These two instances would show that fly larvæ such as *Sarcophaga*, or other omnivorous larvæ, find no difficulty in entering the chrysalis under the wing covers during the first few days of the chrysalis stage and before the wing covers begin to fit tightly around the edges.

There seems to be a peculiar odor to the chrysalids that attracts flies, and a dead chrysalis proves to be a still greater attraction. Dead chrysalids that happened to be left in uncovered jars and were afterwards examined and dissected were in many cases found to contain large numbers of larvæ of the small flies of the *Phoridæ* family, and the adult flies could be noticed flying around the jars in large numbers after dead chrysalids were left uncovered for a few days.

From work carried out it appears to be definitely proven that this pest is parasitized during the chrysalis period and is free from parasites during the entire caterpillar stage.

Owing to unavoidable causes these observations on *B. isthmia* have not been as complete as could have been wished, but they cover the ground as thoroughly as the circumstances would permit.

I wish to express my thanks to Dr. S. T. Darling, former Chief of Laboratories, for his advice and assistance during nearly the whole of this work; to Major F. F. Russell, Chief of Laboratories, for examining and making cultures of the entomogenous fungi of this pest; to Dr. H. C. Clark for making pathological examinations of chrysalids killed by this fungus disease, and to Mr. J. E. Jacobs, Chemist, for determining all weights given in this paper.

NOTES ON THE LIFE-HISTORY OF MARMARA ELOTELLA BUSCK, A LEPIDOPTEROUS SAP FEEDER IN APPLE TWIGS[1]

By Stuart C. Vinal

For several years the writer has observed quite noticeable serpentine mines in the bark of apple twigs in the vicinity of Amherst, Mass. In 1914 a sample of this work was sent to Washington for determination, and identification showed the sap feeding larva responsible to belong to the genus *Marmara* of the Tineina but the adult moths had never been reared from apple. Accordingly, at the suggestion of Dr. H. T. Fernald, investigation was started during the winter of 1915 with the object of obtaining adult insects and studying the life-history. In July some moths were bred from the apple twig mines and sent to Mr.

[1] Contribution from the Entomological Laboratory of the Massachusetts Agricultural College, Amherst, Mass. This paper is presented as part of a thesis for the degree of Master of Science.

Busck of the National Museum, who identified them as *Marmara elotella* Busck.

Special acknowledgments are due Dr. H. T. Fernald, Dr. G. C. Crampton, and Dr. W. S. Regan for their encouragement and assistance throughout the progress of this paper. For the identification of this species and helpful suggestions the writer is deeply indebted to Mr. August Busck of the United States National Museum and to Rev. J. J. DeGryse of Staunton, Virginia.

History and Ecology

The Tineina, to which this species belongs, constitutes a large and important group of minute moths including many destructive miners. These fall roughly into two distinct classes according to their manner of feeding.

1. Tissue feeders. Those which feed on the internal parenchyma tissue of leaves early in life and later may become external feeders.

2. Sap feeders. Those which mine just beneath the cuticle destroying only a few layers of cells and feeding on the plant sap thus liberated.

This sap-feeding habit has been found only in two families, the Phyllocnistidæ and the Gracilariidæ. The Phyllocnistids are sap feeders throughout their larval life and include the following genera: *Marmara*, *Camermaria*, and *Phyllocnistis*, while the Gracilariids in their early instars are true sap feeders but in later instars become tissue or external feeders and include the genera *Gracilaria*, *Ornix*, *Acrocercops*, and *Phyllonorcyter*.

Many interesting articles have been written based on the specialization shown by these sap-feeding larvæ and their significance in showing evolutionary steps from the more generalized tissue-feeding type. The sap feeders are considered a very highly specialized group and are probably of comparatively recent origin in the Lepidoptera.

Practically all miners confine their feeding to foliage, but a few larvæ of the genus *Marmara*, established by Clemens (*Proc. Ent. Soc. Phila.*, vol. 2, 1863–64, pp. 6–7) mine just under the epidermal layer of bark. Clemens described *Marmara salictella* which "mines the bark of yellow willow tree" and gave a brief account of its life stages. He also described *Marmara* (*Gracilaria*) *fulgidella* (*Proc. Acad. Nat. Sci. Phila.*, 1860, p. 6) mining in twigs of white oak and chestnut. Chambers described *Marmara* (*Phyllocnistis*) *smilacisella* (*Cin. Quar. Jour. Science*, 2, p. 107) bred from leaves of smilax. This species was redescribed with biological notes added by Braun (*Ent. News*, vol. 20, p. 432, 1909). Busck described a new species, *Marmara guilandinella* (*Proc. U. S. Nat. Mus.*, vol. 23, p. 245), mining leaves of *Guilandia*

bonducella in Florida, and in *Proc. U. S. Nat. Mus.*, vol. 26, p. 772, he described *Marmara arbutiella* mining leaves of arbutus trees in Seattle, Washington. In *Proc. Ent. Soc. Wash.*, vol. 8, p. 97, he also described *Marmara opuntiella* mining leaves of Opuntia sp. in Southern Texas. *Marmara* (*Gracilaria*) *elotella* was likewise described by him in *Proc. Ent. Soc. Wash.*, vol. 9, p. 102, but the host plant was not given. A *Marmara* sp. mines orange peels in southern California but the adult has never been determined.

Clemens (*Proc. Ent. Soc. Phila.*, vol. 2, 1863–64, pp. 6–8) claims that *Marmara salictella* changed from the flat mining larva to a more cylindrical form which has fairly well developed legs and prolegs, and escapes from its mine to spin its cocoon in some convenient protected place, this cocoon being covered with a characteristic globular or frothy ornamentation. Busck also ascribes the above habits to *M. opuntiella*, *M. guilandinella*, and *M. arbutiella* although no actual observations were made on the last named species. *M. fulgidella* and *M. smilacisella* it is also claimed form the frothy characteristic cocoon of this genus. *Marmara elotella*, however, differs from all the above species in regard to the formation and situation of its cocoon.

Present Distribution in Massachusetts

An examination of apple twigs at various points throughout Massachusetts has indicated a rather widespread prevalence for this species within the state. It has been found more abundantly, however, in apple trees on the grounds of the Massachusetts Agricultural College and orchards adjoining, than elsewhere. The reason for this localized occurence is unknown.

Character and Extent of Injury

Infested apple twigs show the long, narrow, tortuous, serpentine mines which are very characteristic of all *Marmaras*. They are readily recognized by the yellowish-brown color and slight swelling of the bark over the tunnels, while the normal bark is dark brownish in color. The moths seem to prefer two-year-old twigs upon which to oviposit, usually selecting sucker-like growths. However, the larvæ are occasionally to be found mining in any branch which has a thin, smooth, epidermal covering. The mouth parts of the larvæ are profoundly altered and specialized for living beneath the cuticle of the bark, which they separate from the "greenbark" below by cutting through a row of cells by the action of their circular, saw-like mandibles. From the origin of each mine the tunnel gradually widens from about 0.5 mm. at the beginning, to 7–8 mm. as it nears completion. The average length is between two and three feet. These tunnels do not penetrate

deeply enough to injure the cambium and therefore this species is of little economic importance. Mines similar in character, undoubtedly caused by different species, were seen during the summer of 1916 on poplar, ash, and pine.

Life-History and Description of Life Stages

Egg.—Description:

Oviposition took place during the month of August while the writer was away, and hatching had occurred before his return so that only the empty egg shells have been available for examination. Judging from these the eggs are elliptical in shape, flattened below and convex above. Approximate measurements: 0.7 mm. in length. 0.5 mm. in width.

Location on the Tree.—These tiny eggs are deposited singly on the smooth bark of apple twigs, oviposition for the most part being upon two-old-year wood, and never on the present season's growth. They are apparently stuck to the bark with a secretion of a mucilaginous nature. Eggs are rarely laid upon older wood excepting where the bark is thin and smooth. The period of incubation is probably about ten days.

Mining Larva.—Description of Full-Grown Mining Larva (Fig. 24, 1):

Length 5.5–6 mm., width at first and second segment 1 mm. Dorso-ventrally depressed, body strongly constricted behind the second segment, the remaining segments tapering gradually posteriorly and deeply incised laterally at their junction points. Body semi-transparent, lemon-yellow in color and consisting of thirteen segments excluding head.

Head large, flat, slightly retractile, with dark chitinous supports. Mouthparts very much modified and exserted (Fig. 24, 5). Labrum (lr) fused with dorsal surface of head and immovable. Mandibles (md) large, flat, and circular saw-like with the distal margin serrated. Labium (li) consisting of a chitinous fold distally covered by short spines and extending far back into the head. Maxillæ rudimentary, situated in close apposition to the lateral sides of the labium at its junction with the head. Antennæ (ant) situated on each side of the head near the mouthparts, consisting of two visible segments, the distal one bearing two papillæ, one large and one small, two large papillæ present on second segment with a small one situated in close proximity to a bristle which extends to the apex of the antenna. Ocelli (oc), two pairs with lenses absent, situated posterior to the antennæ. On the lateral margin of the head mid-way between the antennæ and the posterior margin of the head is a stout spine.

Body. First and second segments widest, approximately 1 mm. Third segment narrower than second and fourth. An internal chitinous shield extends from the posterior border of the head into the prothorax and gives this segment a dark brownish color. No legs or prolegs present. Semicircular fold, probably used in propulsion, situated at the posterior extremity. Body without bristles except on first, second and third segments (thorax) where there are two short, stout spines laterally. Anterior fourth of each body segment banded by closely set spine-like protuberances of the body wall. These are directed backward and probably function in bracing the larva during tunneling operations. Spiracles extremely minute but visible with

high power of microscope, near the anterior lateral border of each abdominal segment except the last two. Meso- and meta-thoracic segments (second and third) without spiracles. Prothorax with a spiracle somewhat larger than those upon the abdomen, situated on each side near the posterior margin.

LARVAL LIFE-HISTORY.—It is very difficult to gather data on these interesting sap feeders because the larvæ if removed from their mines are unable to reënter the bark to continue mining and therefore soon die. On hatching, the young larvæ, without exposing themselves, immediately enter the twig and begin their mines which extend partly around the twig before running lengthwise. They molt twice before winter sets in and hibernate as third instar larvæ in their mines, protected from severe climatic changes only by the dead bark covering the tunnel. With the coming of warm days in the spring they resume activity and molt a third time about the middle of May. During June the fourth instar mining larvæ become full grown.

HYPERMETAMORPHISM.—In this species all the mining larval stages are flat, legless, with exserted mandibles fitted only for separating the tissues of plants and not for masticating purposes. In structure all these stages are alike excepting in the proportionate size of the thorax and abdomen. In the young larvæ the head and thorax are much wider in proportion to the abdomen than in later stages.

Upon reaching maturity the mining larva retreats a short distance and remains quiescent at one side of its mine. During this quiescent period the larval skin remains intact while internally a hypermetamorphic stage is formed, called the intermediate or pseudo-pupal stage. The head of the intermediate stage is formed within that of the mining larva and gradually contracts until the outline of both are readily seen under the microscope. In the meantime the body has gradually become shorter and more cylindrical. The formation of this intermediate stage has been excellently discussed by Rev. J. J. DeGryse (*Proc. Ent. Soc. Wash.*, vol. 18, p. 164, 1916) who observed this phenomenon in *Marmara fulgidella* Clemens.

Within the pseudo-pupal stage is formed the true spinning larva or pre-pupa, and when complete it emerges, casting both the intermediate and mining larval skins at the same time. This is accomplished by forcing its head backward and breaking the skin of both preceding stages transversely at the first abdominal segment. The head and thorax are first liberated, followed immediately by emergence from the abdominal exuviæ.

SPINNING LARVA OR PRE-PUPA (Fig. 24, 2):

Length 5 mm. Color yellowish-brown with tinge of red. Body shorter, more cylindrical, and incisions between segments less pronounced than in mining larva.

Head smaller and more typically lepidopterous than in previous stages (Fig. 24, 6). Chitinous supports reduced in number. Mouthparts markedly different from mining

larval trophi. Labrum (lr) immovably fused with head and bears near its anterior edge six short spines. Mandibles (md) flat, well developed, with median margin serrated, and cross each other similar to the blades of a pair of scissors. In this species their function is still obscure. Maxillæ (mx) present, consisting of three visible segments; a large papilla-like terminal segment bearing laterally a spine near its tip; at the internal distal end of the basal joint are two long bristles which probably correspond to the lacinia of other lepidopterous maxillæ. Labium or spinneret (sp) well developed with labial palpi present. Antennæ similar to those of the mining larva but bear two long bristles on the second joint instead of one as in the mining larva. Ocelli, two pairs with lenses present. On lateral border of head five bristles, three situated near the ocelli and two just anterior to the junction of the head and prothorax. Three more bristles are visible from dorsal view which arise from ventro-lateral margin of head, two near the ocelli and one near the posterior border of the head.

Body. With the exception of the head the body wall of each segment is covered with spine-like processes, like those found on the anterior fourth of each body segment of the larva. From the side of each segment projects a fairly long bristle, with the exception of the first and last two segments which bear two each. A pair of rudimentary legs on each thoracic segment (1, 2 and 3) and a bilobed structure on the ventral side of the last abdominal segment which may function as anal prolegs or may be only a part of the thirteenth segment. No true prolegs of any kind. Last three abdominal segments shrunken and drawn forward.

Formation and Situation of Cocoon.—Heretofore all species of this genus have been described as emerging from the mines and spinning their cocoons in protected crevices, and according to Clemens and Busck, characteristically ornamented by frothy globules.

As mentioned above, the mining larva upon reaching maturity remains quiescent at one side of its mine and gradually becomes more cylindrical during the process of forming the intermediate pseudopupal stage, resulting in an upward pressure upon the epidermal covering of the tunnel which finally splits away from the twig at the opposite side of the mine. In all probability the mining larva weakens the epidermal covering with its mandibles before entering the quiescent stage. As the epidermis breaks away the spinning larva emerges and soon spins a few threads which help cause the cuticle to shrink and form a longitudinal fold under which the white, unornamented silken cocoon is spun (Fig. 24, 7).

Upon completion of the cocoon the spinning larva transforms to the pupa, which occurs during the latter part of June and early July. The spinning larva exuvium is very delicate and shrinks to form a compact ball at the posterior end of the cocoon.

Pupa (Fig. 24, 3):

Length 3.5 mm., width 0.7 mm. Newly formed pupa pale yellow showing a reddish tinge beneath the dorsum of the third, fourth, and fifth abdominal segments, but later becoming brownish with black markings on the wings. Proximal part of the labial palpi not covered by maxillæ. Maxillæ more than half the length of wings and longer than prothoracic legs. A very stout spear-like projection covered with blunt

teeth situated medianly on the front of the head, doubtless enables the pupa to pierce or saw through the cocoon on emergence. Appendages not fused to the body. Metathoracic legs and antennæ equal in length and reach to the last abdominal segment. Two pairs of bristles present on the thorax, one pair laterally on the dorsum of both the meso- and meta-thorax. A smaller, stouter bristle is situated on the lateral sides of the abdominal segments dorsal to each spiracle. Spiracles situated on anterior lateral margins of the abdominal segments project as tuberosities. The anterior fifth of each abdominal segment is banded by spine-like projections similar to those found in the larva and pre-pupa but less distinct. Cremaster absent. Last four abdominal segments movable.

EMERGENCE OF ADULT.—Just previous to the emergence of the adult, the pupa works its way forward, puncturing the cocoon with its spear-like projection and forcing itself half out of the cocoon. In this position the pupa case splits, liberating the tiny moth. This takes place in the vicinity of Amherst, Mass., from the middle to latter part of July. The duration of the pupal stage is at least fourteen days.

ADULT (Fig. 24, 4):

"Labial palpi white, second joint dark fuscous exteriorly; maxillary palpi white on the inner side, fuscous exteriorly. Antennæ white, annulated with brown. Face, head and thorax shining silvery white. Fore wing white with golden-brown and black markings; at the base of the wing is a brown costal spot, on the middle of the wing is a golden-brown transverse fascia, broader on the costal edge than on the dorsal and edged posteriorly by a sharp black, somewhat angulated line; at apical third is an outwardly strongly oblique fascia attenuated towards dorsum and edged posteriorly with black, and a similar fascia also edged with black, but hardly so oblique is situated between this and the tip of the wing. Across the cilia and the extreme tip of the wing is a transverse streak of mixed brown and black. Fore and middle legs with swollen black femora and white tarsi. Hind legs white, shaded externally with brown; tibiæ smooth.

"Alar expanse: 6 to 7 mm."—Busck's description of *Marmara* (*Gracilaria*) *elotella* in *Proc. Ent. Soc. Wash.*, vol. 11, 1909, p. 102.

At the end of this description Mr. Busck states that this species is very close to *Marmara* (*Gracilaria*) *fulgidella* Clemens, and on comparing the two descriptions I find they practically coincide. However, Mr. Busck has made slide mounts of the male genitalia of *M. fulgidella* and *M. elotella* and has found that the two species are abundantly distinct. The fact that *M. fulgidella* mines in the bark of white oak and chestnut, while *M. elotella* mines in apple, coupled with their distinct genitalia proves that these are different species, but, nevertheless, are difficult to separate by descriptions.

As a supplement to the original description of *M. elotella* the following notes are added:

Fore and middle femora black at both ends. Distal end of middle tibia black and bearing two scale-covered spines which are usually black at base and white apically. Tarsi either white or marked with black at the distal end of each segment. From near the base of hind tibia originate two white scale-covered spines, the larger one

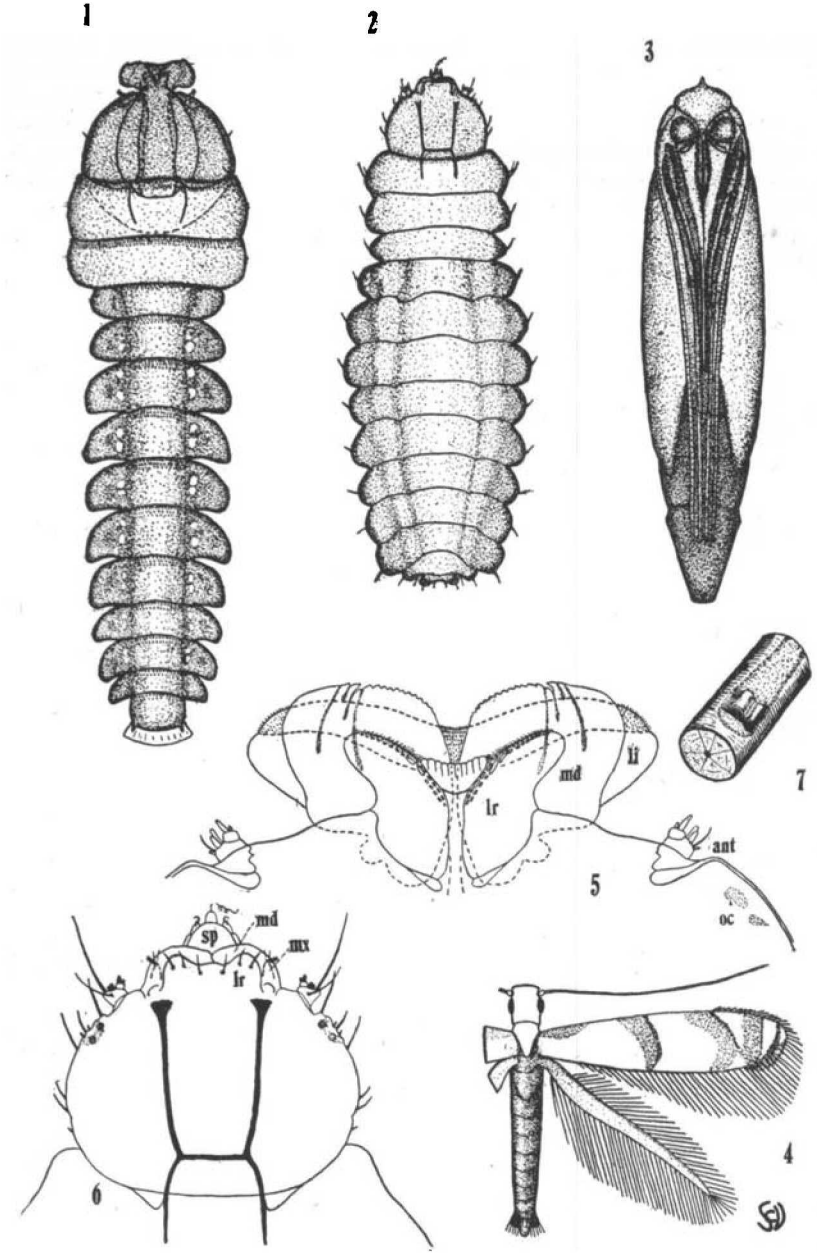

Figure 24. 1, Full grown larva; 2, Spinning larva or pre-pupa, 3, Pupa; 4, Adult. Head, thorax and wing coloration: White, white; Stippled portion, golden-brown; Short black lines, black. 5, Mouthparts of the larva. Labrum (lr); Mandibles (md); Labium (li); Antennæ (ant); Ocelli (oc). 6, Head of spinning larva or pre-pupa. Labrum (lr); Mandibles (md); Maxillæ (mx); Labium or spinneret (sp). 7, Twig showing epidermal fold under which the cocoon is spun.

banded in middle with brown. Two white scale-covered spines arise from the distal end of the hind tibia. Abdomen sometimes wholly white but more generally the anterior fifth of each segment is fuscous.

HABITS OF THE ADULTS.—These tiny moths are very inconspicuous and, like other members of the group, assume a peculiar attitude while at rest. The fore legs are extended while the others are partly folded under the body. In this way the insect rests on the fore legs and the end of the abdomen. The antennæ are held at right angles to the axis of the body and are in constant vibration. During the day these moths are seldom active and remain hidden until dusk, at which time they may be seen flying around their host tree in quite large numbers during early August. In the course of a few days they begin laying eggs for the next generation. Thus it takes a full year for *Marmara elotella* Busck to complete its life cycle.

NATURAL ENEMIES

An undetermined Chalcid parasite is quite efficient in controlling these miners. Many of the larvæ become full grown and spin their cocoons but instead of containing the lepidopterous pupæ, the pupæ of the Chalcid parasite appropriates the comfortable quarters of the sap feeders.

GENERAL CONSIDERATIONS

Although adult characters of *Marmara elotella* correspond to the systematic ideal of the genus, the peculiar method of cocoon formation when taken in comparison to the characteristic Marmaran cocoon, which is ornamented by froth-like globules and has been observed in all species thus far described, shows that one of two things should be done. Either the generic cocoon character must be changed so that it includes the type shown by *M. elotella* or a separate genus should be erected. As stated elsewhere in this paper, I have observed bark miners on pine, ash, and hemlock which form the same characteristic cocoon as *M. elotella*, all of which will probably prove to be different species. Another fact showing difference between this species and other members of the genus may be found in that there are no prolegs in the spinning stage of *M. elotella*, while in other species the prolegs are present.