E. W. B.

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Connecticut Agricultural Experiment Station

New Haven, Connecticut

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THE BIRCH LEAF SKELETONIZER

Bucculatrix canadensisella, Chambers

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The Biology of

THE BIRCH LEAF SKELETONIZER*

Bucculatrix canadensisella, Chambers

ROGER B. FRIEND

I. INTRODUCTION

The biology of *Bucculatrix canadensisella,* or, as it is more commonly called, the birch leaf skeletonizer, is known to only a very slight extent. Not only does the insect have peculiar habits and a specific structure, but its great abundance during certain years, coupled with its habit of feeding on native birches, renders it of interest economically as well as biologically. In the following pages are the results of investigations, made during the years 1924, 1925, and 1926, into its habits, reactions, distribution, history, and morphology. The work is not complete, but it is intended that the gaps shall be filled, in part at least, in the future.

I am indebted to Professor Alexander Petrunkevitch of Yale University and Dr. W. E. Britton of the Connecticut Agricultural Experiment Station for criticism of the work; to Professor G. C. Crampton of the Massachusetts Agricultural College for assistance in certain details of the morphological part; to Messrs. A. B. Gahan, R. A. Cushman, and C. F. W. Muesebeck of the United States Department of Agriculture for determining the species of parasites; to Dr. Annette F. Braun of the University of Cincinnati for some notes on the geographical distribution; to Mr. C. B. Hutchings of the Entomological Branch, Canada, for the use of an unpublished manuscript, and to Mr. B. H. Walden of the Connecticut Agricultural Experiment Station for the photographic work.

II. HISTORY

The earliest reference to the genus *Bucculatrix* is found in the first volume of de Geer's "Mémoires," in which is given the life history of a "little caterpillar with sixteen legs, smooth, green, which feeds on the lower side of the leaves of Frangula." It was the manner in which this caterpillar spun its cocoon which attracted the attention of de Geer, as the following extract from his

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* This paper is a dissertation presented in partial fulfillment of the requirements for the degree of Doctor of Philosophy at Yale University.

"Mémoires" shows: "Quand elles sont parvenues à leur juste grandeur, ce qui arrive dans le mois susdit, elles filent contre les feuilles mêmes de trés-jolies petites coques alongées. qui meritent extrèmement d'être connues, à cause de leur figure particulière. Ce sont ces coques qui m'ont déterminé à donner l'histoire de ces Chenilles." He gives a detailed description of the manner in which the cocoon is woven, and also gives brief attention to the pupal and adult stages. There is a plate of illustrations of the larva, the structure of the cocoon, the adult, and the injury to the plant. The species described was *Bucculatrix frangulella* and the host plant, *Rhamnus frangula,* the buckthorn.

In 1832 de Haan published a posthumous volume of Lyonet's works in which there is a description of a "chenille extrèmement petite, mais qui emploie une adresse inconcevable à se filer une coque cannelée." This description formed part of a letter from Lyonet to Réaumur written December 22, 1744. and was later sent to the president of the Royal Society of London to be published if the society saw fit to do so. Most of the description is devoted to the details of the structure and weaving of the cocoon. In his illustrations Lyonet figures the larva, cocoon and its structure, and adult. The larvae were found by Lyonet on the leaves of the oak. This species was *Bucculatrix ulmella* Mann (Zeller).

The history of the genus up to 1862 is given by Stainton in his "Natural History of the Tineina." Linnaeus and Fabricius neglected it entirely, and in 1783 Goeze, in his "Entomologische Beiträge," gave the name *Tinea frangulella* to de Geer's species. Neither de Geer nor Lyonet gave names to the species they described. Retzius, writing contemporaneously with Goeze, and Villers six years later, both gave different names to the *Tinea frangulella* of Goeze. The next person after de Geer to describe a species of this genus was Haworth, who in 1829 in "Lepidoptera Britannica" described *Tinea cuculipenella* with the varieties *beta, gamma,* and *delta.* Stainton notes that although Haworth's descriptions are very vague, *beta* was probably *Bucculatrix boyerella, gamma, B. crataegi,* and *delta, B. ulmella* (Lyonet's species). Three years later, in 1832, appeared the posthumous volume of Lyonet's works, in which is described what proved to be *Bucculatrix ulmella,* as mentioned above. In 1834 Stephens translated Haworth's description of *Tinea cuculipenella* without mentioning the varieties *gamma* and *delta.* In 1833 Treitschke had redescribed de Geer's species as *Elachista rhamnifoliella,* and a new species, *Elachista gnaphaliella.* In 1838 Duponchel figured four species in his "Lepidoptères de France," in the genus *Elachista,* namely, *E. boyerella, E. rhamnifoliella, E. gnaphaliella,* and *E. hippocastanella.* In 1839 Zeller, in "Isis," placed the following species in section A of his genus *Lyonetia: L. rhamnifoliella* (giving reference to de Geer), *L. albedinella* (*boyerella* of Duponchel), *L. hippocastani* (*hippocastanella* of Duponchel), *L. cristatella, L. nigricomella, L. cidarella,* and *L. crataegi.*

In 1848 Zeller established the genus *Bucculatrix* with nine species, the descriptions appearing in "Linnaea Entomologica," volume III. The nine species, with the authors credited by Zeller, were:

1. *Bucculatrix cidarella* Tischer
2. *ulmella* Mann
3. *crataegi* Zeller
4. *boyerella* Duponchel
5. *gnaphaliella* Treitschke
6. *frangulella* Goeze
7. *hippocastanella* Duponchel
8. *nigricomella* Zeller
9. *cristatella* F. R.

The species *gnaphaliella* had been previously (1839) placed by Zeller in *Lithocolletis.* He included *Bucculatrix* in a group of leaf-mining moths possessing eye-caps. Much of the history of the genus from Zeller on does not concern us here and will be omitted. Stainton, from whose work much of the above information has been derived, listed in 1862 nineteen species of *Bucculatrix* of which he considered fourteen good and five doubtful. The fourteen were known in the larval form and their food plants were given. Twelve of the fourteen are described by Stainton very fully. This work covers practically all that was known of the genus up to the time of writing.

For the earliest described American species we must turn to the writings of Clemens, who, in the Proceedings of the Academy of Natural Sciences, Philadelphia, for 1860, published the descriptions of four new species of *Bucculatrix: B. coronatella, B. pomifoliella, B. agnella,* and *B. trifasciella.* These descriptions were again published in 1872 in a posthumous volume of the writings of Clemens, edited by Stainton. This volume also includes a description of the genus by Clemens. Chambers, in the Canadian Entomologist, volume V, 1873, described and mentioned nine American species of this genus and stated these to be all the described American species known to him. These nine are: *B. trifasciella* Clemens, *B. capitealbella* n. sp., *B. pomifoliella* Clemens, *B. obscurofasciella* n. sp. (possibly synonymous with *B. coronatella* Clemens), *B. luteella* n. sp., *B. agnella* Clemens, *B. packardella* n. sp., *B. coronatella* Clemens, *B. thuiella* Packard. Although Chambers considered his *obscurofasciella* possibly synonymous with *coronatella* Clemens, Forbes (1923) gives *trifasciella* Clemens and *obscurofasciella* Chambers synonymous with *packardella* Chambers. It is not proposed to give a discussion of systematics and synonymy here, however. This briefly concludes the history of the genus in America up to 1875, when the species *canadensisella* was described.

In the Canadian Entomologist, volume VII, 1875, Chambers described *Bucculatrix canadensisella,* having received his specimen from Canada. This description (see page 401) concerns the adult only and does not mention the larva nor the larval food plants. *B. cidarella* of Europe Chambers considered close to *B. canadensisella,* although quite distinct. The larva of the European species *demaryella* feeds on birch, but according to the description given by Stainton (1862) it also is quite distinct from *canadensisella.*

For twelve years after the description by Chambers there occurs no mention of the species, but in 1887 Lintner recorded the occurrence of the insect in Monroe County, New York, where the larvae were very abundant on the leaves of *Betula lutea* during the fall of 1886. In 1890 Packard recorded what was in all probability this species on the leaves of the white birch at Brunswick. Maine. Lintner again reported it from New York in 1893, this time as injurious to all the native birches in the region of Ausable Forks during September, 1891. The same year Fletcher stated that all the birches around Ottawa, especially *Betula papyrifera, B. lutea,* and *B. alba* (European white birch) were severely injured. From this time on the reports of the insect become more frequent and the injury caused by its larvae more noticed. Hutchings published a brief life history in the 56th Annual Report of the Entomological Society of Ontario (1926), and this treats of the insect more fully than any other publication to date. The species is of some economic importance, and most of the literature on it concerns the injury done to the birch trees.

Systematically the genus has been neglected, and when mentioned it is referred to as aberrant. Forbes (1923) published a key to the species found in northeastern United States with descriptions. For descriptions of species discovered in the present century in America the writings of E. Meyrick, A. F. Braun, and A. Busck should be consulted; and for Old World species see the writings of E. Meyrick, especially his "Exotic Microlepidoptera."

The history of the insect is interesting in view of the fact that at frequent intervals it appears in extraordinary numbers and severely attacks birches over wide areas. In 1886 Lintner found it abundant in Monroe County, New York, and in 1887 it was reported as abundant in Massachusetts. During the years 1890, 1891, and 1892 a serious outbreak occurred in Ontario, New York, and New England. In 1901, 1902, and 1903 it was again very abundant and severely attacked birches throughout this same area. In 1907 a small outbreak occurred on Staten Island, New York, and in 1910 the insect was abundant at Kinderhook, New York.

In 1909 and 1910 birches in Minnesota were extensively skeletonized, and the insect's depredations were severe in Ontario in 1910, 1911, and 1912, and in New England in 1909, 1910, and 1911, growing less serious in 1912 and 1913. The third outbreak of this insect thus covered Ontario, Minnesota, and New England between 1909 and 1912, with small outbreaks in New York in 1907 and 1910. In 1919 the larvae were again beginning to appear in large numbers. This year they were abundant in New Brunswick and were noticed in Connecticut. In 1920 birches were heavily skeletonized and defoliated in Ontario, Quebec, and New Brunswick. In 1921 the infestation continued in these regions, and larvae were abundant in Minnesota and appeared commonly in Massachusetts. In 1922 the injury to birch trees was conspicuous over the Great Lakes region and in New England. This last outbreak began to subside in 1924, although the larvae were injurious in Quebec in 1925. Beginning about 1890 there have been four serious outbreaks of this insect, one about every ten years. Some of the possible reasons for this periodic abundance will be considered under the section dealing with predaceous and parasitic enemies.

III. Systematic Position

The genus *Bucculatrix* was placed by Zeller in a group of minute leaf-mining moths the adult antennae of which possessed eye-caps. Along with *Bucculatrix* were *Lyonetia, Cemiostoma, Nepticula,* etc. The first general treatise on *Bucculatrix* placed the genus in the Tineina (Stainton 1862). It is usually placed in the Lyonetiidae today and is so classified by Forbes (1923). There are, however, differences of opinion as to the classification of Lepidoptera and of this genus in particular. Thus Forbes places *Bucculatrix* in the family Lyonetiidae of the superfamily Tineoidea, but Mosher (1916) places it in the family Bucculatrigidae of the superfamily Gracilarioidea, basing her decision on pupal characters; and Fracker (1915) places it in the family Bucculatrigidae of the Tineoidea. The grouping of families and genera in the Tineina is still apparently an open question. The genus will here be placed in the Lyonetiidae according to the classification of Forbes and considered as slightly aberrant. For a taxonomic account of the genus and a key to the species of northeastern United States the work of this author may be consulted.

IV. Laboratory Methods

The life history data were secured by rearing individual larvae in glass jars or vials, each receptacle containing wet sand and a fresh birch leaf. Observations were made daily. Adults for oviposition records were caged over a birch twig in a celluloid cylinder with cloth ends. This permitted natural conditions of light and air. The leaves were examined daily with a glass and eggs were marked with a circle of black ink and numbered. Pupae were obtained by simply placing small pieces of heavy cardboard under the plant in a stock rearing cage. The larvae spun their cocoons on the under side of the cardboard. The pupae were kept in a box sunk in the ground until the early summer. Just prior to the period of emergence they were placed singly or in groups of five in glass vials plugged with cotton or in large gelatin capsules, the ends of which were perforated. This made observations on the emergence of adults a simple matter. All life-history studies were made in an out-door insectary. For dissecting fresh material, it was found best to cover the chloroformed specimen with a drop of thick shellac, add one drop of alcohol, allow to set a few minutes, and then immerse in saline solution. The shellac became pitchy and held the insect firmly, but at the same time it could be easily removed from the chitin. For studying the external morphology the insects were boiled in 10 per cent potassium hydroxide until clear and then stained in tetrabromfluorescic acid twenty-four hours. The chitinized plates stained deeply red, and the membranous cuticle a light pink. The body being clear, the internal skeletal structures were readily observed. For the temperature experiments the larvae were kept singly in glass vials or in test tubes, the receptacle in either case being plugged with cotton. The food material was kept fresh and unwilted. The individual insects in all cases were from miscellaneous field collections made in the vicinity of New Haven except where otherwise noted.

V. MORPHOLOGY

The morphological descriptions will be confined to the external appearance of the various stages and certain important anatomical details of the exoskeleton. The genital organs of the adult will be briefly mentioned as they are of considerable interest morphologically and have more or less influence on the external form. The internal anatomy is not further described here, but it is intended that a description of the anatomy and histology will be produced later.

The original description of the genus by Zeller (1848) is reprinted below.

Bucculatrix Zell.

Elachista Tr. Lyonetia ex p. Zell.

"Caput lanatum, comosum.
"Antennae breviusculae, conchula basali parvula instructae.
"Palpi nulli; os squamis epistomii tectum.

"Alae anteriores caudulatae; cellula discoidales acuta postice venulas 6 emittit; vena subcostalis longissime interrupta; subdorsalis simplex:
"posteriores lanceolatae; vena mediana in 3 ramos divisa, subdorsalis simplex.
"Tibiae posticae pilosae.
"Larva 16 pes supra epidermidem foliorum vivit; metamorphosis in folliculo affixo subit."

The presence of palpi will be brought out later, and the vein which Zeller calls "mediana" in the hind wing is designated in this paper the radius.

The following is the original description of *Bucculatrix canadensisella* by Chambers (1875):

Bucculatrix canadensisella n. sp.

"The ornamentation of this species differs from that of any other yet found in this country, and though allied to *B. cidarella* of Europe, it is still quite distinct.

"Head white. Tuft tipped with dark reddish brown, and the face faintly tinged with purplish fuscous. Upper surface of the thorax brown margined all around with white. Base of the fore wings white, followed by an oblique brown fascia, which is nearest the base on the costal margin, and is followed by an oblique white fascia; all of these are placed before the middle and are followed by a large brown patch which occupies the entire wing to the ciliae, except that it contains a white spot on the middle of the costal margin. The brown patch is margined before on the dorsal margin of the wing by a small tuft of raised brown scales. At the beginning of the dorsal ciliae is a white spot placed a little before, but becomes almost confluent with a longer white costal streak. Behind these streaks to the apex the wing is pale brown, with a darker velvety brown apical spot. Ciliae pale yellowish, with a dark brown hinder marginal line before their middle not extending into the costal ciliae. Hind wings pale fuscous. *Al. ex.* ⅜ inch."

A. ADULT

1. External Appearance

As both the above descriptions are rather brief, the external appearance of the adult is here given in a little more detail. By reference to plate XVII and text figure 12 the important markings can be easily followed. Sexual differences are slight and will be referred to in the description.

The general appearance of the adult in repose is shown in plate XVII. The head bears a dorsal tuft of rather long hair-like scales, the center of which is brown and the outer parts white. The "face" is covered with gray or brownish scales. When the insect is at rest the head is bent ventrally so that the labium touches the bases of the prothoracic coxae and the short tongue is curled and concealed between the latter. There are no maxillary palpi, and the labial palpi are very small and concealed beneath the head. The eyes are black and partly concealed by the scapes of the antennae which are expanded to form eye-caps. These eye-caps are white, and from the anterior border of each there extends down in front of the eyes curved slender scales which give the insect the appearance of having "shaggy brows." The pedicel of the antenna is short, and the flagellum contains 29 segments, each of which bears two whorls of brownish scales. The proximal segments of the flagellum have no scales on the ventral side. This "nude" area is usually considered sensory. The first segment of the flagellum (third of antenna) is longer than any of the remaining segments. The antenna is about two-thirds the length of the body and filiform.

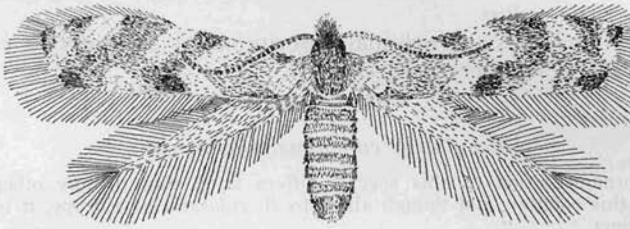

FIG. 12. Adult moth, enlarged about ten diameters.

The ground color of the fore wings is brown, and although typically reddish, it often varies to a yellowish. The wings are marked with transversely diagonal white bars as shown in figure 12. The basal bar is confluent with a white area on the mesothorax. The second bar forms an angle with the apex directed distally. It sometimes extends completely across the wing and is often interrupted in the center by brown scales. The remaining bars do not cross the wing but terminate near the midline. There are two extending from the costal border and one from the anal border, all three directed slightly apically. Close to the tip of the wing is another white area whose exact size varies somewhat in different individuals. It extends from the costal to the distal border of the wing but does not include the apex, this latter being dark, almost sable, in color. There are two other prominent dark spots on the wing, one at the anal angle and one at the distal margin of the second transverse white bar. Both of these are always present, and sometimes there are other dark spots on the costal border. Beginning slightly distal from the middle of the costal border a row of gray cilia extends around the wing almost to the proximal end of the anal border. The tuft of raised brown scales on the anal border of the wing as described by Chambers is usually conspicuous.

The hind wings are gray and their borders are almost completely ciliated. The superficial difference in shape between the fore and hind wings is due to the more extensive development of scales on the former. The scales on the hind wing are less numerous and do not project beyond the wing borders. Both the wings are really pointed.

The dorsal side of the thorax is brown with white areas laterally, these latter being confluent with the white basal areas on the wings. Each tegula bears a group of eight to ten bristle-like scales which extend along the costal border of the wing as far as the metathorax when the wings are folded. The pleural and sternal sides of the thorax are silvery-white. The coxae are large and of the same general color as the sternum of the thorax except that the lateral borders are brownish, particularly proximally. The femora and tibiae are brown laterally and white medially, as is the first tarsal joint. The tarsal joints two, three, and four each have a white ring proximally and a brown ring distally. The fifth tarsal joint is white, and its scales almost conceal the tarsal claws. At the posterior border of the mesothoracic tibiae at the distal end is a pair of spurs, and a pair of similar spurs is found at each end of the metathoracic tibiae. There is a pair of spines at the distal end of each of the first four tarsal joints. A row of thickly set long hairs is found on the anterior and posterior border of the metathoracic tibiae.

The abdomen is covered with silvery-white scales ventrally and brown scales dorsally. The males have seven segments superficially distinct on the ventral side, the second to the eighth inclusive, and the scales from the eighth practically cover the genitalia. The female has six segments superficially distinct ventrally, the second to the seventh inclusive. Scales from the seventh segment conceal the border between the seventh and eighth, and scales from the latter cover the remainder of the abdomen, giving the appearance of one broad segment. The ninth segment in the female is partly retracted within the eighth, and the tip of the ninth projects very slightly beyond the scales of the latter. The terminal fringe of scales on the male abdomen flares slightly but never does so on the female. The female abdomen is slightly larger than the male. On the dorsal side of the abdomen of each sex there are distinctly demarcated eight segments, the first to eighth inclusive.

The body length averages about three millimeters and the alar expanse seven millimeters. The sexes are of equal size.

2. Head (Text figure 13)

The head is somewhat compressed anterior-posteriorly, and the occipital surface is flat. The antennae are filiform and composed of 31 joints, of which the first or scape is expanded to form the eye-cap. The second joint or pedicel is short and subspherical. The third joint (first of the flagellum) is half again as long as any of those following. The length of the antennae compared

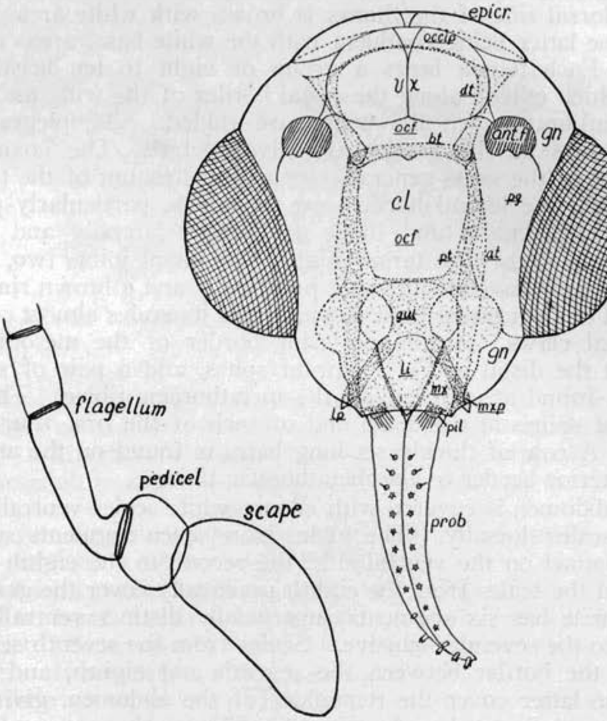

FIG. 13. Head and base of antenna of adult. *ant f*, antennal fossa; *at*, anterior arm of tentorium; *bt*, base of tentorium, *cl*, fronto-clypeus; *dt*, dorsal arm of tentorium; *epicr*, epicranium; *gn*, gena; *gul*, gular region; *li*, labium; *lp*, labial palpus; *mx*, maxilla; *mxp*, maxillary palpus; *occip*, occiput; *ocf*, occipital foramen; *pg*, postgena; *pil*, pilifer; *prob*, proboscis; *pt*, posterior arm of tentorium; *vx*, vertex.

The abbreviations underlined in the figure are on the posterior surface of the head.

with the body length is shown in figure 12. The eyes are black and weakly spherical. There are no ocelli. Between the antennal fossae (ant f) and connecting them is the suture which separates the fronto-clypeus (cl) from the epicranium (epicr). A suture running between the eyes and through the epicranium divides off the vertex (vx) anteriorly. The vertex bears the forward-projecting hairs of the dorsal tuft and is divided by a median light suture. The posterior part of the epicranium is likewise divided by a median suture and bears the upward- and backward-projecting hairs of the dorsal tuft. The occiput (occip) lies between the epicranium and occipital foramen and is not sharply demarcated from the postgenae laterally. The fronto-clypeus appears to extend laterally to the eyes. The labrum is not present as a distinct sclerite and is represented by a pair of pilifers (pil) placed one above each maxilla. There are no mandibles. The proboscis (prob) is reduced, being about the length of the head. Each half of the proboscis (the galea) bears on its anterior surface a row of eleven papillate projections which appear pentagonal in cross section and each of which terminates in a short peg. The particular function of these was not ascertained. Near the base of each half of the proboscis and also on the anterior surface are three or four setae. Near the base of each maxilla and projecting from the lateral side is a small protuberance (mxp) which may represent the rudiment of the maxillary palpus. The bases of the maxillae (mx) are, as usual with Lepidoptera, firmly fixed in the ventral (posterior in this case) side of the head. The labium (li) is a small triangular sclerite, with a forward-pointing apex, on the ventral side of the head and lies between the maxillae. It bears a pair of one-jointed palpi (lp). Between the labium and the occipital foramen (ocf) lies a gular region (gul) which is bounded laterally by the maxillae. Its separation from the labium is indistinct. The postgenae are separated dorsally from the genae (gn) by the suture which divides the epicranium and ventrally by the sutures connecting the maxillae with the lower border of the eyes. The genal regions are not distinctly separated from the fronto-clypeus.

The tentorium is similar to that of other Lepidoptera. The body of the tentorium (bt) separates the occipital foramen into a dorsal and ventral part. The anterior arms (at) come forward from the body and then turn ventrally to terminate at the ventro-lateral angles of the fronto-clypeus. The dorsal arms (dt) extend up from the body to the occiput, bordering the foramen laterally. The posterior arms (pt) extend down each side of the lower part of the foramen to the maxillae. In the figure of the head all the abbreviations of the parts on the posterior (morphologically ventral) side of the head are underlined.

3. Cervical Region (Text figure 14)

The head is supported by a pair of laterally placed cervical sclerites (cerv) which extend from the prothorax. At the cephalic end they meet the body of the tentorium, and at the posterior end they articulate with the episterna and then curve medially to meet in the midline.

4. Thorax

The three thoracic segments are distinct, although the prothorax is much reduced. The mesothorax is the most developed, due to the development of the fore wings and the powers of flight. In the following description the nomenclature of Crampton (1909) has been adhered to as far as possible.

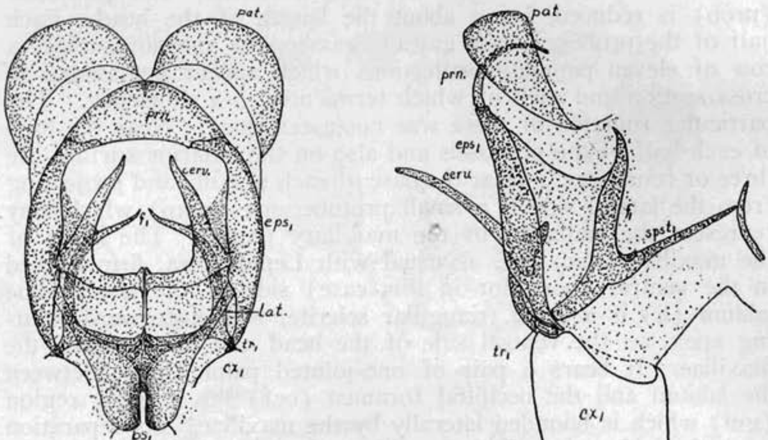

FIG. 14. Prothorax of adult, anterior (left) and lateral (right) aspects. *bs,* basi-sternum; *cerv,* cervical sclerite; cx_1, coxa; eps_1, episternum; f_1, furca; *lat,* precoxal bridge; *pat,* patagium; *prn,* pronotum; *spst,* spinisternum; tr_1, trochantin.

a. Prothorax (Text figures 14 and 15)

The tergal region of the prothorax consists of a central triangular pronotum (prn) and two laterally placed and conspicuous patagia (pat). The apex of the pronotum meets the prescutum of the mesothorax in the midline.

The pleural region contains one narrow sclerite, the episternum, (eps) which meets the pronotum above and the coxa (cx) below. Anteriorly it supports the cervical sclerites and meets the precoxal bridge (lat) of the sternum. There is a very minute sclerite, the trochantin (tr), at the articulation of the coxa. The epimeron is obsolete. From the posterior border of the episternum the pleural apodeme extends into the body cavity and meets the arms of the furca (f_1). Of the sternal sclerites the basi-sternum (bs_1) is the larger and extends laterally in the precoxal bridge to

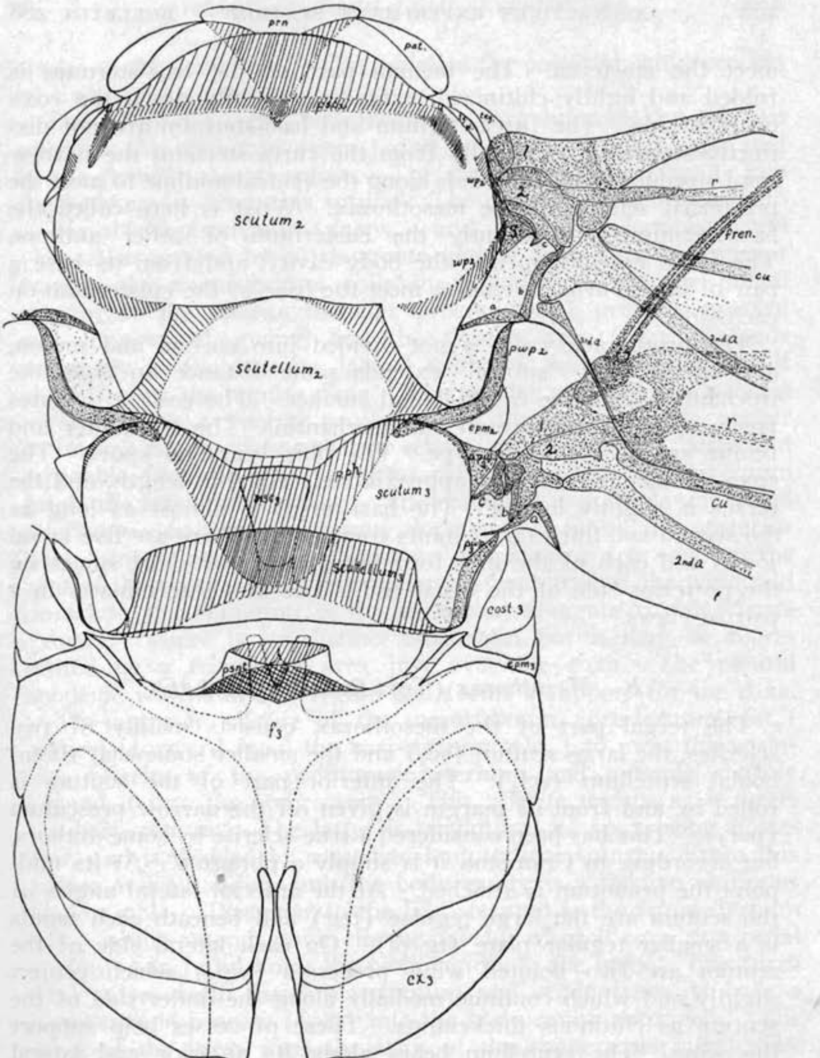

FIG. 15. Thorax of adult, dorsal aspect. *a, b, c,* axillary sclerites; *awp,* anterior wing process; *cost,* costal sclerite; *cu,* cubitus; *cx,* coxa; *epm,* epimeron; *f,* furca; *fren,* frenulum; *msc,* median area of scutum; *pat,* patagium; *pph,* postphragma; *prn,* pronotum; *psc,* prescutum; *psnt,* posterior chitinous plate on metathorax; *r,* radius; *teg,* tegula; *tg pl,* tegular plate; *wp,* wing process; *1, 2,* axillary areas; *2nd a, 3rd a,* anal veins. The inferior numbers indicate the thoracic segment to which the part belongs.

meet the episterna. The median part of the basi-sternum is folded and lightly chitinized, extending slightly down the coxa on each side. The furca-sternum and basi-sternum are not distinctly separated. Caudally from the furca-sternum the narrow spini-sternum ($spst_1$) extends along the ventral midline to meet the presternal sclerite of the mesothorax. What is here called the basi-sternum is apparently the eusternum of other authors. The furca extends up into the body cavity, and from its base a pair of lateral arms extend to meet the base of the episternum on each side.

The prothoracic coxa is not divided into eucoxa and meron, although a faint "suture" extends some distance up from the trochanter along the caudo-lateral surface. The coxa articulates freely with the episternum and trochantin. The trochanter and femur are of the usual type. The tibia bears no spurs. The coxa, femur, and tibia are approximately equal in length, and the tarsus is slightly longer. The basi-tarsus is almost as long as the second and third tarsal joints combined. There are five tarsal joints and each of the first four bears a pair of short spines on the posterior side of the distal end. The tarsus terminates in a pair of claws.

b. Mesothorax (Text figures 15 and 16)

The tergal part of the mesothorax consists mainly of two sclerites, the large scutum (sc_2) and the smaller somewhat rhomboidal scutellum (scl_2). The anterior part of the scutum is rolled in, and from its margin is given off the narrow prescutum (psc_2). This has been considered a true sclerite by some authors, but according to Crampton it is simply a phragma. At its midpoint the pronotum is attached. At the anterior lateral angles of the scutum are the large tegulae (teg) and beneath each tegula is a smaller tegular plate (tg pl). On each lateral side of the scutum are two pointed wing processes (wp_2) which project slightly and which continue medially along the under side of the scutum as chitinous thickenings. These processes help support the wing. The scutellum bears along its anterior and lateral margins a phragma which projects slightly into the body cavity. The posterior lateral angles of the scutellum continue out as the anal borders of the wings. From the posterior margin of the scutellum the large postphragma (pph) projects ventro-caudally into the body cavity. This phragma is made up of a layer from the mesoscutellum and one from the metathorax. The layers are easily separated. There is no true postnotum (or pseudonotum) present as a distinct sclerite. The curved process (pwp_2) which supports the anal area of the wing extends out from the lateral angles of the scutellum. This is called the posterior wing process by Snodgrass (1909).

The pleuron of the mesothorax is largely made up of two sclerites, the epimeron (epm_2) and episternum (eps_2) separated by the vertical pleural suture. The pleural apodeme extends into the body cavity from this suture. The episternum is divided into a dorsal anepisternum ($aneps_2$) and a ventral katepisternum ($keps_2$) separated by a triangular middle area. At its anterior margin the anepisternum rolls in medially. From the dorsal margin of the sclerite the alar process (alp) projects upward and supports the wing, and the tegular arm (tega) extends anteriorly to the anterior lateral angle of the scutum where it abuts against the tegular plate. The tegular arm and alar process together with a ventral projection on the anepisternum appear to form a single anchor-shaped sclerite fused with the latter and separable from it with no great difficulty. The katepisternum meets the sternum ventrally. The epimeron is a single undivided sclerite somewhat membranous dorsally. It meets the posterior wing process and then arches over as a narrow arm to meet the arm of the furca (f_2). Just under the anal area of the wing and dorsal to the epimeron is the somewhat elongate costal sclerite ($cost_2$). There is no distinct trochantin but it may be represented by a triangular area just over the coxa. The pleural apodeme widens at this region and forms a support for the coxa.

The anterior sclerite of the mesosternum (presternum. pst_2) projects forward from the basi-sternum (bs_2) to meet the posterior sclerite of the prothoracic sternum and extends slightly beyond it into the body cavity. This sclerite widens as it meets the basi-sternum. The latter is triangular, its apex being posterior, and is divided by a median longitudinal suture. From this suture and extending into the body cavity is a median chitinous blade (mbl). Posterior to the basi-sternum is the furca-sternum (fs_2) which extends down the medial side of each coxa as a pedal region (pdr_2) and holds the coxa rigidly to the body. The furca (f_2) arises from the furca-sternum and sends from its base a short curved process (fpr_2) into the body cavity anteriorly. The arms of the furca meet the arms of the epimera dorsally. The latero-sternites extend from the basi-sternum laterally to the pleural suture.

The mesothoracic coxa (cx_2) is divided into an anterior eucoxa ($eucx_2$) and a posterior meron (mer_2) by a vertical suture on the outer side. On the medial surface of the coxa lies a heavily chitinized angular plate (cs_2) which meets the pedal region of the furca-sternum. The leg articulates at the trochanter, the coxa being immovable. The tibia bears at its distal end on the posterior side a pair of spurs of which the outer is longer. The tarsus is similar to that of the prothoracic leg. The mesothoracic leg is slightly longer than that of the prothorax.

The wing venation (figure 17) is much reduced. The subcosta and costa are probably represented by the single costal vein. The radius (r) is rather faint at the base and gives off five branches distally. The median vein has disappeared except for the branches m_1 and m_2. The cubitus (cu) is single. There is a faint fold (1st a) which may represent the first anal vein. The second (2d a) and third (3d a) anals are distinct. There is some variation in the origin of r_4, as it sometimes branches off distally to the position shown in the figure. The costal vein bears a retinaculum (ret) for the frenulum. The veins named above are according to Forbes (1923).

The axial sclerites of the wing are as shown on the right side of figure 15. The sclerites a, b, c, 3, and the small sclerite between 1 and 3 are hard chitinous plates, but those marked 1 and 2 are thickenings of the wing similar to veins. The alar process of the pleuron abuts on 2, as does the anterior of the scutal wing-processes. The posterior of the two scutal wing-processes abuts on 3, and the posterior wing-process supports a. The anal area of the wing folds along the outer border of b.

c. *Metathorax* (Text figures 15 and 16)

The scutum (sc_3) of the metathorax is divided medially by a triangular area (msc_3). This does not appear to be a distinct sclerite but simply a more lightly chitinized region. The postphragma of the mesoscutellum is attached to the anterior margin of the scutum, its line of attachment extending to the wing process (awp_3) at the anterior lateral angles. The scutellum (scl_3) is a band stretching across the base of the scutum and appears to overlap the latter, due to the presence of a phragma which projects caudo-ventrally into the body cavity. From the posterior border of the scutellum a membrane drops ventrally to meet a chitinous arm which forms a bridge between the ends of the epimera. The center of this bridge bears a chitinous plate (psnt) to which the tergum of the first abdominal segment is attached. This represents the pseudonotum (Snodgrass), although much modified from a primitive condition. At its lateral angles the scutellum continues into a narrow posterior wing process (pwp_3) which supports the anal area of the wing.

The pleuron of the metathorax resembles that of the mesothorax. The trochantin area at the head of the coxa is more distinct here, however. Dorsally the alar process (alp) continues, directly with the pleural apodeme, and the anepisternum ($aneps_3$) bears another process which also supports the wing. The costal ($cost_3$) sclerite is prolonged anteriorly as a long arm. The epimeron (epm$_3$) extends further posteriorly than does the same sclerite in the mesothorax.

The sternum of the metathorax differs markedly from that of the preceding thoracic segment. From the central basi-sternum (bs$_3$) extend the narrow latero-sternites (not shown in the diagram). The basi-sternum extends caudo-ventrally to meet the furca-sternum (fs$_3$) at the coxal support. There is no pedal region of the furca-sternum, but the coxa is held rigidly by this sclerite plus the basi-sternum. The furca-sternum extends as a narrow arm dorsally and then divides into a furca (f$_3$). The anterior furcal process (fpr$_3$) is very large and the furca is heavy. Dorso-laterally the arms of the furca meet those of the epimera.

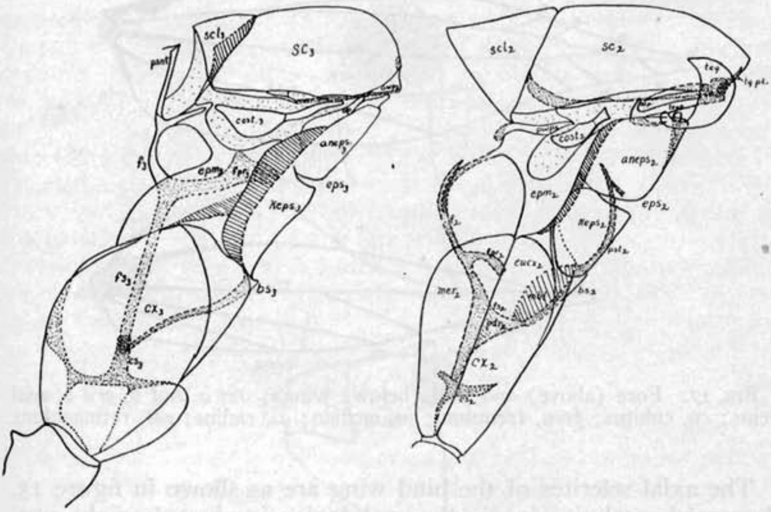

FIG. 16. Meso- (right) and meta- (left) thorax, lateral aspect; *alp*, alar process; *aneps*, anepisternum, *bs*, basi-sternum; *cs*, median coxal support; *eucx*, eucoxa; *fs*, furca-sternum; *fpr*, furcal process; *keps*, katepisternum; *mbl*, median blade; *mer*, meron; *pdr*, pedal region; *tega*, tegular arm; *sc*, scutum; *scl*, scutellum. For other abbreviations see figure 15.

The meron of the coxa is much reduced and occupies a posterior-medial position, only the eucoxa being visible laterally. The tibia bears a pair of spurs on the posterior side of each extremity, and the outer spur of each pair is the longer. The leg is otherwise similar to that of the mesothorax.

The wings (figure 17) show greatly reduced venation. There are, besides the costal, three principal veins, the radius (r), cubitus (cu), and the second anal (2d a), the median being represented by two branches only. The costal vein probably represents the combined costal and subcostal. The radius is single and from it there branch the two divisions of the median (m_2 and m_3). The cubitus is single. The frenulum (fren) consists of two stout setae that are held in the retinaculum of the fore wing.

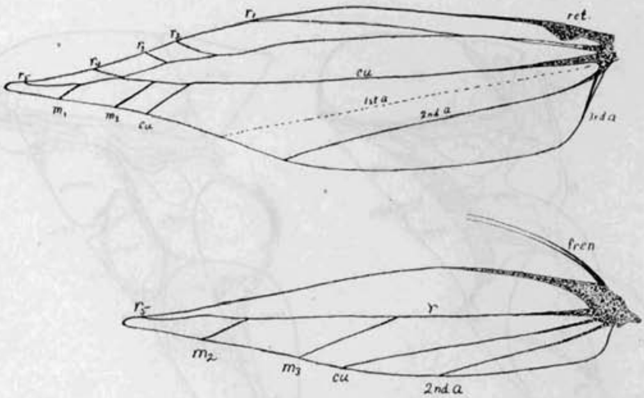

FIG. 17. Fore (above) and hind (below) wings; *1st a, 2nd a, 3rd a,* anal veins; *cu,* cubitus; *fren,* frenulum; *m,* median; $_{1\text{-}5}$, radius; *ret,* retinaculum.

The axial sclerites of the hind wing are as shown in figure 15. An angular sclerite (a) in the anal region is pivoted on the posterior wing process. The anal region folds along the outer side of this sclerite. Two sclerites (b and c) lie between this and the anterior wing process. These three constitute the chitinous axial plates homologous with those of the fore wing. The areas marked 1 and 2 are thickenings of the wing similar to veins and are homologous to the same areas of the fore wing. The sclerite c may correspond to 3 of the fore wing, and the sclerite b to b and c of the fore wing. The alar processes of the pleuron abut on the area marked 2, and the subcostal area (1) meets the anterior wing process and the sclerite marked c.

Snodgrass (1909) has described the typical arrangement of the axial sclerites in the wing, but the tracing of these in the wing here described is uncertain, due to the difference in arrangement, and hence the letters and numbers as given here do not correspond to those of the above author.

5. Abdomen (Text figures 18 to 20)

The abdomen has nine visible segments in the female and ten in the male, although in the latter sex the tenth is reduced to the socii. The apical segments in each sex are modified to form the external genital apparatus. The first segment has a strongly chitinized tergum, probably a development in accordance with its function of supporting the abdomen on the thorax. The sternum of the first segment is indistinguishably fused with that of the second and both are quite membranous. The identification of two sterna is furnished by the presence of two spiracles on each side.

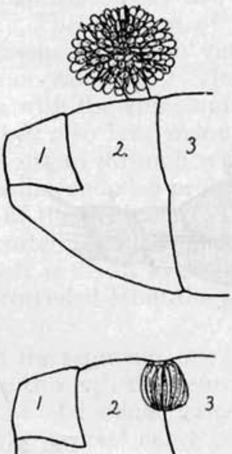

FIG. 18. "Alluring" organ on abdomen of adult male, expanded above, retracted below.

In the female the segments from two to seven inclusive are of the usual unmodified type, but in the male the second segment shows a peculiar sexual dimorphism. On the caudal margin of the tergum of this segment is located a protrusible organ which, for want of a better name, has been termed an alluring gland. Similar organs called alluring glands have been described as occurring on other parts of male Lepidoptera, and until a histological and cytological investigation is made of this particular case, the common term will be used in describing it. In other species of Lepidoptera there is considerable evidence that these organs give off a distinct odor when protruded, but the alluring function of these in a sexual sense is not definitely proved. This "gland" is shown in figure 18 protruded (above) and retracted within the abdomen (below). When retracted it folds in an eversible sac, and when protruded the entire organ, including the sac, projects out from the body, looking for all the world like a composite flower.

The scales composing it are of two kinds, some pointed and some lobular. This organ is found in all males and never in the females. The remainder of the male abdomen up to and including the eighth segment is in no wise unusual. In the female the eighth and ninth segments (figure 19) are modified somewhat. On the sternum of the eighth segment is a slight protuberance which marks the copulatory opening leading into the bursa duct and thence to the bursa copulatrix. At the end of the ninth segment is the external opening of the vagina (ventrally) and the alimentary tract (dorsally). Petersen (1900) has described in some detail the female and male genital organs of Lepidoptera and shows the transitional stages from the type having one genital opening (at the tip of the abdomen) to that having two as here found. The presence of two genital openings is forecast in the pupa. On each side of the copulatory opening is found a tuft of orange-colored scales, and a third tuft is found on the dorsum at the anterior margin of the eighth segment. These three tufts are normally concealed from view under the posterior margin of the seventh segment. The lateral apodemes from the ninth project back into the eighth segment. The tip of the female abdomen is usually telescoped so that the eighth segment is partly retracted within the seventh, and the ninth is retracted within the eighth. The posterior part of the eighth is membranous. In the illustration the abdomen is shown with these segments drawn out into view. The tenth segment is not developed.

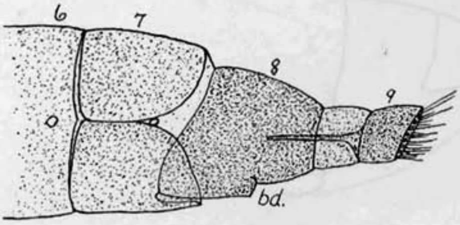

FIG. 19. Tip of abdomen of adult female. *bd*, opening of bursa duct.

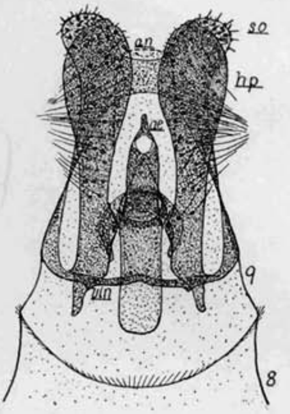

FIG. 20. External genitalia of adult male. *ae*, aedoeagus; *an*, anus; *hp*, harpe; *so*, socius; *vin*, vinculum.

In the male (figure 20) the ninth and tenth segments are much modified and are usually retracted within the eighth. As shown in the figure, they are drawn out to expose the external genitalia. The nomenclature given is according to Eyer (1924). The tergum of the ninth forms a "roof" over the anus (an) which lies just beneath it. It is called the tegumen. Attached to its distal end are the socii (so) which really belong to the tenth segment and form the anal armature. They are paired and bear many short spines and setae. The sternum of the ninth segment consists of a narrow chitinous band, the vinculum (vin), which is fused with the tergum on each side. The paired claspers, called harpes (hp), articulate with the vinculum and are appendages of the ninth segment. They also bear many setae and short spines. The cone-like chitinous organ through which the aedoeagus (ae) projects is called the anellus and also probably belongs to the ninth segment as do the rest of the genitalia. The aedoeagus is a heavily chitinized tube supported by the anellus and tapering to a point distally. The penis itself is a soft eversible tube contained within the aedoeagus and is protruded from the ventral side of the tip of the latter.

There are on each of the segments one to seven inclusive a pair of spiracles, and visible through the ventral wall of the abdomen are the four pigmented abdominal ganglia of the nerve cord. The ganglia of the entire ventral nerve cord of all stages of this insect are deeply pigmented and usually visible externally. In the adult the appendages conceal all but the abdominal, and these are found at the second segment and at the junctions of the third and fourth, fourth and fifth, and fifth and sixth respectively. The last is larger than the others, being a compound ganglion. The third and fourth abdominal ganglia are often contiguous and sometimes are fused to some extent.

6. Genital organs and alimentary tract (Text figures 21 and 22)

The internal genital organs of the male and female are diagrammatically illustrated in figures 22 and 21. In the female the bursa copulatrix (bur) is by far the most conspicuous of these organs, and it occupies much of the anterior part of the abdomen, lying in the region of the third segment. It is connected by a duct to the external opening in the sternum of the eighth segment, and from the dorsal side of this duct near its external end there arises the long slender seminal duct which permits the passage of spermatozoa from the bursa into the oviduct and thence into the seminal receptacle (rec sem). The common oviduct divides into two ducts (ovid) from each of which are given off four ovarioles (ov), each of which terminates in a filament. The filaments on each side unite with each other. The ovarioles extend from the oviduct along each side of the bursa to its anterior end, curve dorsally and posteriorly, then dorsally and anteriorly to a common point just above the bursa where the group from each side is attached by the filament tips to the dorsal wall of the abdomen.

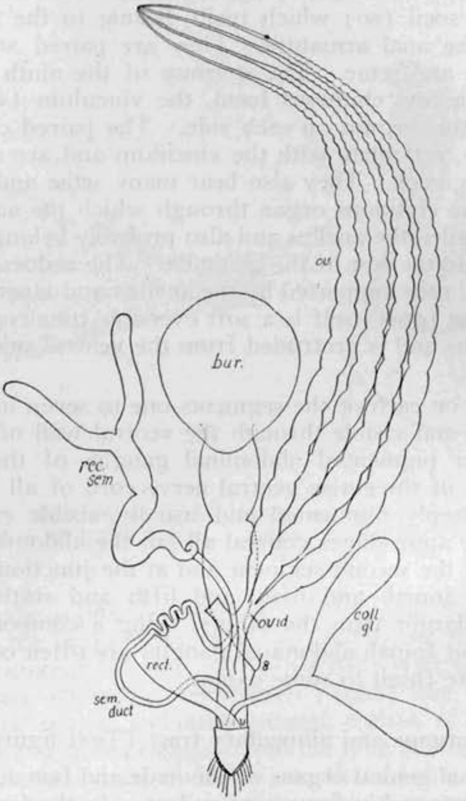

FIG. 21. Reproductive organs of female. *bur,* bursa copulatrix; *coll gl,* colleterial glands; *ov,* ovarioles; *ovid,* oviduct; *rec sem,* seminal receptacle; *rect,* rectum; *sem duct,* seminal duct.

The alimentary tract passes ventrally and to the right of the bursa, curves dorsally to pass above the union of the oviducts, then goes over the common oviduct to the tip of the abdomen, the rectum lying above the vagina. The ovarioles are of the polytrophic type, that is, the nutritive cells alternate with the ova. The seminal receptacle is bilobed and is attached to the dorsal wall of the common oviduct. The colleterial glands (coll gl) are paired and are connected by a common duct to the dorsal wall of the vagina. They secrete the adhesive substance which attaches the egg to the leaf. In the illustration the genital organs are shown spread out and not in their normal positions.

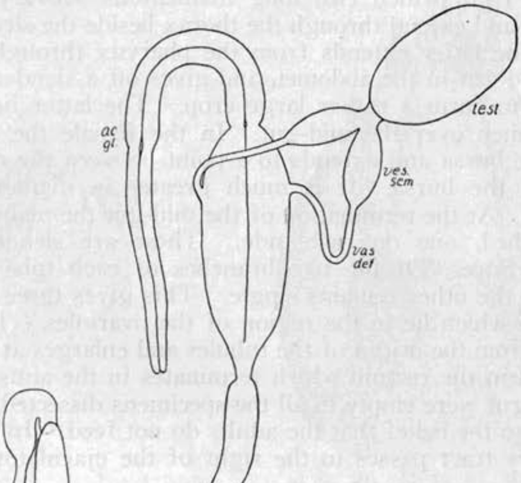

FIG. 22. Reproductive organs of male. *ac gl,* accessory glands; *aed,* aedoeagus; *ejac duct,* ejaculatory duct; *test,* testes; *vas def,* vas deferens; *ves sem,* seminal vesicle.

In the males the testes (test) are united and enclosed in a common scrotum. The vesicula seminales (ves sem) are paired and unite just under the testes. From the vesicula seminales, which are really enlargements of the vasa deferentia (vas def), the latter ducts pass to enlarged chambers which lead to the ejaculatory duct (ejac duct) which in turn terminates in the aedoeagus (ae). The accessory glands (ac gl) which presumably secrete a substance which mixes with the spermatozoa, are paired and are connected with the enlargements at the terminations of the vasa deferentia. In some insects these glands secrete a substance which forms the spermatheca (especially Orthoptera). They occur here attached to each other rather loosely.

The alimentary tract begins anteriorly in a large muscular pharynx from which two long filamentous salivary glands are given off and extend through the thorax beside the slender oesophagus. The latter extends from the pharynx through the thorax to the mid-gut in the abdomen and gives off a slender tube which enlarges to form a rather large crop. The latter lies mainly in the abdomen over the mid-gut. In the female the mid-gut lies under the bursa and extends to a point between the common oviduct and the bursa. It is much greater in diameter than the pharynx. At the termination of the mid-gut the malpighian tubes are attached, one on each side. These are slender and each branches once. Of the two branches of each tube one divides once and the other remains single. This gives three branches of each tube which lie in the region of the ovarioles. The hind-gut extends from the origin of the tubules and enlarges at its posterior end to form the rectum which terminates in the anus. The crop and mid-gut were empty in all the specimens dissected, which adds evidence to the belief that the adults do not feed. In the male the alimentary tract passes to the right of the ejaculatory duct.

B. The Egg (Text figure 23)

When first laid the egg is a translucent white, but it becomes more opaque after a few days. In shape it is flatly ovoid, and the longest diameter is 0.25 mm. It is made to stick to the leaf by an adhesive substance which surrounds it on the leaf surface in a narrow encircling band. The hexagonal sculpturing of the surface is quite distinct, and the micropyle occurs close to one end. When it leaves the oviduct the egg is soft and flexible, and its shape changes from approximately spherical when it is placed on the leaf surface. The eggs are always laid singly and scattered over the leaf, as shown on plate XVII.

C. Larva (Text figures 24 and 25)

When first hatched the larva is minute (.35 mm. long), translucent, apodous, and flattened, a typical leaf-mining type. When it leaves the mine at the close of the third instar it has assumed a cylindrical form, the head has shifted from its former horizontal plane to a plane nearly at right angles with the body, and all the legs are present and functional. It measures about 2.5 mm. in length. When fully grown (plate XVII) the larva is about 6.0 mm. long and yellowish green in color with the setae on white tubercles. The prothoracic shield is not conspicuous. The head is brown and typically that of a leaf-eating larva. There are the usual prolegs on abdominal segments, three, four, five, six and ten.

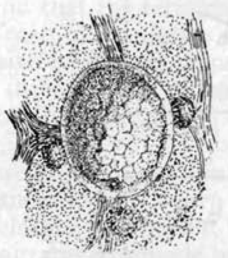

FIG. 23. Egg, much enlarged. Actual longest diameter .25 mm.

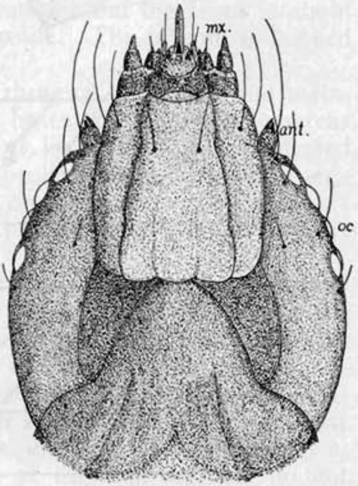

FIG. 24. Head of larva of 5th instar, ventral aspect. *ant*, antenna; *mx*, maxilla; *oc*, ocellus.

The radical change in structure which occurs at the second molt is due to the change in feeding habits and environment of the larva, for the third instar comes out of the mine to the leaf surface. This necessitates the acquisition of legs and the shifting of the plane of the head. The dorsal part of the head capsule is longer than the ventral, and this makes the posterior margin of the epicranium in the leaf-mining instars, where the head is horizontal, push back into the prothorax. Trägårdh (1913) has described structural transitions in several leaf-miners which change their feeding habits. The third instar resembles the fourth and fifth in general, but the setal pattern is somewhat different and there are fewer crochets on the prolegs. The prolegs of the abdominal segments three to six inclusive have one transverse row containing two crochets, and the prolegs of the anal segment bear one crochet.

The fourth instar is like the fifth except for size and no further mention need be made of it. The fifth instar is a typical caterpillar with the mouth-parts well developed. These are shown in a ventral view in figure 24. The antennae are minute, and there are only five ocelli (oc) present on each side. They are arranged

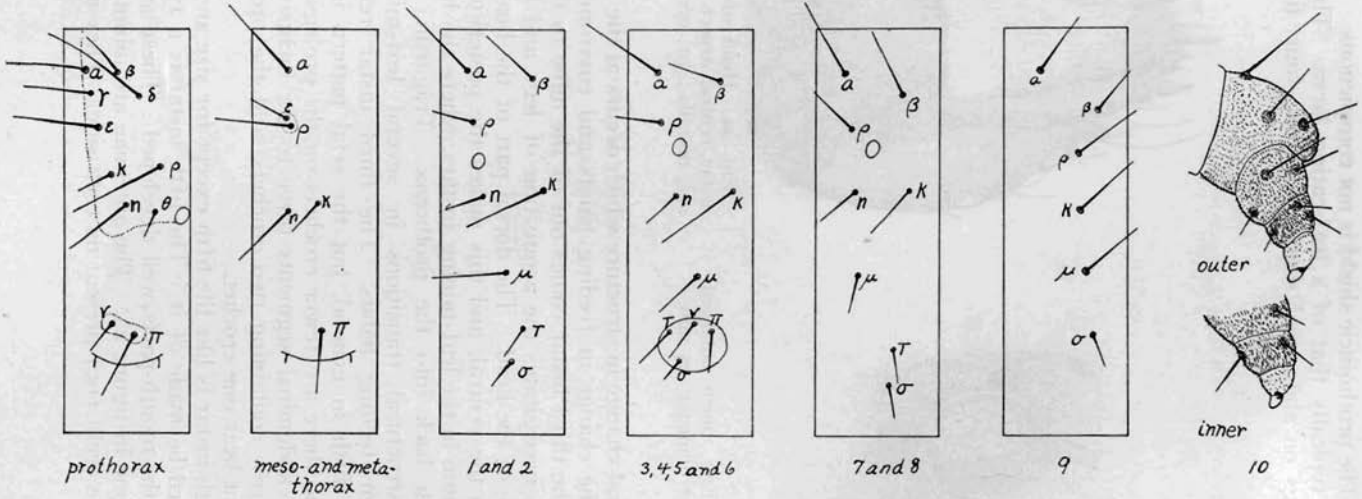

FIG. 25. Setal pattern of 5th instar larva.

in a curved row whose concavity is ventral. The labium is drawn out into a spinneret through which the duct of the silk glands reaches the exterior. The maxillae bear on the inner surface a pair of curved chitinous hooks. Otherwise the mouth-parts are not unusual. On the dorsal surface the adfrontals extend back to the posterior margin of the epicranium and the frons is about one-third the length of the head capsule. The labrum is bilobed and the mandibles bear four "teeth."

The prothoracic legs differ from those of the meso- and metathorax in that the terminal segment bears one claw only, whereas in the case of the latter two pairs of legs the claw is protected by a pair of terminal lappets. The prolegs of the abdominal segments three to six inclusive bear on the planta two rows of crochets, three per row. The anal prolegs have a single crochet only.

The setal pattern of the body of the larva is of some taxonomic importance and is shown in figure 25. In this description the nomenclature of Fracker, though cumbersome, has been followed. The diagrams are made so that the anterior margin of each segment is to the left and the dorsal midline is at the top. Each diagram is that of the left half of each segment projected on a flat surface. Certain segments are alike, and these have been represented by one diagram. The setae of the anal segment do not conform to those of any of the others.

D. PUPA (Text figures 26 to 29)

The pupa is spindle-shaped, about three millimeters long and brown in color. Many of the adult structures are evident, and the head thorax and abdomen are distinct. In the description here given the parts, although often incompletely developed, are named in accordance with the corresponding parts of the adult.

The vertex (vert) occupies most of the dorsal side of the head and is separated from the frons by the Y-shaped epicranial suture, the frons meeting the arms of the suture. The stem of the Y is indistinct. The frons (fr) extends caudally along the ventral side of the head from the epicranial suture to merge into the clypeal region, there being no demarcation between the two. The frons in figure 26 can be easily distinguished by the presence of the pointed cutting plate in its anterior part. This is the so-called "cocoon-breaker" with the aid of which the pupa emerges from the cocoon. The bases of the antennae (ant) are visible on the dorsal side of the head lateral to the epicranium. On the ventral side of the head and lateral to the frons are the eye-pieces (e). The clypeus bears the bilobed labrum, and on each side of the labrum is a small triangular mandibular sclerite. Neither labrum nor mandibles are found in the adult. The labrum bears a pair of laterally placed setae. The maxillae are prominent and form the pair of medially placed appendages extending caudally from the labrum. Neither maxillary nor labial palpi are visible. The antennae extend caudally almost to the tips of the wings. Between the antennae and maxillae lie the folded prothoracic and mesothoracic legs. The tarsal regions of the metathoracic legs are visible between the tips of the antennae, most of this pair of appendages being covered by those preceding. A small part of the metathoracic coxae is visible in the midline posterior to the mesothoracic coxae. The metathoracic legs extend slightly beyond the tips of the wings. The fore wings extend to the seventh segment of the abdomen on the ventral side and conceal the hind wings. The appendages are loosely attached to each other

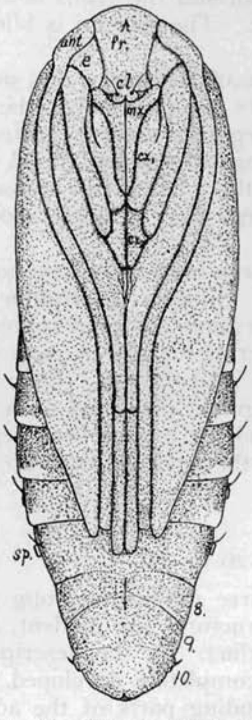

FIG. 26. Female pupa, ventral aspect, much enlarged. *ant*, antenna; *cl*, clypeus; *cx*, coxa; *e*, eye; *fr*, frons; *max*, maxilla; *sp*, spiracle.

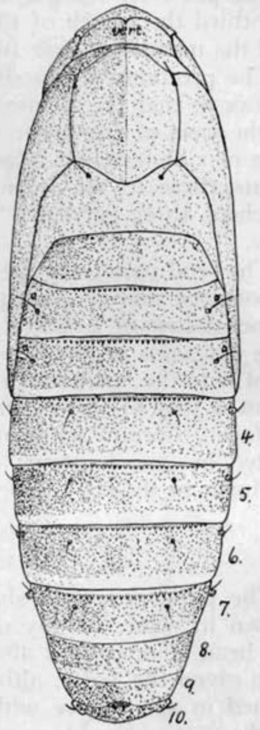

FIG. 27. Pupa, dorsal aspect, much enlarged.

and are free from the body wall. They overlap, more or less, and the covered parts are quite membranous. When dissected out, the regions of the coxa, femur, tibia and tarsus are visible, although often not distinctly demarcated, and the tibial spurs are prominent. The two folds in the legs occur between coxa and femur and between femur and tibia. The tibia merges into the tarsus.

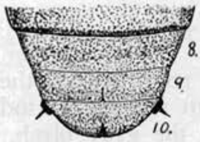

FIG. 28. Tip of abdomen of male pupa, ventral aspect.

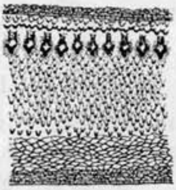

FIG. 29. Section of dorsum of abdomen of pupa.

The female has evidence of two genital openings on the ventral side, one on the posterior border of the eighth abdominal segment and one on the interior border of the ninth. These are short slits in the integument. The male has evidence of one genital opening only (figure 28), on the ninth segment. This condition in each sex corresponds to that of the adult. On the tip of the tenth abdominal segment is the indentation marking the anal opening, and on the lateral sides of this segment are a pair of short strong spines.

On the dorsal side of the pupa the prothorax is constricted in the middle and widens laterally. It lies between the epicranium and mesothorax and abuts on the antennae. The epicranial suture extends to the anterior margin of the prothorax. The mesothorax is a large quadrate sclerite separated by distinct sutures from the prothorax, metathorax, and fore wings. Along its midline it is raised into a very slight ridge. At the anterior-lateral angles are a pair of setae. The mesothoracic wings extend around the body to the ventral side. The metathorax is not so long as the mesothorax and merges indistinctly into the wings laterally. It bears also a pair of setae at the anterior-lateral angles, but these are more approximated than those of the mesothorax. The metathoracic wings are almost entirely concealed by those of the mesothorax, the bases only being visible. There are visible dorsally ten abdominal segments, of which numbers two to seven inclusive bear a pair of setae at the anterior-lateral angles, and numbers one to seven bear laterally placed spiracles. Segments four to seven inclusive bear also a pair of medially placed setae. The spiracles on the first abdominal segment are concealed by the hind wings. At the anterior margin of the tenth segment is a dorsal tubercle bearing a pair of spines. This and the lateral spines on the tenth segment are purely pupal structures. The dorsal surface of the abdominal segments is covered with minute spines (figure 29) and on segments two to seven inclusive there is a row of heavy spines along the anterior margin.

In the male abdominal segments three to seven are movable, and in the female segments three to six are movable. The terminal segments are immovably united in both sexes.

VI. Life History and Habits

All the data here given, except for field records and other cases specifically mentioned, were obtained from records of individual insects reared in New Haven, Conn., on the gray birch, *Betula populifolia*. The field observations in Connecticut and Massachusetts are also of insects occurring on *Betula populifolia* unless otherwise stated. The period during which records were made covers the years 1924, 1925, and 1926.

The first adults appear the last of June in the region about New Haven, and the last disappear the last part of July. In 1924 adults were fairly numerous July 7th, and the last were seen July 31st. During 1926 adults were systematically collected with a net and by hand during July in one locality, a group of birches just north of Mt. Carmel, near New Haven, and these collections indicated a maximum number of adults were present the fourth week in July. During 1926 the season was later than usual. This species was abundant during the second and third weeks in July, but from the 27th to the 31st it declined in numbers from about a maximum to disappearance.

Pupae were kept at normal temperatures in an out-door screened insectary during 1924, 1925, and 1926. Those of 1924 were collected in the field during the spring of that year; those of 1925 and 1926 were reared in the out-door insectary. Records were kept of the emergence of 104 adults in 1924, 135 in 1925, and 36 in 1926. In 1924 the period of emergence was between June 4th and July 9th (only three emerged before June 23d); in 1925 between June 15th and July 19th, and in 1926 between July 2d and July 21st. The period of maximum emergence during 1924 was between June 25th and July 9th; in 1925 between June 18th and July 10th, and in 1926 between July 2d and July 9th. In 1925 all records obtained after July 1st were of individuals taken from New Haven to Woods Hole, Mass. The early appearance of adults in 1925 may possibly have been due to high temperatures early in June of that year, for, during the first ten days of June, 1925, the mean hourly temperature was 75.2°F. as opposed to 60.6°F. in 1926, and 61.2°F. in 1924 (U. S. Weather Bureau, New Haven, Conn., statistics).

Hutchings (1926) reports that in Ontario the adults are found during July (up to the 25th) with a maximum emergence from July 6th to July 14th. In New Brunswick, Gorham (1922) reports adults abundant the first two weeks of July. It would seem from these reports that the adult insect appears at approximately the same time of year over much of its entire range, being at a maximum during the first part of July.

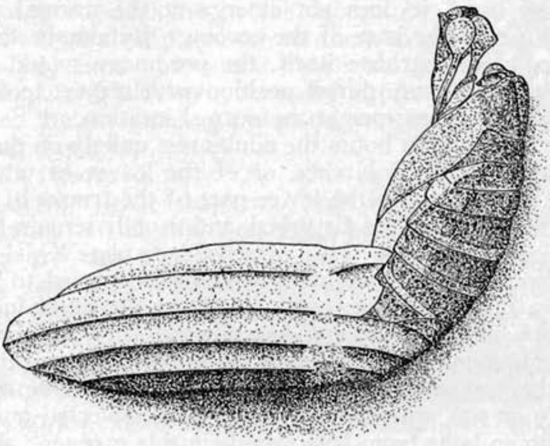

FIG. 30. Cast pupal skin and cocoon.

From the pupae collected in the field in the spring of 1926 there were secured 54 adults of which the sexes were determined. Thirty-three were females and 21 were males. Of 36 adults secured from laboratory-reared larvae, 19 were females and 17 were males. Although the females outnumber the males, the difference is not sufficiently great to warrant an assumption that there is not approximately an equal number of each sex under natural conditions.

When ready to emerge from the cocoon the insect is in the pre-imaginal stage, and the scales of the imago are easily seen through the pupal skin. The pre-imago works its way forward, probably with the assistance of the spines on the tenth abdominal segment, and breaks through the anterior end of the cocoon. The cutting plate on the vertex is of material aid in the process. When about three-fourths of the length is exposed, the body is held at an angle of about 40° from the cocoon. The pupal skin splits at the junction of the vertex and the prothorax and also longitudinally through the prothorax and mesothorax. The eye-pieces remain attached to the antennae and mouth parts. Figure 30 shows a cocoon and an empty pupal skin in the characteristic position.

According to Snodgrass (1922), the emergence from the cocoon is greatly assisted in *Bucculatrix pomifoliella* Clemens by the presence of three "valves" in the anterior end of the cocoon, these acting as an inclined plane to lift the insect. In *B. canadensisella* these structures are not present. The inner part of the cocoon is woven so that its lateral walls curve in at the base, making a "round corner," and this might conceivably give the pre-imago an upward lift. However, if a pupa is pushed gently forward by hand, it does not emerge at the normal place, but lower down near the base of the cocoon. By simply rolling over in its attempt to extricate itself, the pre-imago would bring the cutting plate in a more dorsal position with respect to the cocoon and thus insure emergence at the normal location.

During the daylight hours the adults rest quietly on the surfaces of the lower leaves of birches, or of the leaves of undergrowth under the birches, or on the lower part of the trunks of the trees. They fly very little unless disturbed, and usually remain motionless for long periods of time. The photograph on plate XVII is a three-minute exposure of a live adult which was carried to and from the camera in the position seen. It shows the adult in the characteristic position. They can be collected very easily by simply inverting an empty glass vial over the quiet insect and then gently tapping the opposite side of the leaf on which it rests. It will quickly fly or run up into the vial. I have collected one hundred in less than an hour from fern fronds in this manner. When disturbed, they fly quickly a few feet, very rarely over five or six, and usually much less. If confined in a bottle they run excitedly for a few minutes when disturbed.

From field observations it seems that as a rule the moths remain near the ground during the day and go up into the trees at about dusk. I have often failed to get them in a net by sweeping birches over my head, when many were secured by sweeping within four feet of the ground. Yet, in the same location, by sweeping the birches at dusk, several were netted very quickly at a height of about nine feet from the ground. In 1926 in one particular locality, moths were very abundant during the day on the fronds of ferns growing under the birch trees, but none were seen on the leaves of the birches which were not lower than four feet from the ground. An investigation of the birches at night with the aid of an acetylene lamp showed that the moths were all up on the birch leaves, and none were on the ferns below. The next day over one hundred were easily caught on the ferns, but none were on the leaves of the trees. At times, however, I have found moths on the leaves of the trees during the day five feet from the ground. Gorham (1922) reports that in New Brunswick he found moths on the birches in large numbers at all hours of the day, but he gives no further information on the distribution.

The moths prefer situations out of direct sunlight, and this may account for their position during daylight hours. This nightly migration into the trees may be affected somewhat by conditions of light, moisture, and amount of undergrowth, but it apparently occurs to some extent wherever conditions are normal.

The response of these moths to light is not very definite, due to their habit of remaining quiescent in one spot unless greatly disturbed. Attempts to make them show either a negative or positive response to daylight in the laboratory gave inconclusive results. Several attempts to attract them to a lighted lantern, an acetylene lamp, and automobile headlights at night in the field failed completely, although they were present in considerable numbers on the surrounding trees and were relatively more active than during daylight.

From the above observations it is assumed that oviposition occurs at night. In the insectary eggs were secured from three to seven days after the adults emerged, but in view of the fact that the moths are very inconsistent about ovipositing in captivity, these data may have to be extended under normal conditions.

It was necessary to place several males and females in a cage in order to ensure a supply of eggs. Although I have no data on the number of eggs laid by any one female, an examination of the oviducts shows that there may be a considerable number, for sixty-two fully formed eggs were dissected out from one female caught in the field, and there may have been several laid before she was captured. This number of eggs was never secured from any female in captivity. From four females thirty-four eggs were secured in one day in a cage, and from these same four, fourteen eggs the following day. They died without further oviposition. These females were reared and laid only the eggs recorded.

The adults have been kept alive in cages out of doors for twelve days after emergence from the cocoon, but they usually die sooner. They have never been seen to feed, and apparently they did not touch a honey-and-water mixture placed in the cage. The presence of a 25 per cent solution of honey in the cage did not prolong the duration of adult life. Certainly food is not a requisite and is not necessary to oviposition. All the adults collected in the field died in a few days, so twelve days probably is a fairly long period of life. Humidity and temperature have considerable effect on this, and moths caught in the field can be kept alive four to nine days if held at 10°-12°C., whereas they die in one to three days at room temperature. They will remain active after an exposure to 7°C. for twelve hours, but when the air is cooled to 5°C. they very quickly become inactive.

The eggs are laid singly on either side of the leaf and on any part of the surface. There is some preference shown for a position beside the midrib or some other prominent vein of the leaf.

but not to the exclusion of the rest of the leaf (plate XVII). Eggs are laid on leaves on all parts of the gray birch. Insectary records for 1924 showed a period of oviposition lasting from July 5th to July 21st, and field observations the same year showed unhatched eggs up to August 7th. No field observations were made during 1925, but gray birches sent from Boston, Mass., to Woods Holt, Mass., on July 9th, carried many unhatched eggs on the leaves. In 1926 eggs were found in the field between July 23d and August 3d, but in view of the fact that they were numerous July 23d and that some of those collected that day hatched July 30th, oviposition must have begun as early as July 16th. Many eggs collected August 3d hatched August 15th, so oviposition occurred as late as August 1st. Oviposition takes place usually during the month of July, and unhatched eggs may be found up to the middle of August. In 1926 the incubation periods of 48 eggs from laboratory-reared adults were 15 days on the average, the maximum being 17 days, the minimum 13 days, and the majority (27) taking 14 days. In all but three cases these eggs went through the incubation period between June 25th and July 13th, a month earlier than normal. They were from laboratory-reared adults which emerged earlier than normal. The other three eggs were incubated at the normal time, between July 31st and August 14th, and they took 14 days each, so the figure for all 48 was normal. This agrees with the period given by Hutchings in Ontario in 1925. The eggs have a high degree of fertility, and those that do not hatch are rare.

A short time before the larva leaves the egg it can be seen curled inside (figure 31). When it emerges, the young larva bores through the bottom of the egg into the leaf, and as it feeds it leaves the egg filled with dark excrement. This habit makes it very easy to determine whether or not the eggs are hatched, for after the larva has left, the egg appears brown or black in contrast to its former translucent condition. For several days the young larva mines close to the egg, but it finally straightens its path and mines in a more or less definite direction.

The larva completes the first and second instars and most of the third in the mine. I have found a head capsule in a mine only twice, but the measurements of the width of the head capsules (p. 444) and the descriptions of the larvae clearly indicate three mining instars. While in the mine the larva is always oriented dorso-ventrally with the leaf; that is, its dorsal side is always toward the upper surface of the leaf. For the first week the mine is extended very little and is always close to the egg, giving a blotch appearance, due to continuous turning of the mine in a small area. A mine six days old measured only 1.5 mm. across the mined area. This larva never makes a real blotch mine, but its excavations are always linear and winding, with slightly

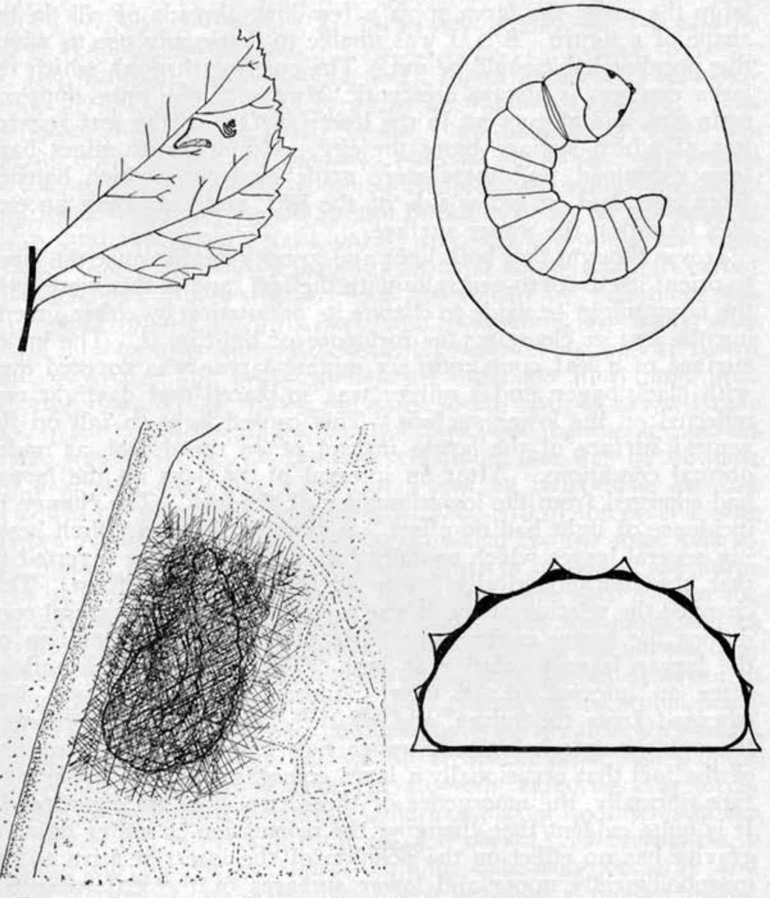

FIG. 31. Larval mine in birch leaf, slightly less than normal size (upper left); embryo in egg (upper right); larva in molting web (lower left); diagram of cross section of cocoon (lower right).

enlarged ends. During the last part of its mining life the larva lengthens the mine very rapidly and broadens it somewhat. Most of the mines are about three-fourths of an inch long when finished (figure 31).

When ready to emerge from the mine, the larva cuts a crescentic opening in the lower epidermis, an operation taking about fifteen minutes. It then works its way out until, by bending its body ventrally, it can grip the leaf surface with its thoracic feet. It then quickly pulls itself out of the mine, the entire performance consuming about two and one-fourth minutes. While emerging from the mine. the larva spins a few long threads of silk in the shape of a figure "8." I was unable to detect any use to which this peculiar habit could be put. The opening through which the larva emerges is always crescentic, always of the same approximate size, and always cut in the lower surface of the leaf regardless of which surface bears the egg. Hundreds of mines have been examined, and these were made by larvae which hatched from eggs laid on either side of the leaf, and only once an exit was found on the upper surface.

It was thought that both light and gravity might cause the larva to orient itself dorso-ventrally with the leaf, and if this were true, the larva might be made to change its orientation by either inverting the leaf or changing the incidence of light on it. The upper surface of a leaf containing six mining larvae was covered over with black paper, and a mirror was so placed that daylight was reflected on the lower surface. This caused light to fall on the ventral surface of the larvae instead of on the dorsal, as under normal conditions. After an interval of 15 days all the larvae had emerged from the lower surface of the leaf. The change in incidence of light had no effect. A branch of a gray birch bearing several leaves which contained mining larvae was inverted so that the morphologically lower surface was uppermost. This changed the relation of the larvae to gravity. Under natural conditions the leaves never hang horizontally, so the orientation of the larvae is only relative at best. The leaves were examined after an interval of 18 days. Approximately 50 larvae had emerged from the mines, and of these only two had emerged through the morphologically upper, now lower, surface. In view of the fact that occasionally a larva emerges from the upper surface normally, the emergence of these two is of no significance. It is quite evident that changing the orientation to either light or gravity has no effect on the position of the insect relative to the morphologically upper and lower surfaces of the leaf after the mine is well under way; nor will the surface of the leaf through which the larva emerges from the mine be changed by any such procedure. In the above cases all the mines were about half finished when the conditions were changed. The orientation of the larva must be determined after it bores through the epidermis of the leaf from the egg and before it mines to any great extent, for all larvae examined were found with the ventral side toward the lower side of the leaf even when the mine was only two or three days old.

Where the insect is abundant it is by no means unusual to find 25 to 40 mines in one leaf. The mine shows more clearly through the upper epidermis of the leaf than through the lower, but this may be due to differences in the structure of these parts of the leaf rather than to the nature of the mine. The larvae are disinclined to gnaw through large veins, and usually the mine turns aside at these obstructions.

The duration of the mining stage varies greatly. The maximum period observed was 50 days, the minimum 13 days. This variation may be due partly to the conditions under which the larvae were reared. In 1924 and 1925 all the larvae were reared at the normal season and fed on leaves in normal condition. During these two years the maximum duration of larval life was 37 days, and the minimum 24 days. In 1926 several larvae were reared from eggs laid by laboratory-reared adults a month earlier than normal—in June, in fact—and the foliage of the birches was in a more rapidly growing and tender condition, especially since these birches were more or less sheltered and were well fertilized and watered. The water content of the leaves must have been greater than larvae would normally meet. All of these larvae but two were in the mines over 32 days, and the average period of 20 was 44 days. Of the two remaining, one was in the mine 16 days and the other 13 days. These 22 individuals are not included in computing the mining period. All of the other larvae reared during 1926, 35 in number, on which records were kept of the mining period, were in the mines 30 days or less. The duration of the mining stage during 1924, 1925, and 1926 was on the average 22 to 27 days for 50 individuals, not including the 22 mentioned above. This figure is probably correct for normal conditions. Hutchings (1926) gives the mining period as seven to eight days in Ontario, but such a short mining period would bring the larvae to a fully grown condition much earlier than they really appear in the field. There is a difference in food plants to be considered, for larvae in New Haven were reared on gray birch, whereas the common birches in Ontario attacked by this insect are the yellow (*B. lutea*) and white (*B. papyrifera*). Nevertheless in Connecticut the larvae appear feeding externally on gray and white birches at the same time, which indicates a similar mining period.

Mining larvae have been observed in the woods about New Haven as early as August 6th, and eggs collected on leaves have hatched July 30th when brought into the laboratory a week earlier. Larvae have been found out of the mines August 6th, but this is unusually early. The period when mining larvae occur around New Haven lies approximately between August 1st and September 15th, with a maximum number present the fourth week in August. The rearing records coincide with these limits.

When once free from the mine, the larva wanders over the leaf for a short time, an hour or two, and then spins its first molting web. A larva has never been seen to feed between the emergence from the mine and the spinning of the web. There may be a difference in different species of the genus, for Chambers (1882) observed that *Bucculatrix ambrosiaefoliella* feeds two days between emerging from the mine and molting. The larva which emerges from the mine is structurally more like the following external feeding instar than the preceding mining instar. This may argue for possible external feeding, but there is no evidence that it occurs at this time. The exact interval of time between emergence from the mine and either beginning or completion of the first molting web was determined for three larvae, all typical cases. One larva emerged from the mine at 8.20 A. M. and completed its web at 10.45 A. M.; one emerged from the mine at 9.40 A. M., began its web at 10.40 A. M., and completed it at 12.10 P. M.; one emerged from the mine at 10.09 A. M., began its web about 10.42 A. M., and finished it at 12.12 P. M. The larva often selects a position beside a large vein for its web, but it will also spin on the flat upper surface of the leaf. There seems to be a preference for a hollow over which the "roof" of the web may be spun, as the angle between the base and sides of a glass bottle or the hollow beside the midrib of the leaf. Having selected a suitable location, the larva lays down a thin basal "floor" web on the surface of the leaf. This is about 1.5 mm. in diameter. Then it spins another web over this, making long tacks from side to side by swinging the entire thorax and the first two abdominal segments from one side to the other. The body is held facing out and the threads are always straight. In shifting its position the larva swings the abdomen quickly almost 180 degrees. The periphery of the web is thus built up first, the center being weak. A series of short tacks is now made over the "frame" of long threads, and the center is strengthened. This is followed by a series of short tacks all around the edge, a proceeding which evidently strengthens the web. A hole is quickly made through the web near the center, and the larva crawls in head first between the "floor" and the "roof." In crawling into its molting chamber the larva doubles ventrally so that its back is down on the "floor" and its feet touch the "roof"; that is, it is oriented dorsally to the leaf. Before it is all inside, the larva swings its head to and fro, weaving a mat on the under side of the "roof." Since the diameter of the web is not much more than half the length of the larva, the latter is forced to turn around, and when completely inside, its head almost touches the last abdominal segment, the body being bent in a U shape and to the right or left (figure 31). It is plainly visible through the web. The larva is not content with getting inside, but actually makes a turn around its molting chamber. All this time it swings its head, weaving figure "8" loops, and in due time it incidentally has to cover the hole in the "roof" by which it entered. Although this opening is always covered, the larva seems to make no deliberate attempt to cover it, doing so eventually as it works around inside. Most of the weaving is done after the larva is inside. In two instances to which particular attention was given, the time spent weaving prior to entering the web was eight minutes in each case, and the weaving time inside the web was 56 and 52 minutes respectively. In two other instances the larvae were weaving inside the web 60 and 70 minutes respectively. The principal part of the web is woven from the inside and is supported on the lighter structure previously woven from the outside. The entire process of spinning the web takes about one or one and one-half hours, varying somewhat with the larva. The procedure is essentially as described by Snodgrass for *Bucculatrix pomifoliella.* When the larvae are numerous, the birch leaves in August and September are spotted on both sides with many white webs. I call these "molting webs" rather than "cocoons," "pseudococoons," or "cocoonets," as termed by others, because I believe the word "cocoon" should be restricted to that structure, in which the pupal stage is passed.

Having completed its web, the larva retracts its appendages somewhat and remains quiescent a day or two. The tarsal claws and the crochets of the prolegs are not attached to the web, the larva lying freely with its ventral side away from the leaf. If the upper part of the web is removed, the larva falls out. Under such conditions it must molt in some sort of a chamber or fall off the leaf, which might be disastrous, for if food is not available after the molt, the larva dies in a few hours. The small size of the web holds the insect tightly, and the strong attachment to the leaf secures the web against being washed off or lightly brushed off. The web also offers protection from such enemies as ants during a period of helplessness. It is not essential to the process of molting, and seems to be an obstacle to quick molting rather than an aid. If removed from the web, the larva molts perfectly normally. Inside the web it has to pull itself around to get clear of its old skin. After one or two days in the web, the larva molts, and in a few hours, sometimes in one hour, it breaks out through the edge, at the junction of "roof" and "floor" (plate XVII). In molting, the head capsule separates from the rest of the old skin and is cast off first anteriorly. The larva then works its way clear of the remaining skin, casting it off the posterior segment of the abdomen. The molted head capsule and skin are left inside the web and separate from each other.

The manner of leaving the web shows how precisely instincts can regulate action. After it has molted, the larva normally bites a hole through the side of the web and emerges, but before molting it will not bite through and hence cannot get out even though it so desires. An individual which had just entered the web (in this case the second molting web) was rendered inert by hydrocyanic acid gas. After four minutes it regained sensibility and for the next 14 minutes made spasmodic movements while recovering, being apparently normal at the end of this time. It then attempted to get out of the web by pushing against the sides, having "forgotten" the reason for its imprisonment. It pushed vigorously back and forth for seven minutes, stretching the sides of the web in its endeavors to escape, but to no avail. Half a minute's work with its mandibles would have set it free, and had it molted, escape would have normally been accomplished in this manner. The instinct to bite its way out was totally lacking. Finally it began to move around inside the web and spin irregularly, then it began to weave the normal figure "8" loops, and in 28 minutes the web was finished. The larva cannot use its only means of escape from the web until the act of molting is accomplished. This individual later molted and developed normally, not being in any way injured by its treatment.

If removed from the web before it is finished, or, if it is finished, before the pre-molting quiescent stage begins, the larva will spin another web or as much of another web as is possible and will molt normally. An effort is always made to complete another web, but sometimes lack of the necessary silk, or exhaustion, or some other factor, compels the larva to stop after a few strands have been spun, and it then molts in the most convenient place. If it has entered on the quiescent stage prior to molting and has become fixed in the shape of a horseshoe, it does not straighten out when taken from the web, but retains its curved shape until it molts.

Because of the fact that the larva leaves its web so soon after molting, the duration of the instars has been calculated to include the time spent in the web made by the particular instar in question. Thus the feeding period plus the subsequent quiescent period spent in the web gives the length of the instar.

The time spent in the first molting web is much affected by temperature, and usually varies between one and four days in this climate. Many larvae spend less than 24 hours in this web, but most of the larvae are in it about two days. If this period is added to the days of mining life, we get a period of 24 to 29 days for the first three larval instars. This is not remarkably long when compared to the length of the next two instars, which together total about two weeks.

After emerging from its first molting web, the larva feeds from one to nine days, the individuals varying greatly under the same conditions. If food is withheld from the newly molted larva, it dies in a few hours, a much shorter time than if starved after feeding a day or two. This is probably the result of remaining a day or two in the molting web without feeding. During the fourth instar the larvae are restless and wander about more or less. This probably accounts in part for the variation in the length of the instar, for the rapidity of development is much dependent on the amount of food eaten. The average duration of the feeding period for 73 individuals recorded was about four days. In only one instance was the feeding period as short as one day. Temperature affects the duration of this period to some extent, as will be brought out later. The effect of different species of birch as food will also be discussed in another section of this paper.

The feeding occurs normally on the lower side of the leaf, and the veins and the upper epidermis are left intact. The entire leaf is never consumed. It is due to this habit of skeletonizing a leaf that the insect bears its common name. The larvae will eat whichever surface of the leaf is toward the ground, and normally this is the lower epidermis. A birch leaf was inverted so that the normal lower surface was uppermost and covered with a black paper. A mirror was so placed that it reflected light on the leaf from below. The larvae normally feed on the lower side of the leaf, and under normal conditions this side is not so light as the upper. If the larvae fed on the lower side of this inverted leaf, they would feed on the lighter side and at the same time on the side normally uppermost. The two sides of the leaf differ in physical as well as chemical constitution of the surface. Of ten larvae placed on the upper side of this inverted leaf, four migrated to other parts of the plant (a normal movement), one remained on the upper side and was feeding when examined, and five went to the lower side of the leaf and were feeding. Seventeen hours elapsed between the placing of the larvae on the leaf and the final observation. Larvae were then placed on the uppermost side of an inverted leaf and watched. Usually they wandered about restlessly for a time until they came to the edge of the leaf. They then turned to the side underneath. Light reflected on the lower surface by a mirror seemed to have no effect. At times movement to the lower surface was long delayed and at times direct. It very evidently is a reaction to gravity that impels these larvae to feed on the lower leaf surface and not any dislike for the upper surface nor any negative reaction to bright light. What factors developed the habit of feeding on the lower surface only is another matter. The habit of the larva is to feed continuously over a limited area, and it does not wander far unless the food supply gives out. If disturbed, the larva usually drops off the leaf, spinning a long thread as it falls. After falling a few inches it hangs on the end of the thread a moment and then quickly ascends. The thread is spun out the tip of the spinneret, and when the larva stops its descent, it is attached to the end of the thread by means of the spinneret. When it ascends the thread, it moves its head rapidly back and forth and winds the silk on the prothoracic legs which are held forward. If there is too much silk for the prothoracic legs, the mesothoracic legs are brought into use. On regaining its support, the larva simply drops the bundle of thread and walks away. This performance can be easily watched under the binocular if a larva of the last instar is used. The spinning activities of the larva, the quickness with which it drops from a leaf, and the distance it drops are much greater in the last instar than in the fourth. The speed with which these little insects can spin a thread while falling a few feet is remarkable. If touched, they snap the body back and forth rapidly and thus wriggle off the leaf and drop toward the ground. Yet after they have fallen some distance, they suddenly check their descent and can be seen to be hanging by the end of a thread. The silk of which this thread is formed must be spun from the silk glands and out of the spinneret as rapidly as the larva falls. The act of spinning apparently occurs automatically when the larva is disturbed.

Because of their small size and their greenish color, together with the comparatively small amount of leaf tissue eaten, larvae of the fourth instar are not so noticeable as those following. In localities where Bucculatrix is abundant, however, ten to fifteen larvae may often be found on one leaf. Heavily infested birches frequently have 25 larvae of the fourth and fifth instars feeding on each leaf. During the majority of seasons no such number is likely to be present.

The fourth instar molts as did the third, in a white silken web. This web is larger than the previous one, being about 2.5 mm. across. The larva builds the web and lies in it as previously described, being clearly visible. There is a slight difference in structure, as this larva weaves an elliptical mat after it is inside the web. This thickened part gives the second molting web a characteristic appearance, as the first molting web has this structure to only a very slight degree. The time spent in this web varies normally from one to three days, the 75 individuals recorded averaging about two days. This is, of course, affected by the temperature, as was mentioned before. When added to the feeding period this figure gives the length of the fourth instar as about six days.

The larva molts as before and emerges from the second molting web as from the first. It normally feeds on the under side of the leaf, skeletonizing it (plate XVIII), and in this instar the feeding is much more extensive. The injury to the foliage is most noticeable at this time, usually during the last of August and most of September. If the larvae are present in large numbers, all the parenchymatous tissue is consumed, and the leaf dies and drops from the tree. These larvae show greater spinning activity than those of the former instar and may be seen suspended from the leaves in great numbers in seasons of abundance. They feed from two to ten days, the period varying with the individual and being affected by climatic conditions, and an average of 48 recorded individuals gives a period of nearly seven days. This period includes the time from emergence from the second molting web to the spinning of the cocoon. Toward the last part of the feeding period the gonads are clearly seen through the dorsal skin of the abdomen of the larva. About twelve hours before the time when the larva will begin to spin its cocoon, it stops feeding. This interval of time varies considerably and may be much less. By this time the larva has turned brown in color, due to the color of the large silk glands which run almost the entire length of the body. When ready to spin the cocoon, the larva drops from the place of feeding to the ground, spinning out a long thread as it goes. Larvae may sometimes be seen suspended from a thread about fifteen feet long. If the trees on which they are feeding are shaken, these fully grown larvae drop to the ground quickly and in considerable numbers. Having reached the ground, they crawl under a stone, a fallen branch, a leaf, or any other object lying on the ground and spin their cocoons on the under side of this. Sometimes the cocoon is spun on the ground itself. In captivity they will frequently place the cocoons on the sides of the cage close to the base. I have reared hundreds of larvae, and they all have dropped to the ground or close to it to pupate. Fletcher (1893) mentions finding three cocoons on the twig of a birch, but all the cocoons which I have found in the field have been on fallen leaves or other objects lying on the ground.

The manner in which the larva spins its cocoon is characteristic of the genus and quite unique. The earliest description of this process in the genus *Bucculatrix* is by Lyonet, who wrote to Réaumur, December 22, 1744, concerning the larva of *B. ulmella* and its cocoon. This description was not published until 1832 and has been referred to in the historical part of this paper (page 396). De Geer, in the first volume of his "Mémoires," published in 1752, described the cocoon of *B. frangulella* (see page 395), and Snodgrass in 1922 likewise described the manner in which *B. pomifoliella* Clemens wove its cocoon. These three papers go into the details of the process by which the larva lays down its threads, and from a microscopic examination of the cocoon of *B. canadensisella* it is apparent that this larva weaves its threads in precisely the same manner as does *B. pomifoliella*. The general process of weaving is similar in all four species, differing only in a few details. Chambers (1882) described briefly the formation of the cocoon by *B. ambrosiaefoliella* Chambers, and McGregor (1916) gave a brief description of the finished cocoon of *B. thurberiella* Busck. In 1892 Fletcher briefly described the general procedure of weaving by *B. canadensisella* Chambers, and in 1893 Lintner mentioned the same subject, but the latter's description is not correct, and Fletcher's description is not detailed.

The larva of *B. canadensisella* Chambers first lays down an oval mat to serve as a base for its cocoon. It does not previously weave a palisade of poles around the site selected, as do many species of the genus. It then commences at one end of the mat to weave an outer supporting ridged structure of comparatively coarse threads (about .005 mm. thick), facing the work and backing away as the woven structure progresses over the mat in an arch. The ridges are formed by the ends of a series of loops made from one side to the other. The diagram in figure 32 gives the principle. Between ridges the threads cross diagonally. This figure is from Snodgrass (1922) and gives his conception of the actual motions made in weaving. As the cocoon becomes higher, the larva raises the anterior part of its body, and the radius of the structural arch is gauged by the raised part of the body as it swings from side to side, most of the body being fixed in the midline of the oval base. Possibly the prothoracic legs are used in the weaving to aid in guiding the work, as mentioned by Snodgrass and Lyonet. Certainly these legs are held up to the structure. When the cocoon is about two-thirds finished, the larva enters it, turns about, and crawls out until its head reaches the other end of the mat. It now has its anterior end outside of the cocoon but its posterior end in the cocoon. Beginning to weave exactly as before, the larva builds up the last third of the cocoon to meet the previously formed two-thirds, gradually enclosing itself as it works. When the two sections meet, they are joined by cross threads. The architecture is not perfect, for the ridges of the two sections rarely coincide, and sometimes the heights of the sections are not equal. The result is a break in the continuity of the ridges at the junction and often a sag in the contour of the cocoon. A completed cocoon is shown on plate XVIII. This outer structure is not closely woven and the insect can be seen clearly inside. It is, however, stiff and gives support to the lining which is to be woven. The sides meet the oval base perpendicularly.

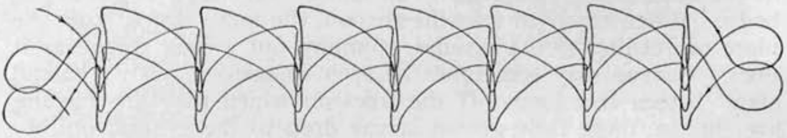

FIG. 32. Diagram of method by which larva of *Bucculatrix pomifoliella* Clemens weaves its cocoon. After Snodgrass.

Having completed its superstructure, the larva weaves a closely knit lining of fine threads (about half the thickness of the threads of the supporting structure) all around the inside by swinging its head in figure "8" loops. Where the walls of the superstructure join the base, the cocoon does not follow but makes a round corner, as the diagram in figure 31 shows. It is this lining which makes the cocoon opaque. Snodgrass has described a series of "valves" in the anterior end of the cocoon of *B. pomifoliella* Clemens, but in the cocoon of *B. canadensisella* these are not present. The cocoon when first finished is almost pure white, but it soons turns brown. This brown color is due not to the pupa inside, for it is present before the prepupa molts, but to a change in the color of the silk when exposed to air. The time necessary to complete a cocoon is from eight to sixteen hours normally. Inside the cocoon the larva remains two or three days before pupating. This prepupal period plus the feeding period makes the fifth instar about nine days long on the average. The larva molts in the cocoon in a manner differing slightly from that which takes place in the molting webs. In the webs the head capsule is cast off entire and anteriorly while the rest of the larval skin is worked posteriorly off the anal segment. In the cocoon the entire larval skin, head capsule included, is worked off posteriorly.

The individuals which were reared in the outdoor insectary under normal temperatures in 1924 pupated from September 4th to September 25th; in 1925 from September 8th to September 13th; in 1926 from September 11th to September 23d. This does not indicate the time of disappearance of the last larvae in the field. During these three years an examination of birches about New Haven was made in order to determine the normal close of the larval period. In 1924 the last larvae were found October 9th; in 1925, September 19th; and in 1926, October 9th. The early disappearance of larvae in 1925, although not caused by any apparent natural enemy or unusual climatic condition, was exceptional. It may have been caused in part by an early season starting the life cycle earlier. In view of the fact that larvae will feed at 48° to 50°F. and will eat birch leaves until they begin to turn yellow very few are caught before pupation by cold weather or lack of food.

The total larval life occupies from 38 to 46 days, as a rule, as the table on page 441 indicates. This is not an average of the completed larval life of a number of insects, but an average of the separate stages of many individuals, rather few of which completed the entire larval period while under observation. Nine larvae carried through from egg to pupa in 1926 averaged 41 days, the maximum being 45 days, and the minimum 36 days. This is as close as could be expected to the 38 days given in the summary for 1926. In the table below, the larval life from the hatching of the egg to the spinning of the cocoon is given for the nine individuals mentioned above. Two days as prepupa should be added to the six days of feeding in the fourth instar to give the total larval period of 41 days. It will be noticed that the larva does not accelerate through one instar if slowed down on a previous instar, but that any retardation during the growing period is permanent as regards time. This is borne out by the other records. Seven larvae were reared in the laboratory in vials containing moist sand, and were under identical environmental conditions. The figures for the stages are given on pages 474-478 (larvae 131-137). The most slowly growing larva was six days in the fourth instar and was feeding six days and fifteen hours in the fifth, while the most quickly growing larva was four days and nine hours in the fourth instar and was feeding four days and nineteen hours in the fifth. It will also be noticed that the quiescent period spent in the molting web is independent of the length of the feeding period, and as the feeding period grows shorter, the proportion of time spent in the web during one instar grows greater. In larva number 9 in the table below, two-fifths of the fourth instar is quiescent, and in number 1, three-sevenths, but in numbers 2 and 4, only one-fourth of the fourth instar is quiescent. The effect of food and temperature on larval growth will be discussed later.

TABLE 1. COMPLETE LARVAL PERIOD

No.	Hatched	In Mine	In Web 1	Total Days	Feeding	In Web 2	Total Days	Feeding	Spun Cocoon	Total Days
1	8-14-26	26	2	28	4	3	7	5	9-23-26	40
2	8-11-26	22	2	24	6	2	8	7	9-19-26	39
3	8-11-26	22	3	25	4	2	6	6	9-17-26	37
4	8-14-26	20	2	22	6	2	8	6	9-19-26	36
5	8- 7-26	27	2	29	4	2	6	5	9-16-26	40
6	8-11-26	30	1	31	5	3	8	4	9-23-26	43
7	8- 7-26	27	3	30	5	2	7	6	9-19-26	43
8	8-14-26	20	2	22	5	2	7	6	9-18-26	35
9	8- 7-26	22	1	23	3	2	5	6	9-10-26	34
Aver.				26±.74			7±.22	6±.16		39±.7

The chart below (text figure 33) gives the periods during which the various stages may be found in the field around New Haven, Connecticut. These limits are computed from field observations and data obtained in the insectary and are broader than actual field observation alone would give. From what notes there are of the occurrence of this insect elsewhere, it seems likely that these periods are approximately correct for the entire region in which the insect is found.

TABLE 2. SUMMARIZED LIFE HISTORY OF *Bucculatrix canadensisella* CHAMBERS

Year	Adult		Egg		Mining instars					Fourth instar					Fifth instar				
	Number of individuals	Period of emergence	Number of individuals	Days in egg	Number of individuals	Days in mine	Number of individuals	Days in 1st molting web	Total length of instars	Number of individuals	Days feeding	Number of individuals	Days in 2d molting web	Total length of instar	Number of individuals	Days feeding	Days prepupa	Total length of instar	Days of larval life
1924	104				5		44			19		19			16				
max.		June 4				32		4			7		3			8			
min.		to				25		*1			1		1			2			
aver.		July 9				27		2	29		3		2	5		6	†2	†8	42
1925	135				10					34		34			27				
max.		June 15				37					8		3			10			
min.		to				24					2		1			6			
aver.		July 19				29		2	31		3		2	5		8	†2	†10	46
1926	36		48		35		34			20		22			15				
max.		July 2		17		30		3			6		3			7			
min.		to		13		18		1			2		1			4			
aver.		July 21		15		22		2	24		4		2	6		6	†2	†8	38

* Several larvæ were in the first molting web less than 24 hours.

† The length of the prepupal stage was determined by removing several individuals from the cocoon at various times after the cocoon was completed. This stage was determined in 1926 and the 1926 figure used in computing the length of the stages in 1925 and 1924.

VII. Determination of the Number of Instars

It is very difficult to determine the number of instars by examining the mines for head capsules. A large number of mines were examined for this purpose and in two cases one capsule was found. The extent of growth and the morphological changes undergone during the mining period indicated at least two and perhaps three larval stages. A number of larvae were collected in the field and the width of the heads measured. The head is not subject to growth changes during any one instar, and according to Dyar (1890) a constant numerical ratio exists between the widths of the heads of any two successive instars of a larva. If the heads of two successive instars are measured, or if a large number of miscellaneous heads are measured, the ratio for the species can be determined and the possibility of missing an instar removed. Any dimension of the head may be used, but the width is the most convenient.

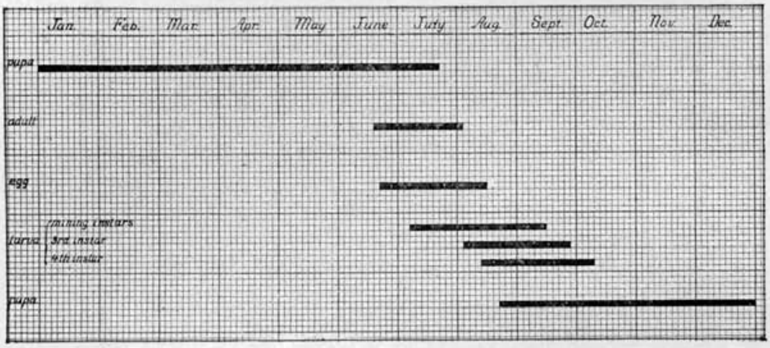

FIG. 33. Seasonal occurrence of the various stages of *B. canadensisella* in the vicinity of New Haven. The larval periods shown should read mining instars, fourth instar and fifth instar.

Several embryos which had developed to the stage where they were about to emerge from the egg and where no further growth of the head could be expected were measured. These were all mounted in Canada balsam. As seen by the table on page 444, the average width is .078 mm., and nine of the twelve measured .076 mm., which latter figure may be considered normal. It is to be expected that the measurements for the first instar would conform to this figure, and of the sixty-one mining larvae measured, eighteen either equal this figure or closely approximate it. All but two of the eighteen equal it. The average width for the first instar is then .077 mm. Thirty-six of the sixty-one measure .114

mm. in width or very nearly so, thirty-four measuring just that figure and the other two measuring .120 mm. The normal and average for this group is .114 mm. The remainder of the mining larvae measured, thirteen, all give a head width of .171 mm. Two larvae were secured just as they left the mine and before they began to weave the molting web, and their heads measured. Both gave a width of .171 mm. These two are marked (ex) in the third column. This checked the group giving this measurement as the last mining instar. Also four larvae were found in the process of molting and with the head capsules just far enough off to permit the measurement of both the old capsule and the new head. Two of these gave the width of the old capsule as .076 mm. and the new head as .114 mm., while the other two gave .114 mm. and .171 mm. for the two widths. This gives a check on the three groups. According to Dyar's principle we should expect

$$\frac{.114}{.077}=\frac{.171}{.114}=R$$

In this case the ratio "R" is 1.5, and the number of instars in the mine is, as the figures indicate, three. To further check this principle, a number of external feeding larvae, also collected in the field, were measured. I have placed these forty-one larvae in two groups as the table shows. According to the principle used above, the measurements should be ,257 mm. (.171 x 1.5 = .257) and .385 mm. (.257 x 1.5) for the fourth and fifth instars. (The actual number of externally feeding instars was determined by actual observation, of course.) In the fourth instar the average width was found to be .245 mm. for the nineteen individuals, with a variation between .228 mm. and .257 mm. The last instar, containing twenty-two individuals, gave an average width of .353 mm. with a variation extending from .304 mm. to .390 mm. It is questionable whether the two larvae whose head widths are .304 mm. belong to the fourth or the fifth instars if one judges by these two measurements alone. The average width is less than that expected in both the external feeding instars, but even so the measurements are sufficiently closely grouped in each case to determine the instar. It is to be expected that the more nearly the larvae approach the fully grown condition, the more widely will they vary in size, for the absolute extent of variation in size under normal conditions increases with age. The change in environment from the mine to the surface of the leaf, with its difference in manner of feeding involved, would also change the shape of the head, because mining larvae have relatively flatter heads. The actual measurements obtained of the heads of the first three instars is much closer to the ideal than would usually be expected.

TABLE 3. HEAD WIDTHS OF THE LARVAE OF *B. canadensisella* CHAMBERS

(All dimensions in millimeters)

	Embryo	First instar	Second instar	Third instar	Fourth instar	Fifth instar
1	.076°	.076*	.114°	.171° (ex)	.257′	.323′
2	.076°	.076*	.114°	.171° (ex)	.247′	.352′
3	.076°	.076*	.114°	.171°	.247′	.323′
4	.076°	.076*	.120°	.171°	.228′	.304′
5	.086°	.076*	.114°	.171°	.247′	.371′
6	.076°	.076*	.114°	.171*	.238′	.380′
7	.086°	.076*	.114°	.171*	.247′	.380′
8	.082°	.076*	.114°	.171*	.247′	.390′
9	.076°	.076*	.114°	.171*	.228′	.380′
10	.076°	.076*	.114*	.171′	.247′	.371′
11	.076°	.076*	.114*	.171′	.238′	.361′
12	.076°	.076*	.114*	.171′	.247′	.361′
13		.076*	.114*	.171′	.247′	.304′
14		.095*	.114*	.171′	.247′	.370′
15		.076′	.114*	.171′	.252′	.380′
16		.082′	.114*		.228′	.352′
17		.076′	.114*		.250′	.361′
18		.076′	.120*		.257′	.361′
19			.114*		.247′	.352′
20			.114*			.332′
21			.114*			.380′
22			.114*			.370′
23			.114*			
24			.114*			
25			.114*			
26			.114°			
27			.114°			
28			.114°			
29			.114′			
30			.114′			
31			.114′			
32			.114′			
33			.114′			
34			.114′			
35			.114′			
36			.114′			
Theoretical average			.114	.171	.257	.385
Average found	.078±.0008	.077±.0001	.114±0001	.171±0.0	.245±.0013	.353±.0036
Standard deviation	.0039	.0045	.001	.000	.0085	.025
Greatest deviation from theoretical	.008	.008	.006	.000	.017	.081

In previous descriptions of the genus *Bucculatrix* it has been tacitly assumed or explicitly stated that the mining period included one instar only, and that the insect always molted on the surface of the leaf. The only mention I have found of a larva molting in the mine is in a description of the larva of *B. ambrosiaefoliella* Chambers by Chambers (1882) in which he states that the larva in question molts once in the mine, once on the surface of the leaf, and once in the cocoon. It would be well, however, to apply Dyar's principle, at least to the early stages, before making any definite statements regarding other species of this genus.

All the measurements given above were made with an ocular micrometer, using a low power of the microscope. The smallest micrometer scale division was .019 mm., and it was found impracticable to interpolate to less than one-fourth this, a measurement of .005 mm. The embryos measured were all mounted in Canada balsam. The larvae of the first three instars, marked with a small circle, "°," were also mounted in balsam; those marked with an asterisk, "*," were mounted in glycerine; and those marked with an apostrophe, "′," were specimens preserved in alcohol. All the fourth and fifth instar larvae were preserved in alcohol after fixation in Gilson-Carnoy's fluid.

VIII. Food Plants

The plants on which the larvae feed are restricted to the genus *Betula,* with the possible exception of the alder, *Alnus incana.* Johannsen, who reports (1911) the single instance of larvae attacking the alder, has also reported (1910) the presence of larvae on red oak. There are other species of *Bucculatrix* which feed on oak, one of which is very common in Connecticut, and it is very probable that the larvae referred to by Johannsen were not *B. canadensisella.* The mines in oak leaves are very similar to those of the birch skeletonizer, but the cocoons are white and are found on the trunk and branches of the trees. I have not bred this species, but Forbes (1923) gives *B. ainsliella* Murtfeldt and *B. packardella* Chambers as indigenous to northeastern United States, and both feed on oak. Alder is closely related to birch, and although the larvae of *B. canadensisella* did not survive in laboratory tests, through one complete instar on *Alnus* (*rugosa?*), under different conditions they may possibly feed on this plant. Of the species of birch on which this insect lives, four are native and one imported from Europe. These are *Betula populifolia* (gray birch), *B. papyrifera* (paper or white birch), *B. lutea* (yellow birch), *B. lenta* (black birch), and *B. alba* (European white birch) respectively. The European birch is a common ornamental tree in northeastern United States and southeastern Canada, and varieties are called the cut-leaf or weeping birch. This tree in Canada seems to be a favorite food plant, but in the vicinity of New Haven it is not quite so severely attacked as the gray birch.

Of the four native food plants, the black birch seems to suffer least, although Maheux reports (1926) that in Quebec this tree has been heavily skeletonized. Which of the other three is most severely injured seems to depend on which is prevalent in the locality. In most of Connecticut the gray birch is the preferred food plant, but on the shores of Highland Lake, where the white and black birches are the only two species common, the white birches were heavily skeletonized in 1925; and in other parts of

Litchfield County, where yellow birch is quite common, it is a favorite host. In Ontario and throughout the Great Lakes regions, the yellow and white birches are the trees which suffer most. The black birch in Connecticut is very slightly injured and usually is untouched, even though its branches intermingle with those of the white and gray birches when these two bear thousands of caterpillars. In laboratory tests the larvae ate the leaves of the black birch very readily. These larvae were taken from gray birch and fed on black birch during the fifth instar. Five of the ten larvae pupated normally, although the duration of the instar was 173 hours on the average as compared with 117 hours for the control. This delay in maturing was partly due to the delay the larvae experienced in getting accustomed to the new food plant.

The red or river birch (*Betula nigra*) is not a common tree in northern United States and southern Canada, and this may be the reason that it is not reported as being attacked by this insect. New England is about its northernmost range, and here it is found only in a few scattered places along river banks. No attempt was made to rear the larvae on the leaves of this tree, as the material is not readily available, and there are no references in the literature to it as a food plant.

There are four other genera of plants belonging to the same family as the birches and growing very commonly in the same localities as these trees. These are *Ostrya* (hop hornbeam), *Carpinus* (ironwood), *Alnus* (alder), and *Corylus* (hazelnut). Under natural conditions I have never observed any of these plants attacked by the larvae of *B. canadensisella,* although they very frequently intermingle with the birches. In the laboratory the larvae have been forced to eat the leaves of *Alnus* but could not maintain themselves on these leaves. The larva itself has really very little to do with the choice of food plants, for this is a leaf-mining insect in the early stages, and if the egg is not laid on a leaf in which the larva can live, death results. Even during the external-feeding stages it is very questionable if a larva could survive long enough to travel from an unfavorable to a favorable plant unless the two plants were very close together.

In an attempt to secure eggs on the leaves of the alder, I placed two alder twigs, each bearing two or three leaves, in a cage with five males and five females. One of the twigs had been dipped in the distillate from an aqueous extract of birch leaves, and the other was normal. The moths were collected in the field. Two females lived six days, one five days, one three days, and one two days, but no eggs were laid. In another similar trial with one female and six males, the female lived four days but laid no eggs. In view of the fact that the females are loath to lay eggs in captivity, the results are merely indicative and not conclusive.

An attempt was made to force larvae to eat the leaves of the alder and the black oak. All these larvae were collected in the field on gray birch. Five larvae in the first molting webs were placed in vials with the leaves of each plant. On the alder all five larvae died in three and one-half days or less without feeding. On the oak some feeding occurred and one larva went through the fourth instar in eight days and then died, starved, in fourteen. Three of the others died of starvation in four and one-half days or less, and one was accidentally killed. Although alder is more closely related to birch than is oak, yet the black oak was preferred as food, though it could not sustain the larvae. Ten larvae were then similarly kept with the leaves of these two plants, but the leaves were previously dipped in a distillate from an aqueous extract of birch leaves. It is sometimes possible to make insect larvae eat materials that have the odor of their food plants. Of the ten larvae used in this case, five were in the fourth instar and five in the fifth. On the alder both instars fed a little. One fifth-instar larva lived ten days, and two fourth-instar larvae lived seven days, but none went through a complete instar. On the oak there was more feeding than on the alder. One fifth-instar larva spun a cocoon after five days, and three others lived between seven and nine and one-half days. One fourth-instar larva lived sixteen and one-half days, molting meanwhile, and three others lived between five and one-half and eight days. In only one instance on the oak was the fourth instar completed. Although the distillate from the birch extract made the alder and oak more attractive to the larvae, and they ate relatively much more of the leaves when so treated, they did not show any growth except in the one instance mentioned above. All but one gradually shrunk in size and finally died of starvation before molting. Control larvae fed on the gray birch were normal in development. On this basis the possibility of larvae under natural conditions living on either oak or alder seems remote, and the reports of feeding on these plants were probably cases of misidentification of the insect in question.

Under laboratory conditions the larvae from the gray birch very readily eat leaves of paper and black birch, and larvae from paper birch just as readily eat leaves of gray birch. In all cases the larvae will mature. The trials conducted were not sufficiently extensive to determine whether or not there is a racial difference in the individuals from different host plants. This racial difference would be primarily manifested by the oviposition response of the adult, and difficulties in securing eggs consistently from females have precluded any definite experimental evidence on this matter to date. When the larvae were reared in the laboratory they were placed on the plants under trial, and if they left these plants, they were put back again. This was continued until they ate the leaves or died. Under normal circumstances, no such condition would be met, and it is conceivable that the larvae might well starve to death in the midst of food which would sustain life, but which, for various reasons, they would not eat. The preference for birch as food, as concerns the larvae, is partly controlled by a chemical sense, for they eat oak and alder leaves more readily when these are first dipped in a distillate from an extract of birch leaves.

IX. Factors Affecting Abundance

The phenomenon of periodic outbreaks of *Bucculatrix* has been dealt with historically in previous pages. Some of the factors which have a bearing on the abundance and rate of increase of this insect deserve consideration. These may be grouped under food supply, climate, and natural enemies (including diseases). Man has not as yet played any direct rôle in the control of this species.

There is no scarcity of food plants in the northern United States and southern Canada, and the endemic population of Bucculatrix has no apparent effect on the growth of birch trees. Between outbreaks the larvae are scarcely noticeable. Paper birch forms a great part of the subarctic transcontinental forest and is a very common tree as far south as the Great Lakes and central New England. Gray birch is common farther south, and in New England and New York it is a weed tree which is constantly encroaching on cleared land. These two are the principal food plants and neither is being extensively cut by man. During an outbreak, when the larvae frequently eat all the foliage on the trees over considerable areas, the birches are not killed, even by several attacks in successive years, due to the lateness of the feeding period. The greater amount of feeding occurs during the last of August and September, and at this time of the year the trees have passed through the most active season and are not so severely injured as they would be by a similar attack earlier in the summer. This insect could probably never eliminate its food plant in any given region. It very probably checks the growth of the trees the year after a severe attack, but this check would not be sufficiently great to cause a decrease in the available larval food supply. Another factor that sometimes has some effect on the abundance of a particular insect is the competition for food with other species of insects. The defoliation of the birches in any region early in the summer would very obviously affect the survival of *Bucculatrix,* which feeds late in the season. At present this factor cannot be considered as of much importance. One of the most serious insect enemies of the birch in New England is the saw-fly, *Fenusa pumila* Klug, whose larvae mine the leaves during the entire summer, as there are several generations. Since this insect confines its work entirely to the new terminal growth, while *Bucculatrix* larvae feed by preference on the older leaves of the tree, the two live together in harmony. There is always the possibility of the last *Bucculatrix* larvae of the brood not having sufficient food, because of the work of the earlier developing part of the brood, and hence being unable to survive. The habit of spending two days in a quiescent state in the molting web increases this danger, for during these two days the foliage on the tree may be entirely consumed. All the observations made in the field indicate, however, that there is no reason to believe that there occurs any decrease in food supply which would have any very important effect in reducing the numbers of this insect even following a year when it was abundant.

No data have been obtained on the effect of climate on the survival of this species. The greatest danger to an insect is during the hibernating period, when severely cold weather sometimes kills off much of the population of certain species. It is a well-known fact, however, that insects which hibernate under the snow are better able to survive extremes of cold than species which hibernate above the snow line. For this reason a very cold winter would not be expected to have a very great effect on the population of the birch *Bucculatrix*. This is an indigenous insect and is inured to the climate of its present geographical range, and the greatest effect of climate on its abundance is probably indirectly through limitations on the distribution of its food plants.

It is not inferred that climatic variations have *no* effect on the population, but rather that climate alone is not responsible for the more or less regular rise and fall in abundance.

The parasites and predaceous enemies of this insect probably account for the increase and decrease in its numbers more than any other one factor. Ten species of Ichneumonoidea and Chalcidoidea have been reared from the larvae and pupae. One of these, *Hemiteles,* is very probably hyper-parasitic, as Viereck (1916) states that all the species of this genus are probably secondary or hyper-parasites. The 10 species with the stage of the host from which they *emerged* are listed below:

	Stage of Host
1. *Bucculatriplex secundus* Viereck Braconidae	pupa
2. *Haltichella xanticles* Walker Chalcididae	pupa
3. *Gelis urbanus* Brues Ichneumonidae	pupa
4. *Cirrospilus ocellatus* Girault Elachertidae	larva (ext. feeding)
5. *Gelis bucculatricis* Ashmead Ichneumonidae	pupa
6. *Mesochorus* sp. Ichneumonidae	pupa
*7. *Pleurotropis bucculatricis* Gahan Entedontidae	pupa
8. *Closterocerus* (*cinctipennis* Ashmead?) Entedontidae	larva (mining)
9. *Derostenus* sp. Entedontidae	larva (mining)
10. *Hemiteles* sp. Ichneumonidae	pupa

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* This is a new species the description of which, by Gahan, is published in Psyche, volume 34, June, 1927.

The family names are those used by Viereck (1916). These species are all small and occur singly in the host. The extent to which they parasitize the host varies, of course, from year to year and in different localities.

In the winter and spring of 1924 there were collected 397 cocoons from which there were secured 29 parasites as follows:

Gelis bucculatricis	14 specimens
Bucculatriplex secundus	7 "
Haltichella xanticles	6 "
Hemiteles sp.	2 "

These cocoons were collected from several localities around New Haven, where the host had been abundant in 1923. A large number of pupae died without metamorphosing, and only 152 adult moths were secured from this lot. In 1925 most of the pupae of which records were kept were from larvae reared in the insectary, and the parasitism, therefore, was abnormally low. Nine individuals of *Bucculatriplex secundus* and two of *Haltichella xanticles* were obtained from 352 cocoons. Conditions during the 1925 season of emergence were not normal, as the cocoons had to be kept in the laboratory. The records are not comparable to those obtained a year later. In 1926 there were collected during April and May 209 cocoons in a locality where the larvae had been very abundant the previous season. No collections had been made in this locality during either 1924 or 1925. All these cocoons contained pupae (as later examination showed), and from them were secured 53 parasites and 58 adult moths. The cocoons were kept outdoors in a shaded place until the emergence period was passed, and then those from which no insects had emerged (98 cocoons) were examined. Five contained dead parasites and 93 contained dead pupae. Of the insects which emerged, then, 47.7 per cent were parasites, and of the total number of pupae collected 27.7 per cent were parasitized. The parasites were of the following species:

Bucculatriplex secundus	37 specimens
Pleurotropis bucculatricis	12 "
Haltichella xanticles	1 specimen
Gelis urbanus	2 specimens
Undetermined (escaped)	1 specimen

It is evident that of the insects which emerge from the cocoons the parasites make up a large percentage, and the parasites are better able to survive than the host. Of the 151 non-parasitized pupae, only 58, or 38.4 per cent, produced adults, whereas of the parasitized pupae, 58 in all, 53 or 91.4 per cent produced parasites. The presence of a parasite in a pupa is very easy to determine after three months, as by this time the parasite has consumed most of the host tissue. A parasite could not have been easily overlooked in the examination of dead pupae. Since these parasites occur singly in the host, the percentages are comparable. There is, of course, the possibility that some of the parasitized pupae died before the parasites had developed far enough to be observed in a dead and desiccated host. The fact that of the 93 dead pupae above mentioned 44 had reached the pre-imaginal stage before dying indicates that this possibility would have no great bearing on the results obtained, for had any parasite been present in any of these, it would have prevented the host from reaching the condition of the pre-imago. It is also true that the parasites are better able to withstand high and low temperatures during the period of emergence than is the host. Three lots of 20 cocoons each were kept at different temperatures, one at 31-33°C., one at room temperature which varied between 18° and 26°, and one at 8-15°. The cocoons were placed in test tubes (50 cc. capacity), 10 in each tube. To serve as a check on the humidity effect, one of the tubes of each lot contained a piece of wet blotting paper which produced a moisture-saturated atmosphere in that tube. The other tube received nothing. All tubes were kept corked except for an interval of about one minute each day when they were opened in the room in order to renew the air supply. The relative humidity of the room averaged 67 per cent, with a variation of 13-14 per cent each side of this for brief intervals of time. The experiment began June 2, 1926. From the cocoons held at room temperature 18 insects were secured, nine from each tube. This represented a normal emergence. Four of these were parasites, all *Bucculatriplex secundus,* and 14 were adult moths. From the cocoons held at 8-15°, two parasites only emerged, one from each tube. One was a specimen of *Bucculatriplex,* and the other was *Mesochorus* sp. From the cocoons held at 31-33° two parasites only emerged, both from the tube containing room air. Both were *Haltichella xanticles*. After being examined July 10th, all the cocoons from which no insects had emerged were removed to the outdoor insectary. Eight adult moths subsequently emerged from the tubes that had been held at 8-15°, four from each tube. After the emergence period was well passed the remaining cocoons were examined. No dead parasites were found, and most of the dead pupae had reached the pre-imaginal stage. Although the number of insects concerned was not large, the parasites were very evidently better able to withstand the extremes of temperature than was the host, for all the parasites emerged under these conditions, but no moths were obtained. The two parasites which came out of the tubes held at 8-15° emerged July 3, and the two from the tubes held at 31-33° emerged June 5 and June 6 respectively. In the case of the latter two, it might be suspected that the difference in development between host and parasites enabled the parasites to complete the metamorphosis and emerge when the host could not, for they were exposed to the high temperature only three and four days. However, from a third tube set up the same as the others but containing calcium chloride and held likewise at 31-33°, there emerged two parasites only, one specimen of *Bucculatriplex secundus* on June 23, and one specimen of *Pleurotropis bucculatricis* on July 4. The cocoons in this last tube were exposed not only to the high temperature, but also to the desiccating effect of the chloride. No adult moths were secured, and no parasites died before emerging.

In addition to this emergence of parasites from pupae, there is sometimes a considerable parasitism of the mining larvae by *Closterocerus* and *Derostenus*. When these parasites were first discovered, it was thought that they were one and the same species, as they were in the larval stage and resembled each other closely. They are therefore grouped together here. If the mines of the *Bucculatrix* larvae are examined in September, many will be seen to contain the remains of the larva and in addition a very minute parasite larva about .75 mm. in length. September 10 and 14, 1925, there were collected 619 *Bucculatrix* mines in gray birch leaves. Of these, 522 were vacant and showed by the exit hole that the *Bucculatrix* larva had emerged normally. The other 97, or 15.7 per cent, contained each the remains of a *Bucculatrix* larva and one parasite larva belonging to one of the two genera in question. The only exception to this was one mine which contained two parasite larvae. The first of October, 1926, the same locality was visited and 289 mines were collected. The mines this year were much less abundant than in 1925. Of these 289 mines, 100 had been normally vacated by the *Bucculatrix* larvae and 58, or 20.1 per cent, contained parasites. The remainder, 131, contained dead *Bucculatrix* larvae, but the cause of their death could not be determined. It could hardly have been the parasites in question, for the *larvae* of these two species were found in the other mines.

The above figures show that there may be a heavy mortality of the host by the combined attack of the parasites. Of these, *Bucculatriplex secundus* is the most commonly found. Only one locality has been examined for *Derostenus* and *Closterocerus,* and it is not known just how widely spread these two species are. *Pleurotropis bucculatricis, Haltichella xanticles,* and *Gelis bucculatricis* are also rather common. One specimen only has been secured of *Mesochorus* and *Cirrospilus ocellatus*. The former emerged from a cocoon in 1926, and the latter was found in the pupal stage in a molting web of *Bucculatrix*. *Hemiteles* may be a secondary parasite and hence of no use in checking the reproduction of *Bucculatrix*. There is a possibility that some of the others also are secondary parasites.

The adults of *Derostenus* appear the last of the summer, but the adults of the other parasites appear about the same time that the host adults appear. This indicates that there may be other hosts for some of the parasites. *Bucculatrix secundus* hibernates as a larva in the pupal cuticle of the host. *Derostenus* and *Closterocerus* kill the host larva before it completes the third instar and hibernate as larvae in the mines of the host. The other species hibernate in the pupal cuticle of the host, but the hibernating stage of these was not determined. All the parasites are minute. The Ichneumonoidea adults are about 1.75-2.00 mm. in length, and *Haltichella xanticles* is about the same size. *Pleurotropis bucculatricis* is about 1.5 mm. long, and *Derostenus* and *Closterocerus* are each about .60 mm. in length.

More important as enemies of the *Bucculatrix* larvae than any one of the above species of parasites, and perhaps than all of them combined, are the various species of ants and other predaceous insects which capture the larvae when they descend to the ground to pupate. Ants will not only capture the larvae before the cocoon is well begun, but will also pull a larva out of the cocoon in which it is almost entirely enclosed. In 1925 ants destroyed the entire stock of larvae in the insectary. On one occasion the litter on the ground under a birch which had borne hundreds of larvae was very carefully examined for cocoons after all the larvae had disappeared, and not over 25 entire cocoons were found. A large number of the cocoons were partly completed. This tree had been under observation and no extensive mortality of the larvae on the leaves was noticed. There is no question that most of the larvae reached the ground, and most of these fell prey to their insect enemies before they could pupate. In collecting cocoons in the field in localities where there has been an outbreak of larvae and the trees have been practically defoliated, it is surprising to find relatively few cocoons that are entire and contain pupae.

Although no detailed observations have been made on the activities of birds, Dr. Britton informs me that he has observed certain warblers apparently feeding extensively on the larvae. While there is no question that birds do have some effect on the abundance of these insects, the effect of ants and other predaceous insects seems to be much greater.

The interrelations of host, parasites, and predaceous foes have been very clearly described in the case of the fall webworm by Tothill (1922), whose conclusions are here briefly summarized, and many of the reasons for the occurrence of outbreaks and the following decline in numbers of this insect are applicable to *Bucculatrix canadensisella*. Under normally balanced natural conditions the parasites are most effective and keep the host in an endemic and harmless state for a number of years. The predaceous enemies are also effective, for without their help the host might increase in spite of the parasites. The combined attack of parasites and predaceous foes reduces the numbers of the host, but at the same time the number of parasites is reduced, for a competitive struggle for food occurs among the species of parasites and among the members of one species. During the last few days of its life in the host, the parasite is much more destructive to the host tissue than at any other time, and although several parasites may start life in one host, which is particularly the case when the host becomes scarce, the only individual that survives is the one which first reaches this rapidly destructive stage, the others perishing from lack of food. The predatory enemies apparently do not discriminate in favor of the parasitized larvae, and this also tends to reduce the number of parasites. Some species of parasites may become locally extinct, and not being strong fliers, do not come in again from the surrounding territory for some years. Any environmental change favorable to the host now gives it an opportunity to increase in the absence of a large part of its enemies, and it soon reaches a stage of great abundance. After a period of years the parasites, which have now found themselves provided with an abundant food supply, increase, and finally, with the aid of the predaceous foes, overcome the host and again reduce its numbers to an endemic state. Over a long period of years the result of these opposing factors is a series of outbreaks following each other at more or less regular intervals. When the host begins to decrease markedly, the parasites also begin to decrease, since they have more difficulty in finding the host, so during the decline of the host population there is not necessarily an increase in the percentage of parasitism. For example, during 1925 the parasitism of *Bucculatrix canadensisella* mining larvae by *Closterocerus* and *Derostenus* was 15.7 per cent, and the following year, in the presence of a very marked reduction in the abundance of mines, the parasitism from these two species was increased only 4.4 per cent.

When the larvae of *Bucculatrix* are abundant there may be expected up to 20 per cent parasitism in the mining instars and an equal percentage of parasitized pupae. To this must be added a heavy mortality due to predaceous enemies. There are also certain undetermined factors, possibly both internal and external, which prevent the development of the insect beyond the pupal stage and cause the mortality of a number of pupae. These last factors are more effective on the host than on the parasite. Aside from the effect of parasites, a considerable number of the mining larvae may sometimes succumb from some cause unknown to the writer. All the factors except parasites maintain a constant attack on the various stages of *Bucculatrix canadensisella,* and when the *Bucculatrix* population begins to decline, the severity of this attack is more keenly felt. A parasite population fluctuates with a host population and has direct bearing on the periodic abundance of the host but cannot entirely eliminate it, as the parasites decrease when the host decreases.

A species of fungus belonging to the genus *Verticillium* has frequently been found growing on the dead pupae of this insect, and it was thought at first that this might possibly be the cause of these fatalities. Several attempts to inoculate healthy normal pupae with cultures grown on oat agar failed completely. The procedure followed was to make a small opening in the cocoon and expose the pupa within. A drop of water containing a suspension of the spores and mycelium was placed on the pupa, which was then set aside in a petri dish for future observation. Although a number of inoculations were made, in not a single case did an infection of the pupa develop, and it was concluded that the fungus concerned is entirely saprophytic. Several species of *Verticillium* are found on dead insects. I am indebted to Dr. McCormick of the Connecticut Experiment Station for determining this fungus and for carrying out the inoculations.

X. GEOGRAPHICAL DISTRIBUTION

This insect, as far as reports in the literature and information acquired directly from entomologists indicate, is found only in the northern United States and in Canada. Its southern limit is North Carolina, and in Canada it occurs in New Brunswick, Quebec, Ontario, Manitoba, Saskatchewan, Alberta, and British Columbia. Mr. Hutchings, of the Entomological Branch, Ottawa, informs me that it probably occurs up as far as the Yukon. It is recorded as far west as Minnesota in the United States. In Ontario, Quebec, New Brunswick, the New England States, New York, Michigan, Wisconsin, and Minnesota it is very common and sometimes appears in such numbers that the birches are defoliated. On the map (figure 34) is marked with a cross every locality from which I have definite records of the occurrence of the insect.

According to data obtained from Sargent's "Silva of North America" (1896), the four native food plants (the paper, gray, yellow, and black birches) of *Bucculatrix canadensisella* occur over a much wider area than that from which the insect is reported. The region occupied by these birches is shaded on the map. The paper birch (*Betula papyrifera*) is very widespread and is a favorite food plant. It is found almost everywhere within the shaded region on the map, but it is not abundant west of the Rocky Mountains nor south of Minnesota, Wisconsin, Michigan, and New York. The red birch (*Betula nigra*) is not a common tree in northern United States and I have no records of its being attacked by this insect. Its range extends much further south

FIG. 34. Distribution of *Bucculatrix canadensisella* Chambers and its food plants. The shaded area shows the distribution of the gray, paper, yellow, and black birches. The crosses indicate localities from which the insect has been recorded.

than that of the other birches. The parts of North America in which these food plants (*B. populifolia, B. papyrifera, B. lutea,* and *B. lenta*) are found corresponds very closely with the boreal and transition zones as outlined by C. Hart Merriam (1898), except for the Rocky Mountain region of the United States. In

Indiana, which is just south of the transition zone, the insects are not plentiful, and in New Jersey they are reported from two counties, Essex and Morris, both in the northern part of the state, and both within the transition zone. In North Carolina adults have been collected in Jackson County. Although the geographical distribution of the birches in the North includes Newfoundland, there are no records of the occurrence of *B. canadensisella* on that island. It is possible that the distribution of this insect coincides with that of the paper, gray, yellow, and black birches, but the map clearly shows that it is most commonly found in the region around the Great Lakes and thence east to the Atlantic Ocean.

That the pupal stage can withstand low temperatures is quite evident, for the region around Port Arthur, Ontario, and the northern shore of Lake Superior very frequently reaches between -20°F. and -30°F. Temperatures would not interfere with the spread of the insect rather far north in western Canada, for the isotherms during the winter run in a curve from Quebec south, and then north through Saskatchewan and Alberta, making the Dakotas, the northern shore of Lake Superior, and the region just north of it much colder than regions directly to the east and west, and this insect is frequently very abundant along the northern shores of Lake Superior. The fact that it hibernates on the ground under leaves and under the winter snow also enables it to endure a very cold climate. It would not be surprising if an examination of white birches during the last of the summer in the northern limits of the range of this tree would reveal the presence of this insect. The southern limit of the insect is also very probably the southern limit of its food plants. This is a very small and inconspicuous moth, and unless it is present in large numbers, it is easily overlooked. As the larval food plants become scattered along the limits of their geographical range, the insect becomes less noticeable. That it has not been reported from more localities is not surprising.

During seasons when it is not very abundant over any great area, the infestations of *B. canadensisella* are often spotted, and a small group of birches may have their leaves completely skeletonized, while one hundred yards away the leaves of others are practically unharmed. This is in all probability due to the fact that the insect flies very little and very rarely goes beyond the shelter of the birch trees.

The insect has probably reached its present geographic range by entirely natural means of spread, for its habits preclude any great distribution by human agencies. It is found on the trees only in the larval state, and then on the leaves only. If birch trees are shipped any distance, transportation always occurs when the tree is dormant and bears no leaves. Birches are cut after the leaves fall, so that there is little probability of cocoons occurring on cut timber. Early records of forest-inhabiting species of insects are none too common in North America, and *B. canadensisella* was probably very prevalent over the entire area from which it has been reported before Chambers described it in 1875. Even today it attracts no attention except during those periods when it becomes extraordinarily abundant and defoliates the trees.

XI. EFFECT OF TEMPERATURE ON DEVELOPMENT

In view of the fact that temperature seems to be a very important factor in the development of these insects, experiments were carried out to determine the effect of different temperatures on the larva during the period when it was feeding externally on the leaf; that is, during the fourth and fifth instars. The temperatures used ranged from 10° to 35°C., and each temperature was held as nearly constant as possible under the conditions. Those at the lower end of the range, 10°, 11°, 12°, were obtained by using ice-boxes. Incubators were used for 25°, 29°, 34° and 35°, and an incubator was cooled with ice for 14° and 15°; 20°, 21° and 22° were laboratory temperatures. Observations were made at 8.00 A. M., 2.00 P. M., and 10.00 P. M., or as close as possible to these hours, each day, and the temperature and condition of the larvae noted. This gives a possible error of four to five hours in the observations, but in a series of observations this error tends to be compensated. The temperature for any given larval stage is the average of all the readings, and the charted temperatures are those obtained daily by averaging the three temperatures for the day. In all cases a fairly constant daily temperature was held. The temperatures were averaged for each individual larva, and the fluctuations of a degree in either direction made the mean temperatures for different larvae kept in the same location vary slightly. For this reason the groups tabulated under 11° and 12° were both held at the temperature charted on line (c), text figure 35, those tabulated under 14° and 15° were held at the temperature charted on line (d), those under 20°, 21°, and 22° on line (e), and those under 34° and 35° on line (h). In some stages there is a difference of only one degree between groups with very little difference in the duration of the stage at the different temperatures. This is due not only to the fact that one degree would not be expected to show much difference under the conditions, but also to the method of averaging temperature readings. The tabulated temperatures are correct within one-half of one degree; that is, if the temperature for one larva during the fourth instar averaged 20.4°C., that larva was placed in the 20° group. A difference of one-tenth of a degree in the average might throw the larva into a higher group, for if the temperature averaged 20.5°C., the larva was placed in the 21° group.

In view of the fact that the larvae kept in ice-boxes were in darkness, eight larvae were reared in a dark box at the laboratory room temperature, 20°-21°C., as a check on the effect of absence of light. Two of these died in the fifth instar and the other six pupated. The mortality was not exceptional. The mean duration of the fourth instar was 125 ± 5.1 hours, with a standard deviation of 21 hours; the mean duration of the fifth instar was 131 ± 4.3 hours with a standard deviation of 18 hours, and the mean duration of the entire external feeding period was 248 ± 6.8 hours with a standard deviation of 25 hours. These periods are practically the same as the periods of larvae reared at the same temperature in the lighted laboratory, and the absence of light caused no error.

The larvae were reared in individual glass vials as described previously, and the relative humidity was kept constant by wet sand in the vials. The leaves used as food were renewed as often as was necessary for keeping the food material fresh and unwilted. At temperatures of 25° and higher, the leaves were renewed daily; at 14°, 15°, 20°, 21° and 22°, every other day; at all temperatures below 14°, twice a week. ·The leaves used were all from the lower parts of gray birch trees, that is, the older leaves, and in all but three or four instances were from the same group of trees. Leaves selected were as uniform as possible. All the larvae used in this experiment were obtained from gray birches bordering a field about eight miles north of New Haven. The large number of larvae reared at room temperature (20° and 21°) was due to the fact that a control of each lot of larvae was kept at this temperature.

Four larval periods were considered: (1) the quiescent period in the second molting web; (2) the fourth larval instar, which includes the period in the second molting web; (3) the fifth larval instar up to the spinning of the cocoon; (4) the entire period of life spent outside the mine, which includes the fourth and fifth instars. Although the fifth instar really includes a prepupal period in the cocoon, observations on this period were not possible without disturbing the conditions of the experiment, so this prepupal period was omitted. The actively growing period of the larva is over when feeding ceases, and the omission of the prepupal period does not affect the results. In each case the end-point is sharply defined.

The chart on page 465, figure 35, gives the temperatures at which the different groups of larvae were kept, and the letter in parentheses at the left of each temperature curve corresponds to the same letter opposite each temperature in tables 4 to 7 and indicates the curve for that temperature group. In the tables are given the number of each larva, the day it began the period represented by the table, the duration of that period, the mean duration for each temperature group, and the standard deviation for each temperature group (in parentheses after the mean). The temperature at which any larva or group was held, together with the temperature fluctuations during the period, may be ascertained by examining the temperature chart (figure 35). Fluctuations occurred one degree each side of the mean except in a few cases where a brief fluctuation of two degrees is found. The latter cases were so few and the variations in temperature for any one larva were of such brief duration that the results are not affected. Table 8 on page 481 is a condensation of the other tables and gives the data which form the basis for the curves shown in figures 36 to 40. These curves show the relation between temperature and development.

Each figure contains two curves. The curve marked A gives the duration of the period in hours for each temperature within the limits of the curve. The abscissae represent degrees centigrade, and the ordinates, on the left of the figure, hours. The number of degree-hours (developmental units) required for development at any temperature may be calculated from this curve by multiplying time by temperature. If the curve conformed to the formula of a true equilateral hyperbola, the number of degree-hours for each point on the curve would be the same, according to the mathematical definition of the curve, and this constant figure would be the so-called "thermal constant." In no two consecutive temperatures of the experiment were the number of degree-hours equal or approximately equal, and the curves clearly show that no thermal constant exists in the development of the larvae under these experimental conditions. The curve marked B gives the index of development for each degree of temperature. The abscissae are the same as those of the A curve, and the ordinates, on the right of the figure, are the reciprocals of the ordinates of the A curve. Each point on the B curve gives that fraction of the total development which is completed in one hour at that particular temperature. The curve thus gives the rate of development directly and changes in that rate corresponding to changes in temperature. If curve A conformed to the formula of an equilateral hyperbola, the curve B corresponding to it would be a straight line by definition, but A is not an equilateral hyperbola, and B is not a straight line. Where a thermal constant exists, the rate of development curve B is always rectilinear, and if a thermal constant exists for any narrow range of temperatures, within that range the developmental curve is straight. According to the data and the curves, there is no thermal constant over any range of temperatures greater than the error of the experiment. In drawing the curves, the points were plotted for the A curve from the experimental data, and the curve was made to conform to these points as closely as possible. These points are enclosed in small circles in the figures. The index of development curve B was then drawn to conform to curve A, and the reciprocals of the plotted points in A are enclosed in circles in B. In the absence of a thermal constant, the rate of development of the larvae and the degree-hours required for the completion of any stage must be calculated from the curves directly. No attempt has been made to project the curves beyond the limits of the experimental data.

The lowest constant temperature at which larvae would survive the fourth and fifth instars and pupate was found to be between 10° and 12°C., and the highest temperature was found to be slightly under 34°C. Eight larvae in the first molting web were held at 6°C. [line (a)] 6 days, during which time they did not molt, and four larvae were held at 3°-6°C. [line (a)] 10 days. during which time no molting occurred. The duration of the period in the molting web at 21° is about 40 hours. All twelve of these larvae molted within 29 hours after removal to the laboratory, where the temperature was 20°-21° [line (e)]. Development thereafter was normal. Six larvae in the first molting web were kept at 9°-10°C. [line (b)]. None of these completed development, but three molted within 9 days and lived 50 days. 39 days, and 10 days respectively, after the molt. The other three died in the web without molting. Ten larvae in the second molting web were kept at 9°-10°C. [line (b)], and all molted within 8 days. Four died in 24-45 days, and six pupated in 18-30 days. Controls of all these larvae kept at 20°-21° in the laboratory were normal and had a mortality of zero (25 larvae in all). It is quite apparent that although some development occurs at 9°-10°C., the continuous exposure of larvae in the fourth instar to this temperature is fatal. If the larvae are in the fifth instar, they may or may not complete development, depending on individual hardiness. Ten larvae in the first molting web were kept at 11°-12°C. [line (c)]. All molted within 4 days, 8 completed the fourth instar, and 7 pupated. Ten larvae in the second molt web were held at the same temperature. Eight of these molted within 3 days and pupated. Controls of these two lots were kept at 20°-21° in the laboratory [line (e)], were normal in development, and had a mortality of 2 larvae in 22. At 11°-12°C., development is slow but otherwise is normal. It may possibly be that the fifth-instar larvae are more able to withstand low temperatures than the fourth. Death at 9°-10°C. seemed due to starvation, the cold preventing the larvae from feeding, and even under normal conditions the fifth-instar larvae eat more constantly than do those of the fourth instar. The larvae at this low temperature were always sensitive to touch, and sometimes spun silk threads. It appears as if the first effect of the cold was to stop feeding activity. The larvae then shrunk in size and finally died from lack of nourishment. The curves (figure 39) of development for the period including the fourth and fifth instars necessarily begin at 12°C., in accordance with the above facts.

At the high temperatures (34°-35°) the effect was somewhat different. The procedure was essentially similar to that described for the low temperatures, and the temperature line (h) in figure 35 depicts the temperature used. This temperature was also fatal to fourth-instar larvae if maintained continuously, but the larvae were able to molt, complete the fourth instar, molt again and begin the fifth instar. None pupated, however. Feeding was very actively carried on until about 12-24 hours before death, and starvation was not a factor to be considered. Fifth-instar larvae molted and pupated without difficulty. The data for the larvae at these temperatures is given in the tables. Since the total feeding period could not be completed at 34°-35°C., the curve of this period stops at 29°C., the highest temperature at which the larvae completed two instars and pupated. At the high temperature, as well as at the low, the fifth-instar larvae seemed better able to endure the adverse conditions and fed more consistently. The lethal high temperature, using the curve as a guide, is in all probability very close to 34°C.

The above data demonstrate that a real threshold of development ("developmental zero") and a real maximum lethal temperature are determinable only when the length of exposure to those temperatures is considered, and that some development may occur at temperatures beyond the lethal high and low (for the entire period) if these exposures are not too prolonged. The difference between that temperature which gives a maximum speed of development and the lethal high is much less than the difference between the same maximum and the lethal low, but development occurs at both extremes. For example, at 9°-10°C., the fourth-instar larvae will ultimately die, but some development will have occurred meanwhile. The same is true of 34°-35° and even higher, for in another experiment an exposure to 37°C. for a few hours caused neither cessation of feeding nor other deleterious effects. In calculating the effect of low temperatures on the life cycle of insects, it has been customary to eliminate all "ineffective temperatures"; that is, all temperatures below a given threshold, this threshold depending, of course, on the insect in question. Theoretically the developmental curve B (figures 36 to 39) should cut the temperature axis at the threshold of development. The corresponding theoretical point on the time-temperature curve A would be at infinity. The curve B, however, shows no marked inclination toward the temperature axis at its lower end, and it would be rash to predict from any data obtained by a time-development study just where it is going to cut that axis. Under natural conditions the temperature fluctuates considerably, and even though it should rise above or sink below that point at which the larvae could not complete development, some development would probably take place at these extremes of the fluctuations. The fact that the curve A is not a true equilateral hyperbola and the curve B is not a straight line makes it inadvisable to project these curves beyond the experimental data in order to determine theoretical points, and no attempt has been made to determine an absolute threshold of development.

The curves A and B in figures 36 to 39 show clearly the depressing effect of high temperatures on the larvae. According to these figures the maximum rate of development would occur at 30°-31°C., and the experimental data give the maximum rate at 29°C., no experiments being carried out between 29°C. and 34°C. Either side of the 30°-31° point, the rate of development is slower, whether the temperature rises or falls.

The curve B shows the rate at which the speed of development varies and the direction of this variation for each degree of temperature. Beginning at the lowest point in the curve, the rate at which development is speeded up increases with each increase in temperature until at a certain point, the steepest part of the curve, a maximum is reached. At this point fluctuations in temperature have their greatest effect on the development of the larvae. As the temperature increases above this point, the rate at which development is speeded up with the rising temperature decreases until the point of maximum rate of development is reached, 30°-31°C. Any increase in temperature beyond this causes an actual decrease in the rate of development. It is this variation in rate of development which forbids the "summing" temperatures on a "developmental unit" basis.

In all four figures (36 to 39) the curves are sigmoid. In the curves representing the total external feeding period, those temperatures beyond 12°C. in one direction and 29°C. in the other are omitted, due to the non-survival of larvae beyond these points, but the curves take the same general form as the others. The effect of temperature in these experiments was similar for both quiescent and active periods. The shorter periods give the better developmental curves, for as the period lengthens the index of development becomes less numerically, and the curve "flattens," if the system of coördinates remains unchanged. In figure 40 the rates of development as actually obtained have been plotted on logarithmic paper, and the curves give a correct impression of the relative effects of temperature for the different stages. The curves are much more nearly parallel than those plotted on arithmetic paper and show that the effect of temperature on the rate of development of the different stages is somewhat similar.

Due to the small scale on which the curves are drawn, the steepest part of any one of the curves is somewhat difficult to determine by mere examination. However, a calculation of the tangents of the curves at all temperatures shows that for the period in the second molting web this steepest part lies between 21° and 22°; for the fourth instar, between 23° and 24°; for the fifth instar, between 24° and 25°; and for the total external feeding period, between 23° and 24°. The tangents of these parts of the curves are 1.8855, .6335, .4280, and .2300 respectively. These tangents are calculated for the rate curves as drawn. The lower temperature at which this is found in the period spent in the second molting web may be due to the inactivity of the insect. The temperature relations for the two feeding instars approximate each other fairly well.

A theoretical use of such curves as those marked B in the figures in considering the development of an insect under natural conditions where fluctuating temperatures occur is in the prediction of the time taken to complete a stage of development. In making such calculations, if the mean temperature of a short duration of time, a few hours, for example, be ascertained and the index of development at this temperature be multiplied by the number of hours during which this mean temperature is considered effective, the amount of development completed during this time can be approximately determined. When the sum of these last determinations equals 1, the development is theoretically completed. This is the method proposed by Sanderson (1908) and seems to be more logical than any alternative method. In practice it has been customary to determine the mean temperature for each hour. The method more commonly used in determining amount of development during short intervals of time under conditions of fluctuating temperatures depends on the assumption that the changes in velocity of development vary directly with increases in temperature and that the velocity curve (B in the figures in this paper) is a straight line for a certain temperature range, if not for all temperatures between the "threshold" and the "maximum." With such an assumption there exists a thermal constant within certain temperature limits ("medial" temperature according to Shelford—1926) and the number of developmental units required to complete development is this thermal constant, i. e., the product of time by temperature. If the amount of development completed during a brief interval of time be computed, it will represent a fraction of the thermal constant (*not* of 1), that is, a certain number of developmental units. When the sum of these determinations, the total of developmental units, equals the thermal constant, development is theoretically completed. The fault with this method lies in its uselessness when the velocity curve is not a straight line, and even if part of this curve is assumed to be straight, the method is not good for fluctuations outside of this temperature range. The small scale on which curves are plotted sometimes gives an erroneous impression of rectilinearity.

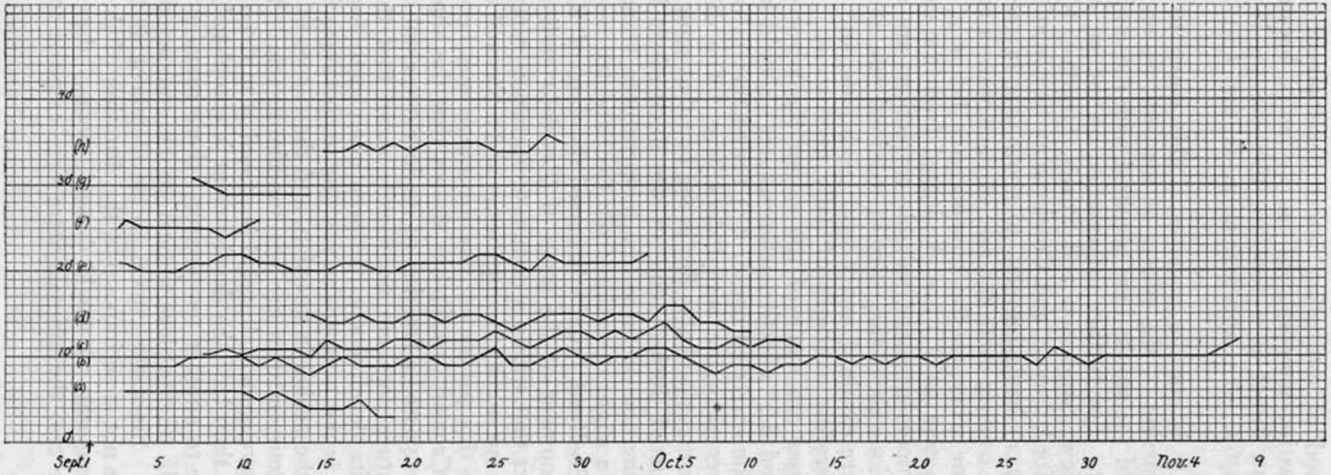

FIG. 35. Chart of temperatures of incubators, etc.

Any method of estimating insect development by averaging widely fluctuating temperatures has its faults, because the development of an insect at a constant temperature is not uniform (Crozier 1926). An approximation is the best that can be attained.

Although it is not the purpose of this paper to enter into a detailed discussion of the effects of temperature on insect life, a comparison of the results here obtained with those of some others is of interest. For further information on the subject the works of Bachmetjew, Sanderson and Peairs, Headlee, Krogh, Glenn, Peirce, Shelford, Payne, and Crozier may be consulted.

Glenn (1922) has attempted to show that in the case of the pupae of the codling moth the rate of development curve becomes a straight line when all the temperatures below a physiological zero (in this case 52°F.) are eliminated from the calculations of the mean temperatures and suitable corrections are made for the high fluctuations above the point of maximal rate of development. The data were obtained under field conditions, and the temperatures are therefore averages of daily fluctuations. However, if the calculations are made of the values the lower points (5.1°, 6.8°, 7.0°, and 8.6° effective temperatures) should have in order to fall into the corrected curve, it is found that in every case the value is lower than the actual data give. The differences are small, but the error probably lies in the fact that some development actually occurred during some of the fluctuations below 52°F., and the elimination of these low temperatures from the calculations caused a slight deviation from the expected results.

Recently Shelford (1926) has used the data of Krogh (1914) on the development of the pupa of *Tenebrio molitor* to demonstrate the fact that within a certain temperature range the rate of development curve may be rectilinear and a thermal constant may be used. In this particular case the range was between 18.5°C. and 28°C. Crozier (1926) has shown that the simple fact that an animal has passed a fraction of its developmental time at a certain temperature does not necessarily mean that that particular fraction of its development has been completed, for the rate of development is not uniform at any one temperature for the entire duration of the period in question, and the curves of development at any two temperatures are not superimposable. Thus, if one-half of the developmental period is passed at a given temperature, more or less than half the development is completed, and when a shift is made to another temperature, there remains more or less than one-half of the development to be completed at the new temperature. Since the curves of development at the two temperatures are not superimposable, the duration of the total period at the two temperatures would depend, among other things, upon which of the two the animals were first exposed to. This fact

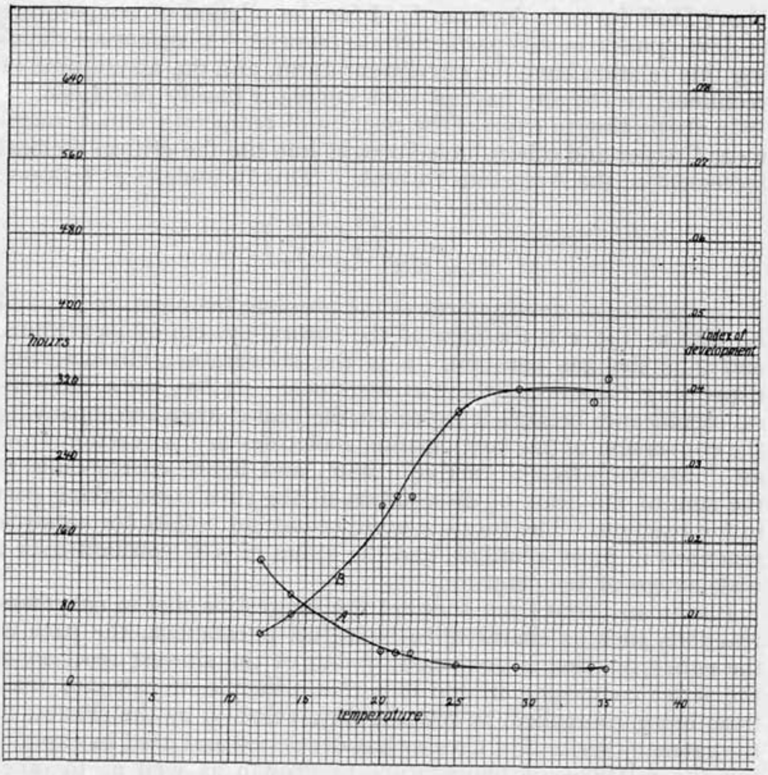

FIG. 36. Effect of temperature on the period in the second molting web. A is the time-temperature curve, and B is the rate of development curve.

alone would throw doubt on the justification of using a thermal constant for any range of temperatures. Moreover, the actual data of Krogh show that the curve is not truly rectilinear even between 18.5° and 28°, but is slightly sigmoid. The calculations were made from Krogh's data, and the last figures are added to show the trend of the curve outside the range in question.

Temperature	Tangent to curve	Angle of curve
18.0 -20.9° C.	.8143	39° 9′
20.9 -23.65	.8291	39 40
23.65-27.25	.8500	40 22
27.25-32.7	.5321	28 1

If the curve were rectilinear between 18.5° and 28°, the second and third tangents at least of those given above should be equal. Moreover, according to Krogh's own statement the Q 10 of the

Van't Hoff formula does not hold for the relation of temperature to development in this particular experiment. Most curves showing this relation have the curvilinear form, and the assumption of rectilinearity for any part of such curves is hardly justifiable.

In attempting to express the relation of temperature to development Crozier and others have brought into use the critical thermal increment of the Arrhenius formula. This formula is as follows:

$$K_2 = K_1 e^{\frac{\mu}{2}\left(\frac{1}{T_1} - \frac{1}{T_2}\right)}$$

K_1 is the rate of development at the absolute temperature T_1, and K_2 that at T_2; e is the base of the natural system of logarithms, and 2 is the gas constant. μ is the temperature characteristic expressing the critical thermal increment. It has some theoretical significance because it expresses the heat change accompanying the conversion of the participating molecules in the reaction from an "inactive" to an "active" state, and hence corresponds to the sum of the heats of dissociation of the substances taking part in the reaction. The formula gives consistent results for catalytic reactions in pure solutions, and the value of μ is constant over a wide range of temperature.

Blackman (1905) put forward the suggestion that in enzymatic reactions such as characterize biological phenomena, the pace of the entire reaction is governed by that of the slowest reaction of the series composing it, and it is this principle of catenary reactions being controlled, as regards their velocity, by the slowest of the catenary series that Crozier has developed and used in explaining the relations of temperature to growth as well as to other biological processes. Within a certain range of temperatures a certain reaction may be the slowest in the process and hence will govern the speed of the whole, but when the temperature rises above a definite point, another reaction of the chain becomes the slowest and hence the governing one. Within the temperature range governed by one reaction of the series, the temperature characteristic for that reaction is the temperature characteristic for the whole process, and when the second reaction becomes the governing one, a different characteristic, that of this second reaction, governs. In a monomolecular reaction the curve obtained by plotting the logarithm of the rate against the reciprocal of the absolute temperature is rectilinear, as can be readily seen from the formula of Arrhenius. The problem becomes one of getting the value of the critical thermal increment (temperature characteristic) for the process at different temperatures and plotting the above curve. If this is rectilinear, the value of μ is constant, and a temperature constant for the process is obtained.

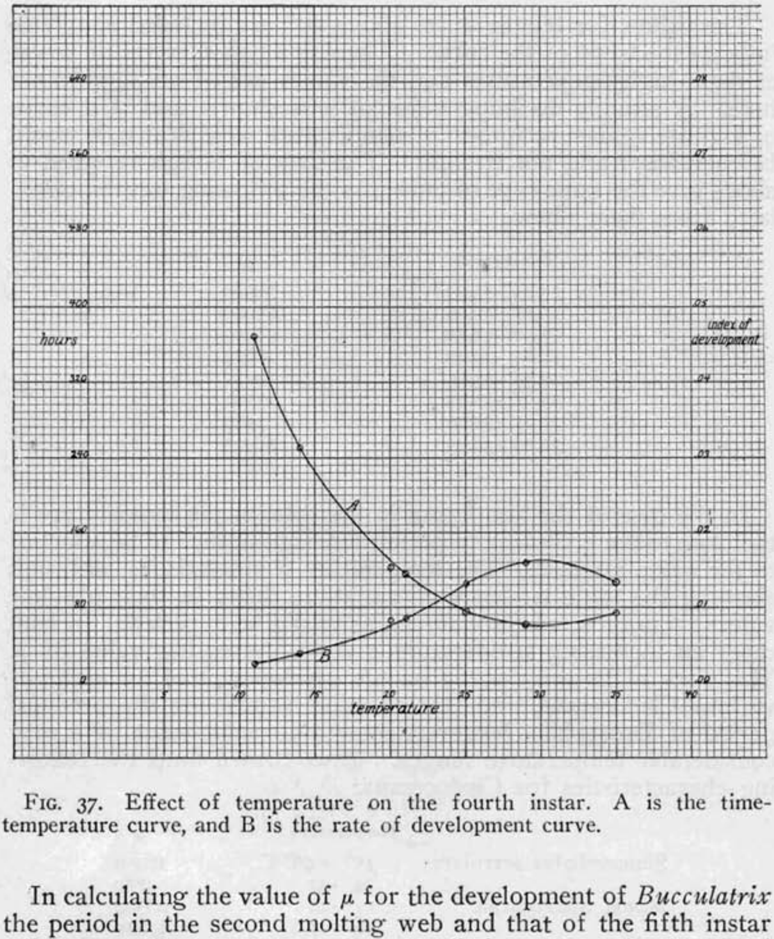

FIG. 37. Effect of temperature on the fourth instar. A is the time-temperature curve, and B is the rate of development curve.

In calculating the value of μ for the development of *Bucculatrix* the period in the second molting web and that of the fifth instar will be considered, as they give two distinct phases in the larval life, and in this particular case contain the data for the most larvae. The values are as follows:

Second Molting Web Temperature	μ	Fifth Instar Temperature	μ
12°-14°	24468	12°-15°	20644
14 -21	23003	15 -21	16637
21 -25	16396	21 -25	14709
25 -29	3431	25 -29	9694
		29 -34	—7793

The values for temperatures above 29° are included simply to indicate the trend of the curve. There is a non-survival of larvae at these high temperatures and the values are of no significance here. A steadily declining value of μ is shown, and if a curve of log rate against reciprocal of temperature were drawn, it would be curvilinear and not straight. The data of Krogh referred to above give the same type of curve, as the following figures, calculated from them, show:

Temperature	μ
13.45°-15.55°	32989
15.55 -17.00	25040
17.00 -18.80	28400
18.80 -20.90	26673
20.90 -23.65	19475
23.65 -27.25	15362
27.25 -32.70	7589
32.70 -32.95	18203

In the case of the last figure in the column the temperature is too close to the preceding to permit any significance to be attached to the value attained. The temperature characteristics, although showing the same tendency of variation, differ in their absolute values from those of *Bucculatrix,* as would be expected. In both cases an increasing temperature gives a decreasing value of μ. The work of Brown (1926) on the development of an instar of various Cladocerans, and that of Bliss (1926) on the prepupal period of Drosophila, however, show a constant value of μ over considerable temperature ranges. Thus Brown finds the following characteristics for Cladocerans:

	Temperature	μ
Simocephalus serrulatus	15° -24.6° C.	16950
	24 -32	4780
Monia macrocarpa	11 -20	28500
	20 -27.6	17210
	27.6-33	7410
Pseudosida bidentata	14 -27.5	19800

Bliss derives the following values for Drosophila:

Temperature	μ
12° -16°	33210
16 -25	16850
25 -30	7100

Crozier (1926) has stated that "there is as yet scarcely sufficient evidence to verify the prediction that the curve relating log velocity of growth to 1/T, when velocity equals reciprocal of

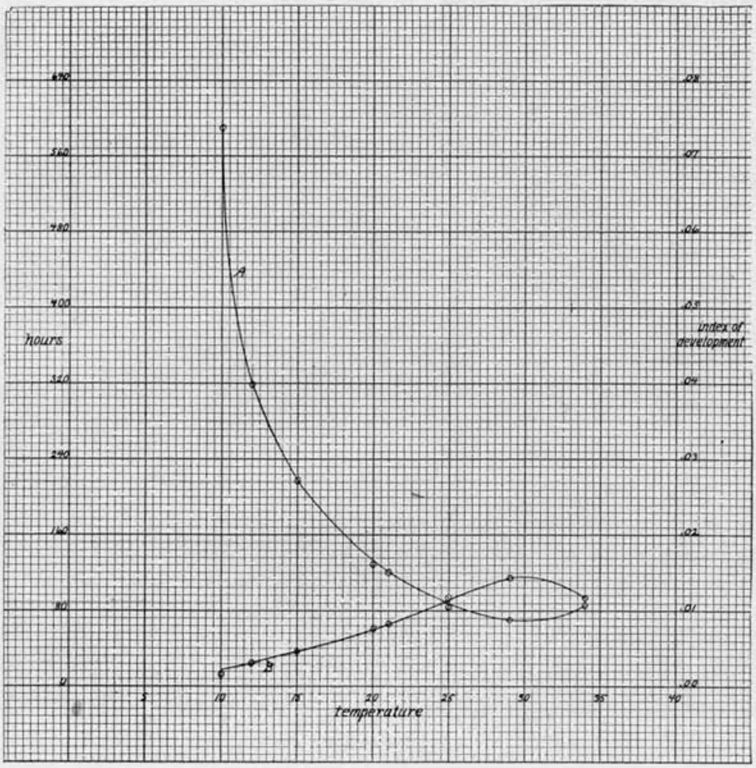

FIG. 38. Effect of temperature on the fifth instar. A is the time-temperature curve, and B is the rate of development curve.

time required to reach a defined stage, should be slightly curvilinear. But there is an indication that growth velocities, where evidenced as constant rates of increase, adhere satisfactorily to the Arrhenius formula; and even when we may quite reasonably expect that an autocatalytic system is involved, the agreement is quite as good as might be desired. The values of the temperature characteristics of growth phenomena are quite varied, yet they cluster quite definitely about the following magnitudes: 7-8,000; 11-12,000; 16-17,000; 20,000; 24,000; 27,000." He brings a considerable mass of evidence to support this view, and for a detailed discussion his works may be consulted. It is simply desired here to compare the values for *Bucculatrix* with those for other animals and to call attention to the fact that different species vary. Heilbrunn (1925) has offered some criticism of the

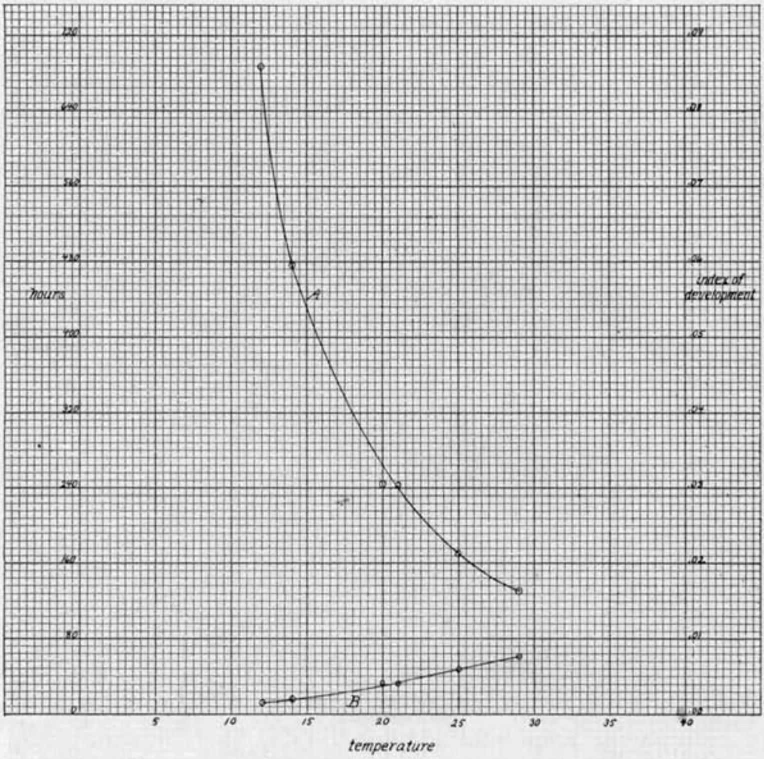

FIG. 39. Effect of temperature on the total external feeding period. A is the time-temperature curve, and B is the rate of development curve.

use of the critical thermal increment of Arrhenius in relation to biological processes of a complex nature and involving several physical as well as chemical reactions, and the identification of basic biological processes by comparing temperature characteristics is open to question.

The effect of temperature on the development of the larvae of *Bucculatrix canadensisella* may be summarized as follows:

The lowest constant temperature at which larvae will complete development is between 10° and 12°C., and the highest temperature is slightly under 34°C.

The curve of the rate of development is sigmoid, and above 30°-31° the temperature has a depressing effect.

In view of the fact that larvae will live for a considerable period of time at 10° and even develop somewhat, although this tempera-

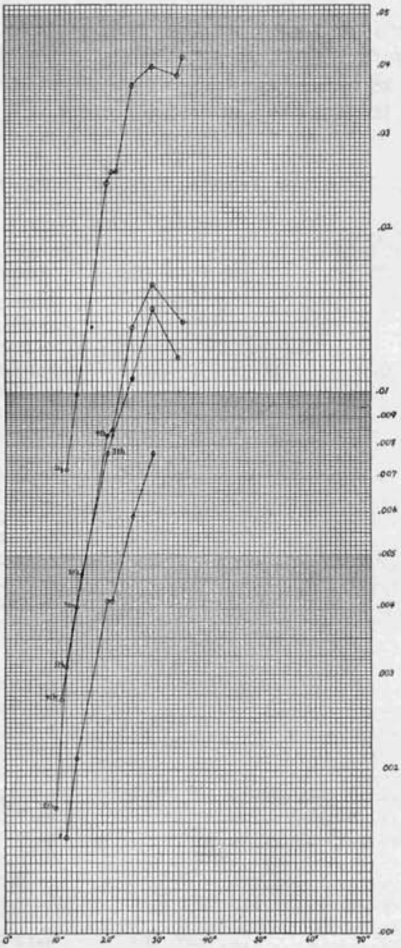

FIG. 40. Effect of temperature on rate of development. W_2 represents the period in the second molting web; 4th, the fourth instar; 5th, the fifth instar; t, the total feeding period. The data are the same as those used in making the B curves in figures 36 to 39 but the plotting paper is arith-logarithmic, and no attempt has been made to smooth the curves. This figure shows the comparative effect of temperature for the different stages.

ture is lethal if continuous, this cannot be considered a physiological zero.

Fluctuations in temperature have their greatest effect on the growth of the larvae when they occur around 21° to 25°.

The temperature characteristic (critical thermal increment) calculated according to the Arrhenius formula is not constant but steadily declines in value as the temperature increases. This temperature characteristic is not the same for the quiescent premolting period as for the feeding period, and the rate of its change with changing temperature is also different.

TABLE 4. EFFECT OF TEMPERATURE ON DEVELOPMENT, 1926

Time in Second Molting Web

Larva No.	Temp. (C.)	Entered web (date)	Hours in web
164	12° (c)	9-21-26	178
165		9-18-26	130
167		9-17-26	136
169		9-24-26	128
170		9-21-26	111
173		9-19-26	138
Mean			137 (20)
251	14° (d)	9-23-26	96
254		9-22-26	112
255		9-23-26	100
256		9-22-26	101
257		9-24-26	95
258		9-22-26	103
259		9-22-26	95
260		9-25-26	104
Mean			101 (5)
122	20° (e)	9-12-26	39
125		9-13-26	54
127		9-12-26	39
128		9-13-26	47
226		9-14-26	41
235		9-12-26	39
131		9- 7-26	40
132		9- 7-26	42
133		9- 6-26	32
134		9- 8-26	39
Mean			41 (5)
123	21° (e)	9-12-26	47
129		9-12-26	33
135		9- 8-26	48
136		9- 7-26	40
137		9- 8-26	48
228		9-11-26	23
229		9-10-26	40
230		9-11-26	23
231		9-11-26	39
232		9-11-26	39
233		9-11-26	39
234		9-13-26	38
281		9-20-26	42
282		9-21-26	40
283		9-21-26	40
285		9-22-26	32
286		9-21-26	40

TABLE 4. EFFECT OF TEMPERATURE ON DEVELOPMENT, 1926—*Concluded*

Time in Second Molting Web—*Concluded*

Larva No.	Temp. (C.)	Entered web (date)	Hours in web
287		9-20-26	49
288		9-21-26	40
289		9-20-26	49
Mean			39 (7)
237	22° (e)	9-23-26	34
238		9-23-26	42
239		9-24-26	39
240		9-24-26	40
Mean			39 (3)
110	25° (f)	9- 5-26	31
111		9- 4-26	32
112		9- 5-26	15
113		9- 5-26	28
114		9- 5-26	28
115		9- 6-26	33
116		9- 5-26	30
118		9- 5-26	22
119		9- 4-26	25
120		9- 4-26	25
121		9- 5-26	28
Mean			27 (5)
155	29° (g)	9- 9-26	23
156		9 -9-26	25
158		9- 9-26	25
159		9-10-26	25
160		9- 9-26	23
161		9- 9-26	31
162		9-10-26	24
163		9- 9-26	25
Mean			25 (2)
261	34° (h)	9-17-26	23
262		9-17-26	23
265		9-17-26	33
270		9-17-26	23
Mean			26 (4)
263	35° (h)	9-16-26	24
264		9-17-26	24
266		9-17-26	24
268		9-16-26	24
Mean			24 (0)

TABLE 5. EFFECT OF TEMPERATURE ON DEVELOPMENT, 1926

Duration of Fourth Instar

Larva No.	Temp. (C.)	First molt web vacated (date)	Duration of instar (hours)
164	11° (c)	9- 9-26	465
165		9- 7-26	381
166		9- 9-26	343
167		9- 9-26	359

TABLE 5. EFFECT OF TEMPERATURE ON DEVELOPMENT, 1926—*Continued*

Duration of Fourth Instar—*Continued*

Larva No.	Temp. (C.)	First molt web vacated (date)	Duration of instar (hours)
168		9- 8-26	319
173		9-11-26	345
Mean			369 (47)
251	14° (d)	9-18-26	231
252		9-15-26	239
253		9-15-26	217
254		9-15-26	281
255		9-17-26	263
256		9-17-26	225
257		9-18-26	240
258		9-15-26	264
259		9-16-26	255
260		9-17-26	281
Mean			250 (21
128	20° (e)	9- 9-26	144
131		9- 4-26	105
132		9- 3-26	143
133		9- 3-26	111
136		9- 4-26	120
281		9-18-26	105
Mean			121 (16)
122	21° (e)	9- 9-26	112
123		9- 9-26	134
124		9- 9-26	119
125		9- 9-26	158
126		9- 9-26	119
127		9- 9-26	112
129		9- 9-26	90
134		9- 4-26	135
135		9- 4-26	144
137		9- 4-26	144
226		9- 9-26	161
228		9- 8-26	81
229		9- 8-26	81
230		9- 8-26	81
231		9- 8-26	97
232		9- 8-26	97
233		9- 8-26	97
234		9- 8-26	144
235		9- 9-26	105
237		9-20-26	106
238		9-21-26	105
239		9-21-26	111
240		9-20-26	145
282		9-18-26	113
283		9-18-26	113
285		9-18-26	130
286		9-18-26	120
287		9-18-26	118
288		9-18-26	113
289		9-17-26	118
Mean			117 (21)

TABLE 5. EFFECT OF TEMPERATURE ON DEVELOPMENT, 1926—*Concluded*

Duration of Fourth Instar—*Concluded*

Larva No.	Temp. (C.)	First molt web vacated (date)	Duration of instar (hours)
110	25° (f)	9- 3-26	85
111		9- 2-26	76
112		9- 2 26	69
113		9- 3-26	77
114		9- 3-26	77
115		9- 3-26	94
116		9- 3-26	79
117		9- 3-26	79
118		9- 3-26	71
119		9- 3-26	64
120		9- 3-26	64
121		9- 3-26	75
Mean			76 (8)
154	29° (g)	9- 7-26	71
155		9- 8-26	55
157		9- 8-26	48
158		9- 8-26	55
159		9- 8-26	80
160		9- 8-26	55
161		9- 7-26	71
162		9- 7-26	80
163		9- 8-26	56
Mean			63 (11)
261	35° (h)	9-15-26	77
262		9-15-26	77
263		9-15-26	62
264		9-15-26	63
265		9-15-26	95
266		9-15-26	79
268		9-15-26	62
270		9-15-26	77
Mean			74 (11)

TABLE 6. EFFECT OF TEMPERATURE ON DEVELOPMENT, 1926

Duration of Fifth Instar

Larva No.	Temp. (C.)	Second molt web vacated (date)	Duration of instar (hours)
531	10° (b)	9-23-26	567
533		9-24-26	452
534		9-28-26	738
536		9-25-26	587
537		9-24-26	604
Mean			590 (91)
164	12° (c)	9-28-26	249
165		9-23-26	239
167		9-24-26	285
168		9-21-26	388
169		9-30-26	486

TABLE 6. EFFECT OF TEMPERATURE ON DEVELOPMENT, 1926—*Continued*

Duration of Fifth Instar—*Continued*

Larva No.	Temp. (C.)	Second molt web vacated (date)	Duration of instar (hours)
170		9-25-26	278
173		9-25-26	284
542		9-25-26	357
543		9-25-26	339
544		9-24-26	259
545		9-24-26	250
546		9-23-26	379
547		9-26-26	403
549		9-23-26	267
550		9-23-26	311
Mean			319 (69)
251	15° (d)	9-27-26	220
254		9-27-26	226
255		9-28-26	211
257		9-28-26	187
258		9-26-26	213
259		9-26-26	229
260		9-29-26	242
Mean			218 (16)
123	20° (e)	9-14-26	120
124		9-14-26	135
126		9-14-26	135
127		9-14-26	152
129		9-13-26	150
230		9-12-26	104
235		9-14-26	107
Mean			129 (18)
122	21° (e)	9-14-26	104
125		9-15-26	120
128		9-15-26	120
131		9- 9-26	115
132		9- 9-26	126
133		9- 7-26	153
134		9- 9-26	93
135		9-10-26	159
136		9- 9-26	135
137		9-10-26	92
226		9-16-26	123
228		9-12-26	135
231		9-12-26	123
232		9-12-26	99
233		9-12-26	99
234		9-14-26	148
237		9-25-26	115
238		9-25-26	170
239		9-25-26	153
240		9-26-26	122
281		9-22-26	129
283		9-23-26	131
285		9-24-26	126
286		9-23-26	94

TABLE 6. EFFECT OF TEMPERATURE ON DEVELOPMENT, 1926—*Concluded*

Duration of Fifth Instar—*Concluded*

Larva No.	Temp. (C.)	Second molt web vacated (date)	Duration of instar (hours)
287		9-22-26	115
288		9-23-26	114
291		9-20-26	91
293		9-20-26	120
294		9-20-26	97
295		9-21-26	120
296		9-20-26	97
297		9-20-26	86
298		9-20-26	112
299		9-19-26	104
300		9-20-26	104
551		9-24-26	146
552		9-23-26	99
553		9-23-26	175
554		9-23-26	112
555		9-24-26	116
556		9-23-26	156
557		9-24-26	104
558		9-24-26	178
559		9-23-26	99
Mean			121 (24)
110	25° (f)	9- 7-26	92
111		9- 6-26	97
115		9- 7-26	97
116		9- 6-26	108
117		9- 6-26	80
118		9- 6-26	88
119		9- 5-26	133
120		9- 5-26	75
121		9- 6-26	72
Mean			94 (18)
155	29° (g)	9-10-26	77
156		9-10-26	55
157		9-10-26	80
158		9-10-26	55
159		9-11-26	82
160		9-10-26	81
161		9-10-26	65
163		9-10-26	65
Mean			70 (11)
526	34° (h)	9-22-26	90
527		9-23-26	91
528		9-23-26	96
529		9-24-26	66
530		9-23-26	86
Mean			86 (10)

TABLE 7. EFFECT OF TEMPERATURE ON DEVELOPMENT, 1926

Duration of External Feeding Period

Larva No.	Temp. (C.)	First molt web vacated (date)	Duration of period (hours)
164	12° (c)	9- 9-26	714
167		9- 9-26	644
168		9- 8-26	707
169		9- 9-26	803
170		9-11-26	629
173		9-11-26	629
Mean			688 (62)
251	14° (d)	9-18-26	451
252		9-15-26	476
253		9-15-26	456
254		9-15-26	507
257		9-18-26	427
258		9-15-26	477
259		9-16-26	484
260		9-17-26	523
Mean			475 (29)
230	20° (e)	9- 8-26	185
127		9- 9-26	264
128		9- 9-26	264
129		9- 9-26	240
132		9- 3-26	269
Mean			244 (31)
122	21° (e)	9- 9-26	216
123		9- 9-26	254
124		9- 9-26	254
125		9- 9-26	278
126		9- 9-26	254
131		9- 4-26	220
133		9- 3-26	264
134		9- 4-26	228
135		9- 4-26	303
136		9- 4-26	255
137		9- 4-26	236
226		9- 9-26	284
228		9- 8-26	216
231		9- 8-26	220
232		9- 8-26	196
233		9- 8-26	196
234		9- 8-26	292
235		9- 9-26	212
237		9-20-26	221
238		9-21-26	275
239		9-21-26	264
240		9-20-26	267
281		9-18-26	234
283		9-18-26	244
285		9-18-26	256
286		9-18-26	214
287		9-17-26	233
288		9-18-26	227
Mean			243 (28)

TABLE 7. EFFECT OF TEMPERATURE ON DEVELOPMENT, 1926—*Concluded*

Duration of External Feeding Period—*Concluded*

Larva No.	Temp. (C.)	First molt web vacated (date)	Duration of period (hours)
110	25° (f)	9- 3-26	177
111		9- 2-26	173
115		9- 3-26	191
116		9- 3-26	187
117		9- 3-26	159
118		9- 3-26	159
119		9- 3-26	197
120		9- 3-26	139
121		9- 3-26	147
Mean			170 (19)
155	29° (g)	9- 8-26	132
156		9- 7-26	118
157		9- 8-26	128
158		9- 8-26	110
159		9- 8-26	162
160		9- 8-26	136
161		9- 7-26	136
163		9- 8-26	121
Mean			130 (14)

TABLE 8. EFFECT OF TEMPERATURE ON DEVELOPMENT, 1926

Duration of Quiescent Period in Second Molting Web

Number of Larvae	Temperature (C.)	Average Time in Web (hours)	Standard Deviation (hours)	Index of Development	Tangent to Curve B
6	12°	137± 5.6	20	.0072	
8	14	101± 1.2	5	.0099	.6770
10	20	41± 1.1	5	.0244	1.3100
20	21	39± 1.0	7	.0256	1.7100
4	22	39± 1.0	3	.0256	1.8855
11	25	27± 1.0	5	.0370	1.2800
8	29	25± 0.5	2	.0400	.8350
4	34	26± 1.4	4	.0385	
4	35	24± 0	0	.0417	.7700

Duration of Fourth Instar

Number of Larvae	Temperature (C.)	Average Duration of Instar (hours)	Standard Deviation (hours)	Index of Development	Tangent to Curve B
6	11°	369±13.2	47	.0027	
10	14	250± 4.4	21	.0040	.2395
6	20	121± 4.5	16	.0083	.4215
30	21	117± 2.6	21	.0085	.4275
12	25	76± 1.5	8	.0132	.6265
9	29	63± 2.5	11	.0159	.1240
8	35	74± 2.6	11	.0135	.3860

Duration of Fifth Instar

Number of Larvae	Temperature (C.)	Average Duration of Instar (hours)	Standard Deviation (hours)	Index of Development	Tangent to Curve B
5	10°	590±27.4	91	.0017	
15	12	319±12.0	69	.0031	.2885
7	15	218± 4.1	16	.0046	.2610
7	20	129± 4.6	18	.0077	.3580
44	21	121± 2.4	24	.0083	.3725
9	25	94± 4.0	18	.0106	.4280
8	29	70± 2.6	11	.0143	.2935
5	34	86± 3.0	10	.0116	.5956

Duration of External Feeding Period

Number of Larvae	Temperature (C.)	Average Duration of Period (hours)	Standard Deviation (hours)	Index of Development	Tangent to Curve B
6	12°	688±17	62	.0015	
8	14	475± 6.9	29	.0021	.1515
5	20	244± 9.3	31	.0041	.1760
28	21	243± 3.6	28	.0041	.1895
9	25	170± 4.3	19	.0059	.2235
8	29	130± 3.3	14	.0077	.1855

XII. CONTROL

The control of these larvae is a very simple matter on ornamental trees. The trees should be sprayed about the middle of August with lead arsenate at the rate of 3 pounds of powder to 100 gallons of water. Add one pound of casein-lime to aid in spreading the poison and making it adhere to the foliage. The larvae feed on the lower side of the leaves, and this side must be covered with the arsenate. Experiments conducted by the writer have shown that if the trees are carefully sprayed there will be practically no feeding by the insects.

XIII. SUMMARY

The history of the genus *Bucculatrix* up to the description of the species *canadensisella* Chambers has been briefly reviewed, and an account has been given of the periodic abundance of this species in North America up to the present. Systematically the genus is usually placed in the family Lyonetiidae.

A brief description is given of the external morphology of the different stages.

There is but one generation a year of *B. canadensisella.* The adults emerge from the cocoons in June and July and oviposit on the leaves of birches. The incubation period of the eggs averages 15 days. The larvae mine in the leaf during the first three instars, the mining period averaging between 24 and 31 days. The last two instars feed externally on the under side of the leaf, skeletonizing it, and this feeding period averages from 13 to 15 days. The total larval life averages from 38 to 46 days. The cocoon is spun on the under side of debris on the ground, and hibernation occurs in the pupal stage. The last larvae are found in the field the latter part of September. There are five larval instars.

The number of larval instars was determined by applying Dyar's hypothesis to the width of the head capsules.

The principal larval food plants are the gray, paper, yellow, and European white birches. Some feeding on black birch has been observed.

The Hymenopterous parasites, of which ten species have been reared, and the ants and other predaceous foes are the principal factors affecting the abundance of this insect.

The geographical range includes southern Canada and northern United States, the insect being particularly abundant around the Great Lakes and east to the Atlantic Ocean.

Temperature has a marked influence on the development of the larvae. At 10°C and lower, and at 34°C. and higher, they cannot survive. The curve obtained by plotting rate of development (reciprocal of hours taken to complete a given stage) against temperature is sigmoid. Above 30° temperature has a depressing effect. An absolute physiological zero was not obtained because of the ability of the larvae to develop slightly at a low temperature which was fatal if continued a sufficient length of time. There is no thermal constant for any temperature range beyond the experimental error, and the temperature characteristic as computed by the Arrhenius formula steadily decreases in magnitude as the temperature increases.

The use of a lead arsenate spray about the middle of August will protect the trees against injury by the larvae.

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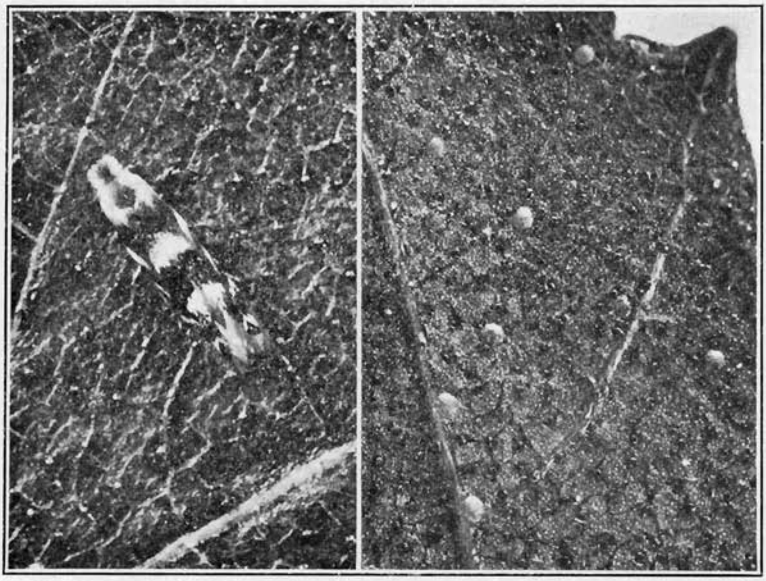
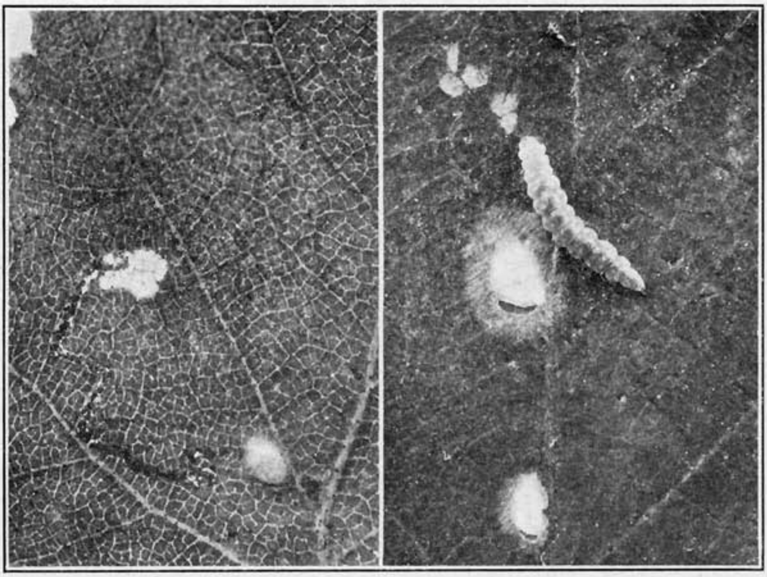


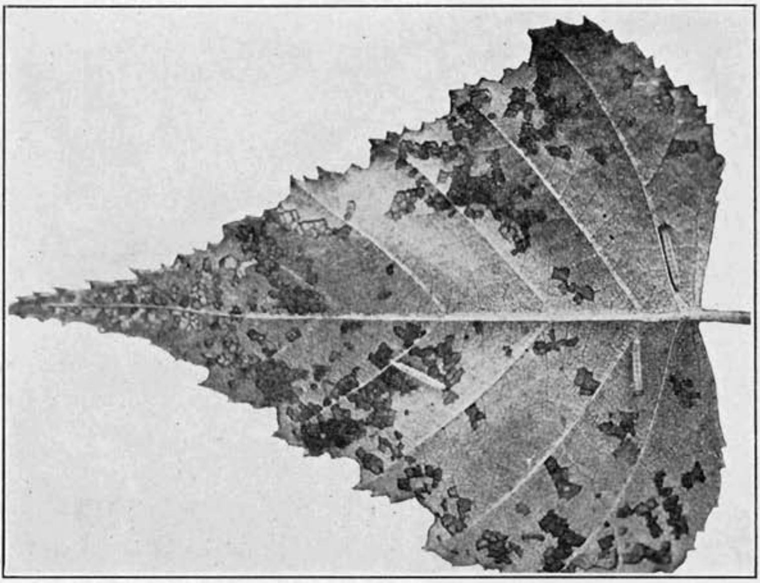
a. Adult (left) and eggs (right) of *Bucculatrix canadensisella* on birch leaves. Adult enlarged eight times, eggs enlarged ten times.



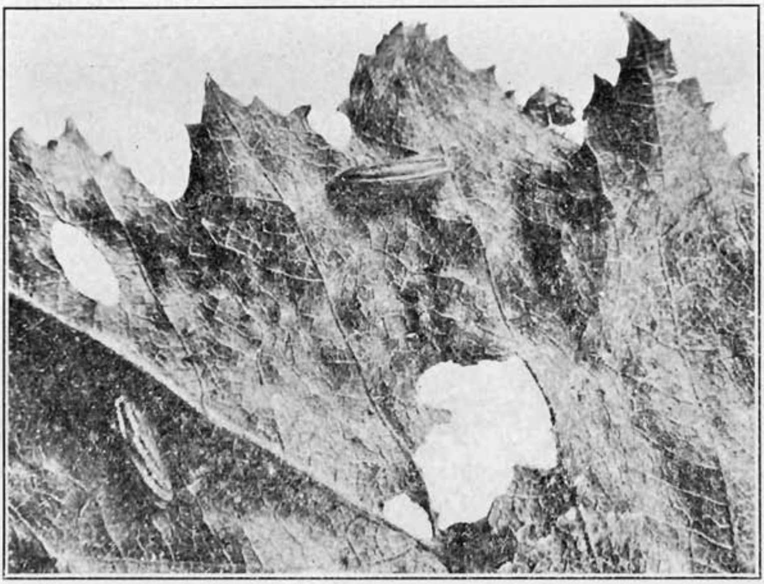
b. Vacant mine of larva in birch leaf (left) and fully grown larva (right) with first (lower) and second (upper) vacant molting webs. Enlarged four times.

BIRCH LEAF SKELETONIZER

PLATE XVIII.



a. Larva of *Bucculatrix canadensisella* skeletonizing leaf of gray birch. Slightly enlarged.



b. Cocoons of *Bucculatrix canadensisella* on dead leaf. Enlarged four times.

BIRCH LEAF SKELETONIZER