a study of all available data. Dark areas represent the stages in the development of the host and clear ones stages in the development of the parasite.

TABLE 16.—Spring development of 97 overwintering *Chelonus annulipes*, and comparison with host pupation at St. Giorgio di Nogaro, Italy, 1939¹.

Date	Total individuals	Condition of <i>Chelonus annulipes</i>						Pupa- tion of host
		Late first-stage larva	Second-stage larva	Last-stage larva	Early pupa	Late pupa	Empty cocoon	
	Number	Number	Number	Number	Number	Number	Number	Per cent
May 1.....	2	2						2.3
May 15.....	3	2	1					3.5
May 17.....	1				1			
May 18.....	2		2					7.6
May 22.....	1		1					10.8
May 27.....	25	8	5	2	8	2		25.9
May 28.....	15	3	6	1	2	3		27.3
May 29.....	8		2		4	1	1	35.4
May 30.....	12	1	1	7	2	1		42.9
May 31.....	8	1	1	1	3	2		70.4
June 2.....	5			2	2	1		
June 3.....	3				3			80.2
June 11.....	3				2		1	
June 12.....	9					8	1	

¹ Data taken on material collected from old cornstalks in the field.

Adult emergence begins the last of May, and continues into the third week of June, as indicated by a study of 32 individuals which were collected as cocoons in the field at St. Giorgio di Nogaro in

the spring of 1930 and from which the adults were reared under outdoor insectary conditions at Hyères, France. Table 17 shows the emergence obtained at Hyères. There seemed to be no marked difference in the time of emergence of the two sexes. The first empty cocoon in the field in Italy was found May 29.

TABLE 17.—Spring adult emergence of overwintered *Chelonus annulipes*, at Hyères, France, 1930

Date	Number of adults emerged			Date	Number of adults emerged		
	Male	Female	Total		Male	Female	Total
June 6.....	3	1	4	June 10.....	1		1
June 7.....	1		1	June 17.....		2	2
June 8.....		1	1	June 18.....			
June 9.....	1	1	2	June 19.....			
June 10.....		1	1	June 20.....	1	1	2
June 11.....		2	2	June 21.....	1	1	2
June 12.....	1	1	2	June 22.....			
June 13.....	1	1	2	June 23.....	2		2
June 14.....	2	3	5	Total.....	15	15	32
June 15.....	1		1				

¹ Includes 1 adult of undetermined sex.

The adults emerging in May and June are in the field during the oviposition period of *Pyrausta* moths in June and July and deposit their eggs during this time.

About the middle of July the full-grown larvae of the first generation of *Chelonus* issue from fourth-instar hosts and spin their cocoons within the tunnels of the borer. The maximum issuance of the *Chelonus* larvae and subsequent spinning cover a period of about a week, and by July 25 most of the parasites are in their cocoons. On July 29, 1926, a full cocoon was found at Piacenza, Italy, and from July 22 to 24, 1929, fresh cocoons were common in the fields around St. Giorgio di Nogaro.

In 1929 near St. Giorgio di Nogaro adult emergence of the first generation of the parasite was first recorded on July 24. On the following day 3.3 per cent of the cocoons collected in the field were found to be empty. A summary of the data upon early emergence for that summer is given in Table 18.

TABLE 18.—Early adult emergence of first-generation *Chelonus annulipes* at St. Giorgio di Nogaro, Italy, 1929

Date	Cocoons collected		Emergence	Pupation of host
	Full	Empty		
	Number	Number	Per cent	Per cent
July 22.....	101			24.8
July 23.....	146			25.0
July 24.....	194		(1)	23.9
July 25.....	204	7	3.3	37.5
July 26.....	578	15	2.5	24.0
July 27.....	417	21	4.8	57.6
July 29.....	361	10	2.7	51.9

¹ First record.

Further data upon emergence in this area were not taken, but it was evident, from the fact that the greater part of the cocoons collected in late July contained advanced pupae, that many adults would soon be in the field. It is therefore safe to say that during the first week of August the emergence of *Chelonus* reached its peak.

During the period August 1 to 9, inclusive, an assistant taking survey data in the "pump lands" around Piove di Sacco collected a total of 115 *Chelonus* cocoons. With the exception of two full cocoons found on August 2 and four others on August 5, all were empty, indicating a practically 100 per cent emergence in that region also, by the end of the first week in August.

The progress of host pupation as shown in the preceding table is evidence that *Pyrausta* moths would soon be out and depositing their eggs in the field. Further, in one field near St. Giorgio di Nogaro examined on July 27 the emergence of second-generation *Pyrausta* moths was found to be 31.4 per cent. While the number of moths in flight was perhaps somewhat less in several neighboring fields, it is certain that a considerable quantity of borer egg masses were available at the time *Chelonus* adults became abundant.

The longevity of *Chelonus* females would presuppose an oviposition period, in this second generation, extending to the time when all *Pyrausta* eggs in the field had hatched, or during the remainder of August and the greater part of September.

Chelonus larvae hatching in the fall pass through the earlier part of their first stage of growth, and then enter a condition of rest synchronous with the dormant period of the *Pyrausta* host larvae.

HYPERPARASITES

Chelonus annulipes itself suffers from the attack of other insect parasites. In one lot of 232 cocoons collected in Italy in 1929 the total hyperparasitism was 8.8 per cent, and in a collection of 1,432 *Chelonus* cocoons received from Italy the same year, D. W. Jones, of the Arlington, Mass., laboratory, found that 2.1 per cent produced hyperparasites.

Six specimens of *Eaeristes roborator* Grav., all small in size, one colony of chalcids determined as *Eupteromalus* sp., and several adults of another chalcid, *Hypopteromalus poecilopus* Cwfd., have been reared from cocoons of *Chelonus annulipes*.

METHODS OF COLLECTION AND SHIPMENT

During the latter week of July, 1929, cocoons of *C. annulipes*, most of which were freshly spun, were collected in the cornfields near St. Giorgio di Nogaro, Italy. The worker, provided with a cardboard box and a knife, examined two rows of corn at a time, observing the tassel and upper stem of each plant. Every tassel infested with *P. nubilalis* was carefully cut open and examined. If a *Chelonus* cocoon was found within the borer tunnel the corn stem was at once cut at a distance of about one-half inch on each side of the cocoon, and the green piece containing the cocoon put in the collecting box. Practically all of the cocoons were found in the tassels, and a maximum of six was at one time removed from a single tassel. Possibly parasitism was equally distributed among *Pyrausta*

occurring in other parts of the plant; it was not possible to procure data on this point. Later all the material so collected was examined by the writer and each parasite cocoon carefully removed from its position in the tunnel of the plant. The free cocoons were then placed in an ice box and kept until the end of the collecting season.

For shipment the cocoons were packed in small cardboard boxes, 50 to a box, and put within a large wooden box, which was transported in cold storage direct to the shipping point and dispatched to the United States Entomological Laboratory, Arlington, Mass.,^a by the first ship. During the trans-Atlantic passage the shipment remained in cold storage.

The collection of *Chelonus* of the second or overwintering generation in the same year consisted in gathering the host larvae within which the parasite passes the winter months. This was accomplished by the usual method of collecting *Pyrausta* larvae. A considerable number of workers were hired to cut the cornstalks brought from a field to a central station. All *Pyrausta* larvae and their parasites were saved for shipment. Those larvae parasitized by *Chelonus*, although smaller than the normal, were included with others which were put into round screened tin cans containing narrow strips of corrugated paper, into the holes of which the borers crawled, sealing them with thin silken webs. Such cans with about 400 host larvae so incased were packed in strong wooden boxes and shipped in cold storage to the Arlington laboratory. In future collections of the overwintering borers all of the small larvae parasitized by *C. annulipes* will be isolated in certain cans and given special attention.

SUMMARY

The braconid *Chelonus annulipes* Wesm., first discovered as a parasite of the European corn borer, *Pyrausta nubilalis*, in corn at Piacenza, Italy, in 1925, has since been found to be of economic importance over a somewhat restricted area near St. Giorgio di Nogaro and in the environs of Piove di Sacco, Italy. Parasitism of the first generation of *Pyrausta* in 1929 at the former point averaged 16.9 and at the latter 8 per cent, with a maximum of 28.6 per cent in one cornfield at St. Giorgio di Nogaro. *Pyrausta* of the second generation that year was much less parasitized; at St. Giorgio di Nogaro the average was only 3.5 per cent. The species, as a parasite of the borer, appears to occur over most of northern Italy.

The adult of this species, determined by C. Ferriere of the British Museum, does not have the more or less typically wasplike appearance of the other known hymenopterous parasites of the European corn borer. It is a black, robust insect with smoky colored wings and an abdomen protected by a single, hard, dorsally convex sclerite. The newly deposited egg is white, smooth, cylindrical, and arcuate. The first-stage larva is characterized by a pair of pointed, curved, chitinous mandibles, a considerable number of dorsal spines, and a partly evaginated anal vesicle. In the second stage the body appears smooth, the mandibles are lightly chitinized

^aFrom D. W. Jones, of the Arlington laboratory, it was learned that out of 1,432 cocoons of *Chelonus* received by him only 11 adults had emerged en route, and but 2 of this number were dead on arrival. From this shipment an emergence of 62.9 per cent was obtained.

and indistinct, and the anal vesicle is prominent. Open spiracles appear on the second thoracic and first six abdominal segments of the last-stage larva, and dorsally, on each of the abdominal segments 2 to 6, are grouped two sets of long brown spines. The mandibles of this stage are brown, well chitinated, and many toothed, and the head in addition possesses a number of characteristic spines and sensory organs. Within a glistening papery white cocoon the pupa, pale yellow for a few days, darkens to the black of the adult.

In general, the internal anatomy of the larva differs little from that of other braconids. In the last-stage larva, however, the arrangement of the integumentary muscles is not complex, and the fibers are not grouped into bundles, the silk glands are not greatly convoluted, and the Malpighian tubes are absent.

The female of *C. annulipes* deposits her egg in that of the host, and the larva passes through three stages within the growing borer. During its last stage the parasite larva issues from the fourth-instar *Pyrausta*, devours all remaining contents of the latter, spins a cocoon, and pupates.

At a constant temperature of 77° F., 2 days are required for the incubation of the egg of *Chelonus*; about 20 days are needed for the total larval growth; and pupation, at that temperature, takes an average of 9½ days. Higher or lower temperatures shorten or lengthen development of the parasite in all stages, and under field conditions it is probable that the egg-to-adult period covers about 40 days.

C. annulipes is easily reared in the laboratory. The female, whether mated or not, will usually start oviposition soon after emergence. Unmated females will reproduce parthenogenetically, the resulting progeny in all known cases being males. Both male and female adults, when given food and water and kept at various temperatures between 46° and 77° F., will live for some time. One nourished female at a fluctuating room temperature lived 84 days (a maximum life period for the species), and a similarly nourished male at a constant temperature of 68° lived 69 days.

In northern Italy *C. annulipes*, like its host, has two generations annually. It overwinters as a late first-stage larva within the fourth-instar borer and in early May resumes development. Pupation and emergence follow toward the middle and end of the month, and in early June a considerable number of adults are in the field to attack the eggs of the first host generation already present on young corn plants. The last-stage *Chelonus* larvae from this lot issue and spin their cocoons in the middle of July, and during the last week of that month and the early part of August the adults emerge and begin ovipositing in the *Pyrausta* eggs of the second generation. Both host and parasite of this generation, after a certain amount of growth, enter a dormant condition for the winter months.

The first importation of this parasite into the United States was made in the summer of 1929, and during 1929 and 1930 a total of 10,767 individuals were shipped from Italy. *Chelonus* are more easily procured during the winter months, when they occur as dormant late first-stage larvae within the hibernating host larvae. The adults are collected as they emerge the next spring.

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