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The Biology and Morphology of *Heterarthrus vagans* FALLEN (*Hymenoptera, Tenthredinidae*)

[Plates XLII—XLVI and 39 text-figures]

Biologia i morfologia zżernicy *Heterarthrus vagans* FALLEN
(Hymenoptera, Tenthredinidae)

Биология и морфология *Heterarthrus vagans* FALLEN
(Hymenoptera, Tenthredinidae)

INTRODUCTION

The subject of this paper is the biology and morphology of *Heterarthrus vagans* FALLEN (= *Phyllotoma vagans* FALL.), whose larvae mine the leaves of alder. On account of the mode of living of its larvae this hymenopteran is placed in the ecological group of mining insects or miners. Very peculiar conditions of larval life are responsible for the development of some adaptive characters of these insects. These adaptations are, above all, the considerable flattening of the larval body, the prognathism, and the development of special organs, i.e., suckers, which are situated on the thorax. Transformations affect mostly the external structure without preventing the larva from feeding and moving inside the mine. The mine is a space in the form of a gallery or a chamber which is left between the two opposite layers of the epidermis of the leaf, after the larva has devoured the green tissue.

So far, the biology and morphology of *Heterarthrus vagans* FALL. have not been worked out in detail. In literature there are some short descriptions, in the form of diagnoses, of the adult insects of the genus *Heterarthrus (Phyllotoma)* in general and the species *Heterarthrus vagans* FALL. in particular (KINEL et al., 1927; SCHMIEDEKNECHT, 1930) and of the larvae of this species (HACHLER, 1947; HERING, 1957; LORENZ & KRAUS, 1957). Other, more numerous, reports refer to the occurrence of this hymenopteran and describe the mines formed by its larvae (NOWAKOWSKI, 1954; NUNBERG, 1947, 1948; OBARSKI, 1933; PIERONEK, 1963; RUSZKOWSKI, 1924; SEIDEL, 1931; SZULCZEWSKI, 1939).

Heterarthrus vagans FALL. is a common insect, known throughout Europe and recorded from Poland. During its larval period it attacks leaves of the black alder *Alnus glutinosa* GAERTN. and the grey alder *Alnus incana* MNCH.

According to ENSLIN (1918), each year there lives only one generation of *H. vagans* FALL., whereas OBARSKI (1933) writes about one or two, and HACHLER (1947), LORENZ and KRAUS (1957) and SEIDEL (1931) about two generations. Other authors do not distinguish generations and confine themselves to the determination of the time of occurrence: from May to September according to BENSON (1952) and from August to September, as stated by HERING (1957).

My studies on the biology and morphology of *H. vagans* FALL. cover the whole life-cycle, from the egg through the larva and puppa to the imago, including the external morphology of the successive stages of development. Most of the observations concern the life of the larva in the leaf and the formation and development of the mine.

My sincere thanks are due to Prof. Dr Adam DZIURZYŃSKI for his guidance and valuable assistance during this work.

MATERIAL AND METHOD

Studies on the biology and morphology of *Heterarthrus vagans* FALL. were conducted for 4 years, from 1960 to 1964. Material for observations, that is, alder leaves with larvae, was collected constantly at the same locality, at Krzemionki in the Podgórze district of Kraków. Only the black alder *Alnus glutinosa* GAERTN. grows in the region of Krzemionki, and most of the material used for the investigations the results of which constitute the subject of my considerations was derived from this species of trees. The mines collected at other localities were used to compare the results with. The material for comparison comes from Kostrze near Kraków (black alder), the Niepołomice Forest (black alder), Krzeszowice (black alder), Radziechowy near Żywiec (black alder and grey alder *Alnus incana* MNCH.), and Rajcza-Nickulina near Żywiec (grey alder).

During this four-year period mines with larvae were collected each year, approximately from May to October, and at the same time observations were carried out on living material. Alder leaves with eggs deposited in them were also often found.

Leaves with both eggs and feeding larvae were kept in Petri dishes or in big jars lined with filter paper moistened with water on the window-sill. In winter, cocoons with larvae were placed in Petri dishes or jars between the panes of a double-window or, partly, on a balcony. The leaves with cocoons were moistened approximately once a fortnight. For the purposes of further breeding the females obtained in the laboratory were kept in glass jars with fresh alder leaves, in which they laid eggs.

The larvae of particular stadia designed for taxonomic measurements and for the study of external morphology were taken out of mines, killed by boiling in water to avoid shrinkage, then fixed in the Carnoy fluid and kept in 70% alcohol. Pupae and imagines were preserved in 70% alcohol except for a part of adult insects, which were kept pinned in the dry state. Dissected organs of larvae and imagines, such as mouth-parts, genitalia, antennae, and wings, were embedded in Canada balsam or in Faure's compound.

Some of the larvae which had gone through the feeding stadia were placed in tightly closed cellophane bags. Here they constructed cocoons, which in contrast with those formed in leaves were almost transparent and made it possible to observe how the cocoons were produced as well as the mode of life of the prepupae, pupae, and imagines enclosed in them.

During the larval feeding stadia the area of mines was measured using a planimeter, profile paper, and a „Perspex" plate with a check of lines, crossing at intervals of 1 mm, incised in it.

The nomenclature used for the larva was adopted from the work by Kraus and Lorenz (1957) and that for adult insects was based on the work of Snodgrass (1935). The paper is illustrated with drawings and photographs. The leaves photographed were intensely illuminated from below.

ADULT INSECT

Female

The body length ranges from 4 to 6 mm (Pl. XLII, fig. 1); the coloration is not uniform, black, brown and orange. Seen from in front the head (Fig. 1) is triangular in outline, flattened and black-brown.

The internal edges of the compound eyes, the labrum, clypeus, frons and mouth-parts, except the mandibles, are whitish. The frontal sutures are obliterated in the anterior part of the head. The large compound eyes occupy nearly the whole sides of the head. The ocelli are large and lie on the vertex of the head.

The antenna (Fig. 2) consists of 10—12 joints covered with short setae. The scape and pedicle are much lighter than the flagellum. Antennal joint III is the longest. The vertex and the region of the ocelli are covered with short setae, whereas the setae on the labrum, clypeus, genae and part of the frons are far longer and slender. The clypeus is a narrow elongate plate with about 30 setae on its external surface. The labrum (Fig. 3 A) is broad compared with the clypeus; its anterior edge is rounded and the posterior one bears two lateral processes (P. L.), which join the trough-shaped plate of the epipharynx. On the external surface of the labrum there are about 20 short thick setae in the middle and about 40 others, several times as long, laterally.

The mandibles (Fig. 3 B) are well developed, and their apical part has the shape of a tooth bent towards the interior of the mouth-parts. The incisor area is very sharp, with a serrated edge and a deep indentation in the middle. The posterior condyle and the anterior articular surface are well developed. The mouth of adult insects comprises all the component parts, not excluding the paraglossae and glossae, which are wanting in the larva. As a whole, the maxillo-labial complex is elongated, which is especially true of the maxillary palp (Fig. 4).

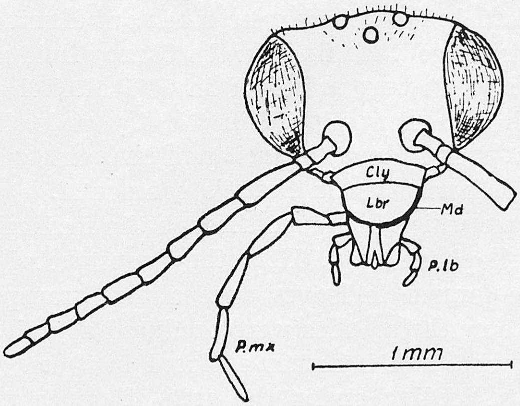


Fig. 1. Head of female *H. vagans* Fall. Cly — clypeus, Lbr — labrum, P. lb — labial palp, P.mx — maxillary palp.

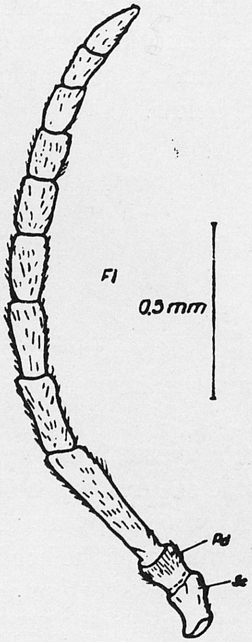


Fig. 2. Antenna of female *H. vagans* Fall. Sc — scape, Pd — pedicle, Fl — flagellum.

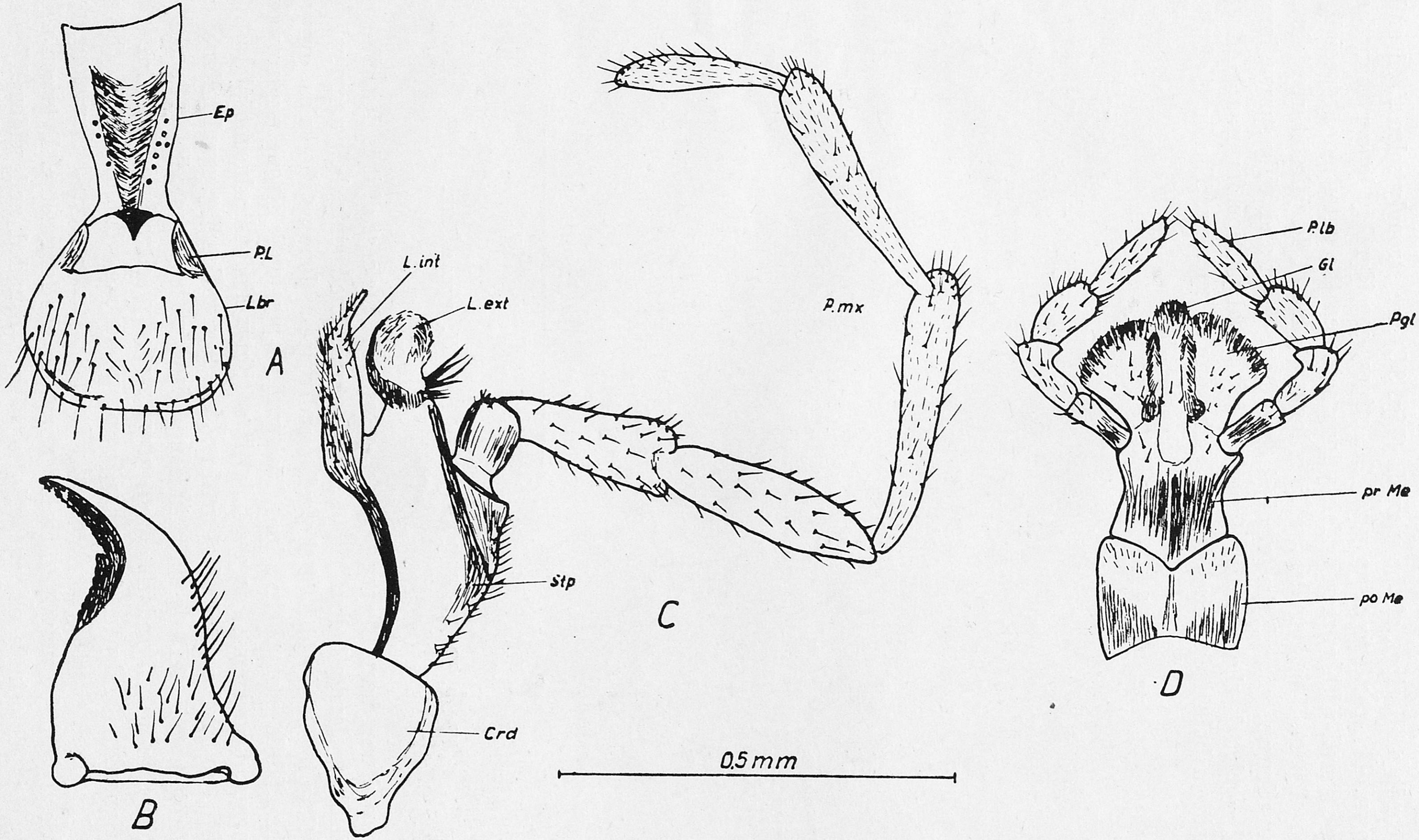


Fig. 3. Mouth-parts of female *H. vagans* FALL. A. Labrum (Lbr) and epipharynx (Ep); P. L — process of labrum. B. Mandible. C. Inner view of the maxilla; Crd — cardo, Stp — stipes, L. int. — lacinia, L. ext — galea, P. mx — maxillary palp. D. Labium, po Me — postmentum, pr Me — prementum, P. lb — labial palp, Plg — paraglossa, Gl — glossa.

The cardo and stipes of the maxilla (Fig. 3 C) are strongly sclerotized and dark brown. The cardo is triangular, the stipes, considerably longer than the cardo, is covered with numerous fairly long setae on the outer side, especially in the basal part. The maxillary palp is long, 6-jointed. The first three joints bear sparse long setae and the terminal three have short and, only sparse, long setae. The galea is short and rectangular, its apical portion forms a kind of spoon, with a hollow in the side facing the mouth opening. The base of the spoon-shaped part bears 7 very long setae, whereas the rest of it is densely covered with long slender hairs forming a kind of fur. The lacinia, being somewhat broader than half the width of the galea and twice as long as the galea, grows out of the middle part of the stipes. Its terminal portion is strongly narrowed and elongate. The lacinia, as a whole, is a thin-walled translucent plate, of which only the basal part is sclerotized and covered with setae equal in length.

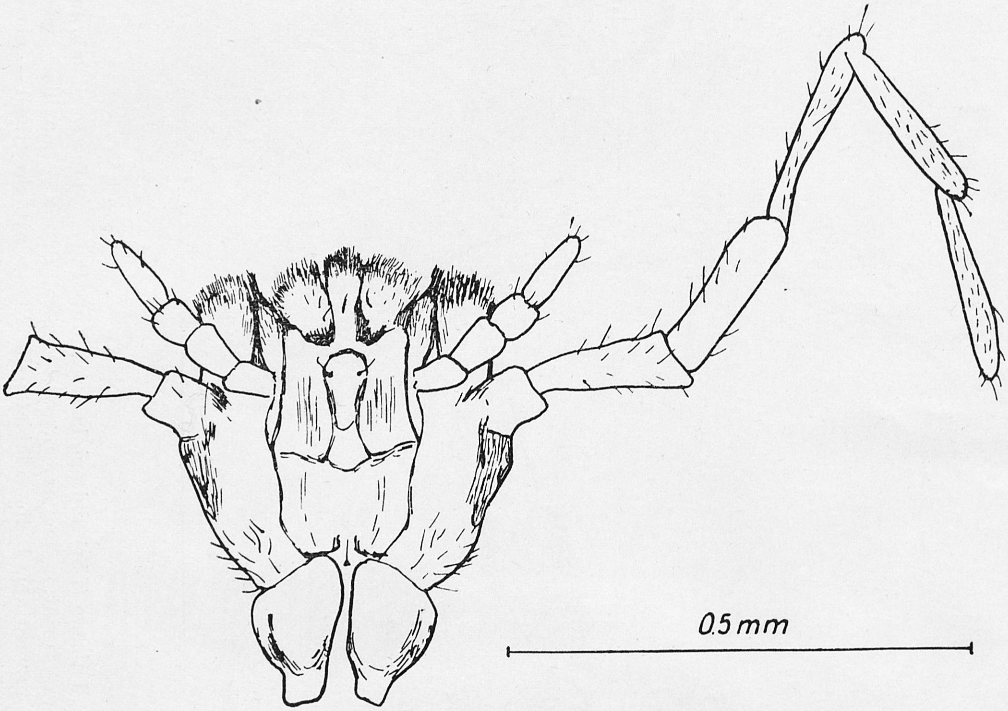


Fig. 4. Maxillolabial complex of male *H. vagans* Fall.

The labium (Fig. 3 D) is short in comparison with the maxilla. The postmentum is thin-walled and the prementum strongly sclerotized, dark brown, with a triangular basal part. The paraglossae, which are triangular plates, bear unequal, long and short, setae, especially in the upper part, and thin elongate plates, mostly on the margin. The inner margin has long setae. Between the paraglossae is the single elongate glossa with a rounded and widened end.

Like the paraglossae, it is covered with setae and plates terminally; there are 3 single setae at the base of the glossa.

The best developed segment of the thorax is the mesothorax, which almost completely covers the prothorax dorsally (Fig. 5). The mesonotum is divided into four parts — the prescutum, the scutum, the scutellum and the postnotum — of which the scutum is the largest. The scutellum has the shape of a rounded pentagon and the adjoining postnotum that of a small wide triangle.

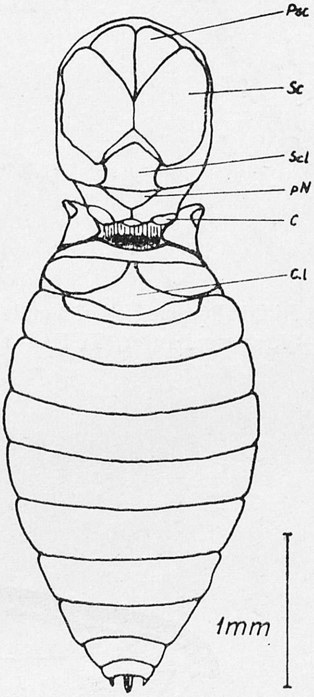


Fig. 5. Thorax and abdomen of female *H. vagans* Fall., viewed from above. Psc — prescutum, Sc — scutum, Scl — scutellum, Pn — postnotum, C — cenchri, C. l — crack-like connection of tergites I and II.

The posterior part of the prescutum and the anterior part of the scutum as well as the whole scutellum are clothed with hair. The pre-, meso- and metanotum, with the exception of two white dorsal cenchri, are black-brown.

The thoracic legs (Fig. 6 A) are relatively slender and more or less uniformly clothed with short hairs. All the three pairs of legs have two trochanters. The second of them (trochanter II) belongs to the femur (Snodgrass, 1935). At the apex of the tibia there are 2 apical spurs. On the front legs one of the spurs is slender, straight and short, whereas the other (Fig. 6 B) is very stout, flattened, longer than the first, arched and split at the end; its surface except the very tip is covered with setae transformed into a kind of scales. The apical spurs on the tibiae of the second and the third pair of legs are subequal and covered with scale-like setae.

The tarsus consists of 5 segments, the first of which, the metatarsus, is the longest and the fourth is the shortest. The tarsus is fairly densely covered with thick setae, which on the metatarsus are still denser and arranged in even

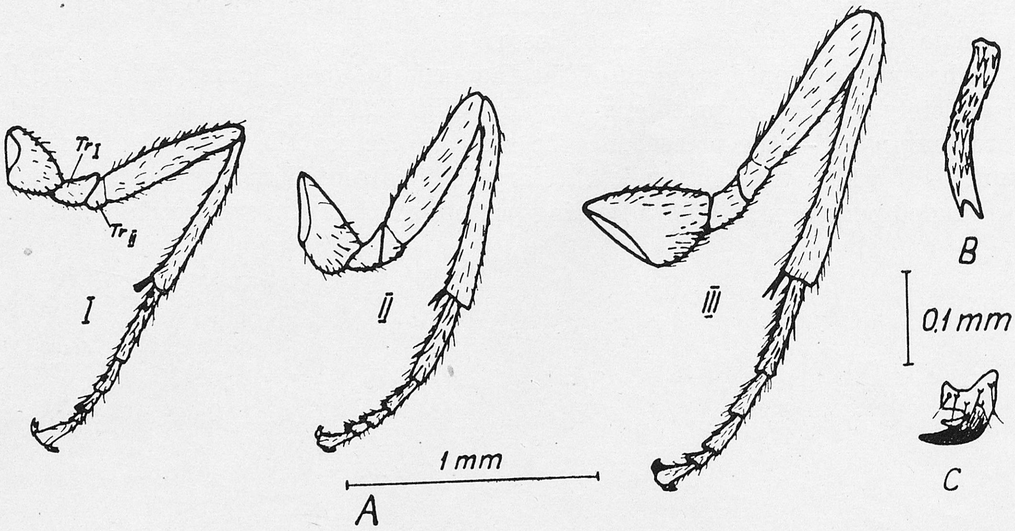


Fig. 6. Right thoracic legs of female *H. vagans* FALL. A. Fore, middle, and hind leg (I, II and III). Tr I — first trochanter, Tr II — second trochanter. B. Spur of tibia of 1st pair. C. Claw of tarsus of 3rd pair.

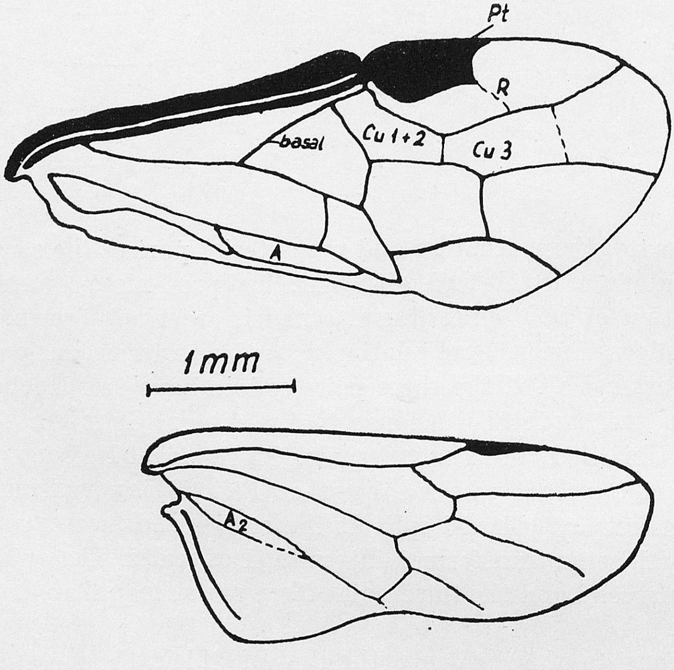


Fig. 7. Wings of female *H. vagans* FALL. Pt — pterostigma, R — radial cell, Cu 1+2 — cubital cell 1+2, Cu 3 — cubital cell 3, A, A_2 — anal cells, basal — basal vein.

rows resembling a brush. Two dark brown claws (Fig. 6C), situated at the end of the tarsus, are bifid, with the basal portion widened. The legs are usually yellow-brown excepting the lower portion of the tibia and the tarsus of the third pair, which are almost dark.

The wings (Fig. 7) are smoky dark brown, uniformly covered with short hair except for the front margin and stigma, where the hair is remarkably more abundant. The venation of both pairs of wings is characterized by great variation. The radial cell of the fore-wing is divided by an indistinct, usually decoloured cross-vein. Cubital cross-vein I is hardly ever present and even then it is very weakly marked; consequently, there are only two cubital cells. Benson (1951) mentions three cubital cells in the genus *Heterarthrus*. Cubital cross-veins II and III are generally partly decoloured and the basal vein is straight. The anal cell in the fore-wing is separated from the front by an oblique cross-vein. In the hind-wing there is no well-defined middle cell, and the anal cell occurs only rarely. The hair is like that on the fore-wing only that in the basal part there are additional setae, pointed and one-fifth as short as the hair.

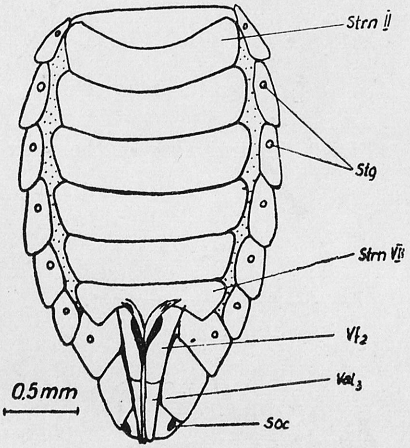


Fig. 8. Ventral view of the abdomen of female *H. vagans* Fall. Strn II — sternite II, Stg — spiracles, Strn VII — sternite VII, Vf_2 — valvifer II, Val_3 — valve III, Soc — socii.

Eight well-developed tergites can be identified on the dorsal side of the abdomen (Fig. 5), whereas tergite IX is considerably shorter and narrower and tergite X is the smallest. The last-named tergite is haired and bears paired sensory processes, the socii. Between tergites I and II there is a medial „cracking", more or less triangular in shape, convex, and whitish in colour. Tergite I and the middle parts of at least two terminal tergites (IX and X) are usually dark brown. The rest of the dorsum of the abdomen is orange-yellow. In dark-coloured specimens tergites II, III, IV and V have also dark brown medial patches.

Spiracles in the form of oval pits occur at the sides of segments I—VIII (Fig. 8). Ventrally, the abdomen has 6 normally developed sternites (Fig. 8), but as the sternite of segment I has undergone a reduction (Berland, 1951; Enslin, 1918; Gussakovsky, 1935), they are, strictlys peaking, sternites II—VII.

The ventral side of the abdomen is usually yellow-orange except the brown external case of the ovipositor and the socii.

In structure the ovipositor of female *H. vagans* FALL. is very much like that in other sawflies (ENSLIN, 1918; SNODGRASS, 1935). It is comparatively short and, when at rest, only slightly projects beyond the end of the abdomen (Figs. 9, 10 A). Its external part is formed by broad paired plates, valves III and valvifers II, which are joined together (Fig. 10 B) into a sheath encasing a pair of valves II and their plates, valvifers I (Fig. 11 A, B). Both valve III and valvifer II are broad, strongly sclerotized, dark brown plates, covered with short hairs on the external side. Valvifer II is joined with tergite IX at the back and with valves I and II at its anterior end. The last-mentioned valves form the essential part of the ovipositor. Valves II are lanceolate, slightly S-shaped,

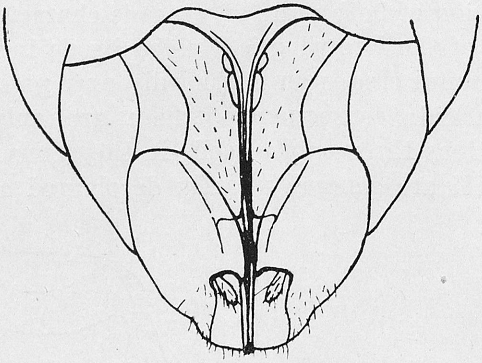


Fig. 9. Ventral view of the apex of the abdomen of female *H. vagans* FALL.

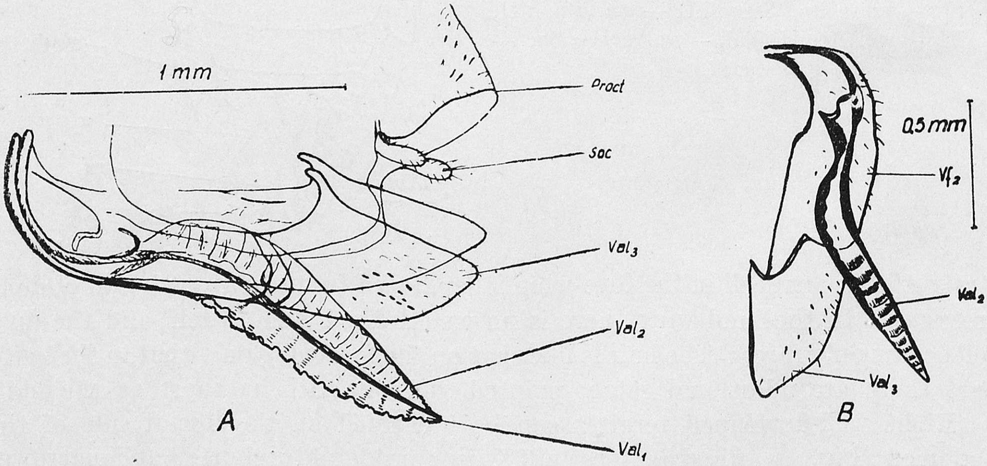


Fig. 10. Ovipositor of *H. vagans* FALL. and its components. A. Lateral view of the whole ovipositor. Val_1, Val_2, Val_3 — valves I, II and III, Soc — socii, Proct — proctiger. B. Valvifer II (Vf_2) and valves II and III (Val_2, Val_3).

convex externally and densely cross-ribbed, and they constitute the dorsal part of the ovipositor. Both valves II are joined together along the thickened dorsal margins, whereas they have a slide articulation with valves I along their ventral edges. Valves I are far more delicate and less sclerotized than valves II and they do not bulge externally. The lower external margin of valve I bears a large number of teeth. At rest both valves I adhere to each other along their lower serrated edges. The posterior part of valve I, resembling a bent stout rod, is united with valvifer I, which is in turn articulated with tergite IX on one side and with valvifer II on the other side.

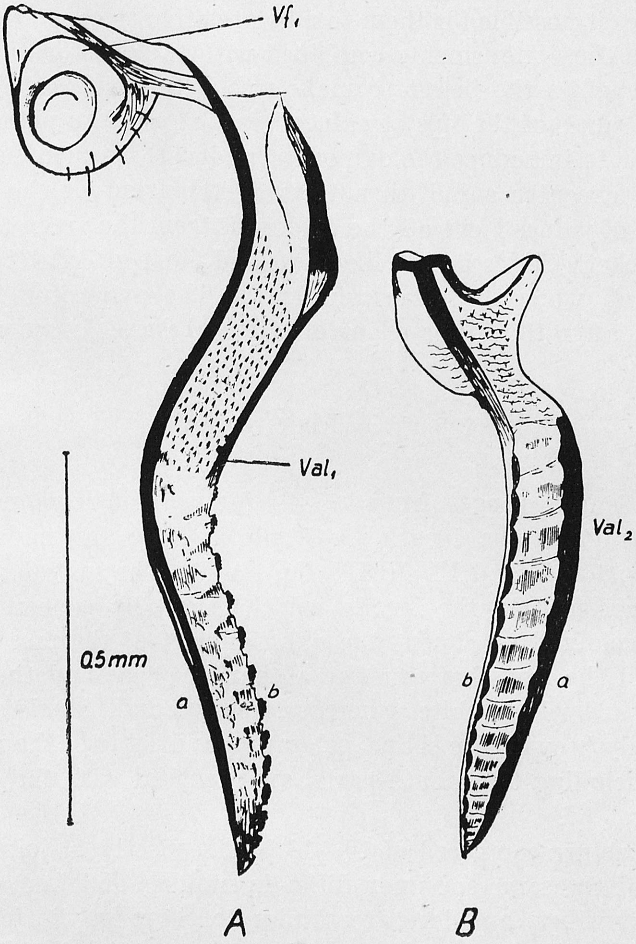


Fig. 11. Components of the ovipositor of *H. vagans* FALL. A. Left valvifer I (Vf_1) and valve I (Val_1). B. Right valve II (Val_2); a — dorsal view, b — ventral view.

Besides the ovipositor, the abdomen ends dorsally in the so-called proctiger (SNODGRASS, 1935) or anal segment (ENSLIN, 1918), with two short haired processes, the socii. The proctiger is covered with long hairs, which are probably sensory hairs, serving, together with the socii and valves III to choose suitable leaves and next places in the leaves for egg-laying.

Owing to the articulations of valvifer I with tergite IX and valvifer II as well as to the suitable musculature, the ovipositor can be protruded and, at the same time, twisted throughout nearly 180°. The sliding joint of valves I with valves II makes it possible for them to move relative to each other. The possibility to perform these movements combined with the work of the sawing blades of the organ enables the insect to make a pocket for an egg in the leaf. The serrated sharp edges of the tips of valves I and II serve to pierce the epidermis of the leaf so as to introduce the ovipositor under it. On piercing the epidermis, the ovipositor executes a half-turn towards the front of the body, and the serrated edges of valves I cut off the epidermis from the green tissue of the leaf and form a pocket. Valves I work like saws and move alternately: one is pushed slightly forward, while the other withdraws. The ovipositor deposits an egg in the pocket, after the lower edges of valves I have drawn aside.

Male

The body length ranges from 2·5 to 5 mm, but it is usually 3·5 mm. BENSON (1952) gives the length, 3—5 mm, jointly for males and females (Pl. XLII, figs. 1 A, B and Pl. XLIII, fig. 1 A, B). The male is generally much smaller and darker than the female, which especially concerns its abdomen.

In lighter coloured specimens the anterior part of the face — the clypeus, labrum, part of the frons between the antennae, genae and the inner margins of the eyes — are yellow-white, whereas in darker individuals also these parts are dark, usually brown. The shape, coloration and setae of the remaining parts of the head, including the mouth-parts, are identical with those in the female (Fig. 4).

The antennae are composed of 10—13 joints, mostly 11-jointed. Sometimes the antennae of the same specimen differ in number of joints, e.g. 11 and 12.

The thorax, wings, and legs are similar to those in the female. In dark-coloured specimens the coxae, the epiphyseal parts of the femora and the tarsi of all the three pairs of legs are also dark brown. In lighter specimens only the terminal parts of tibia III and tarsus III are brown.

The most pronounced differences between the male and female are found in the shape and colour of the abdomen. There are eight fully developed tergites on the dorsal side of the abdomen in the male. Tergite IX is remarkably narrower than the preceding ones, and so is tergite X, which besides is rounded and bears paired sensory processes, the socii. On the ventral side of the abdomen there are 6 sternites of normal width; as in the female, they are the sternites of segments II—VII. Behind them is the hypopygium, in the form of a large oval plate, which according to GUSSAKOVSKY (1935), SNODGRASS (1935) and SZWANWICZ (1956) is the sternite of segment IX (Fig. 12 A).

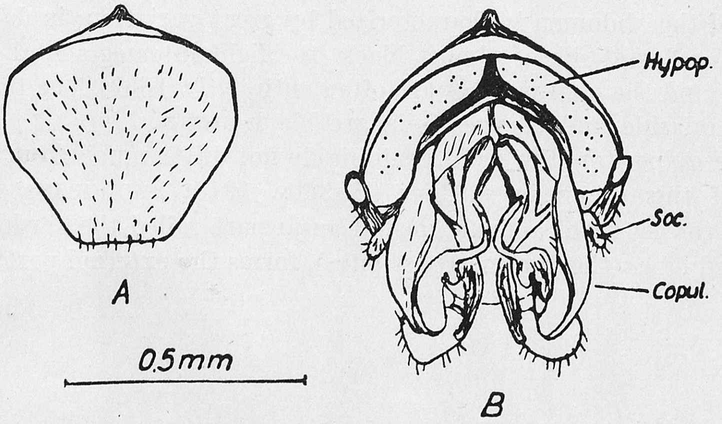


Fig. 12. A. Hypopygium (Hypop). B. Male genitalia (Copul) of *H. vagans* Fall. Soc — socii.

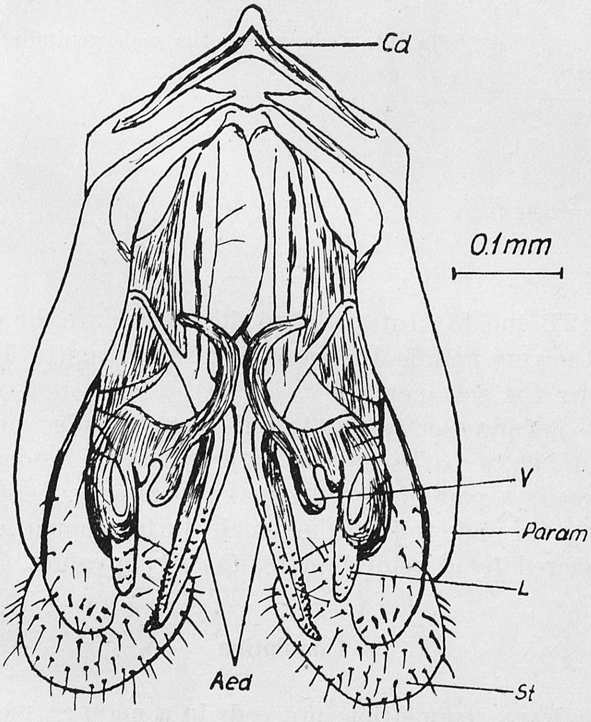


Fig. 13. Male genitalia of *H. vagans* Fall. Cd — cardo, Param — parameres, St — stipal processes, L — lacinia, V — volsella, Aed — aedeagus.

The dorsal side of the abdomen is generally dark brown, only the junction of tergites I and II and often those of other tergites, as well as the oval patches along the upper and lateral edges of the tergites (4 on each), are light brown. The ventral side of the abdomen, at least its terminal part including the genitalia, is dark brown, the remaining parts are yellow-golden. As in the female, the coloration of the abdomen is characterized by great variation; in dark-coloured specimens the dorsal side is almost black, the light intersegmental membranes are wanting and the oval patches are often entirely invisible. The terminal part of the ventral side and the genitalia are black-brown.

Like the ovipositor, the male genitalia do not differ much from the typical structure of this organ in sawflies (ENSLIN, 1918; SNODGRASS, 1935). The phallobase, consisting of a single medial basal part called the cardo and broad lateral paired lobes, the parameres (stipites), forms the external part of the male genitalia (Figs. 12B and 13). Internally to this sheath are the paired lacinia and volsella and, in the very middle, the paired aedeagus (sagitta, Fig. 14), surrounding and stiffening the soft penis.

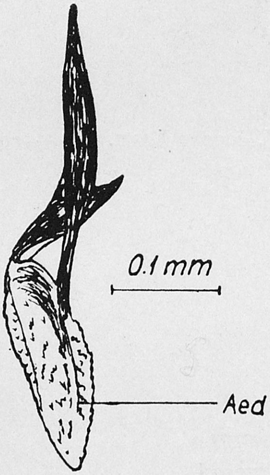


Fig. 14. Aedeagus of the male genitalia of *H. vagans* FALL.

The aedeagus is composed of two trough-shaped blades, pointed at the end, with a large number of barbs on the outer surface. Besides the lacinia and volsella there occurs a pair of dorsal stipal processes, covered with long hair. They are used by the male to hold the female during copulation. Ventrally, the genitalia are covered by a genital plate, the hypopygium.

Copulation

In *H. vagans* FALL. copulation proceeds in a manner more or less similar to that described by BISCHOFF (1927) for other sawflies. The insects copulate with their terminal parts of body turned to each other. The male holds the female's body in the region of the ovipositor with the prehensile parts of its copulatory organs and, as a result, the end part of its abdomen is positioned under the end part of the female's abdomen, while the whole abdomen of the male is arched ventrad.

During copulation, lasting about 15 minutes, the male remains inactive and the female moves forwards, dragging the male behind. In the cases observed the females were decidedly larger than the males copulating with them. After copulation the male becomes very active and the female keeps motionless for about 10 minutes.

The Ethology of Adult Insects

Laboratory insects fed on liquid food, i.e., the secretion of aphids and sweetened or unsweetened water. They lick food, e.g., the secretion of aphids, off leaves with their glossae, paraglossae, galeae, and laciniae. The mandibles do not serve this purpose, but are used by the adult insect to cut out an opening in the hard wall of the cocoon, through which it gets out.

The longevity of adult insects depends on nutrition and other external conditions, especially temperature; they appear to be most vigorous at a temperature of 20—25° C. Generally, they live for a very short time. Females, if nourished, lived 7—10 days, those fasted only 3—5 days. The lifetime of males averaged 1—3 days.

Males are less numerous than females. It may be stated on the basis of my observations that the ratio of males to females is as 1:4. Imagines derived from the larvae collected in September and October begin to emerge in the laboratory, after hibernation and pupation, in the spring of the next year. They appear, at first in small numbers, as early as the beginning of April, then throughout May, June, July and August. The highest number of emerging insects occurs in July and August. It also often happens in the laboratory that the imagines derived from the larvae of the second generation emerge in September and October of the same year. These are both males and females; they all exhibit small vitality and live on the average 1—2 days. The adults obtained from larvae of the first generation usually appear in July and August of the same year.

Parthenogenesis

When studying the biology of *H. vagans* FALL., I found that in addition to bisexual reproduction, parthenogenesis takes place in this species. After emerging from their cocoons, females, completely isolated from males, laid eggs in fresh alder leaves offered them in closed vessels. Under suitable conditions larvae hatched from the eggs and began feeding to form cocoons next. After pupation imagines emerged from the cocoons. The rearing of isolated females showed that irrespective of season the larvae obtained from the unfertilized eggs went only through 5 instars and after pupation gave origin to females only. Thus, this is the arrenotokous type of parthenogenesis, observed also in other sawflies (BERLAND, 1951; BISCHOFF, 1927; ENSLIN, 1918).

Oviposition

The female often begins to lay eggs some dozens of minutes, more rarely several or even more than ten hours, after emergence. It chooses the leaves for oviposition very carefully; it never selects young leaves but almost exclusively the oldest ones or at least those of medium age. The careful selection of leaves is justified, as the green tissue of young alder leaves turns brown and dies owing to even a slight hurt. The very incision of the epidermis of a young leaf with the ovipositor and, what is more, the feeding of a young larva in it bring about the dying of the damaged portions of the green tissue. Under laboratory conditions, when the suitable leaves are wanting, the female lays eggs also in the young leaves. These eggs are, however, fated, because the green tissue surrounding the recess turns dark and the larva hatched from the egg perishes without finding any access to the food. If the damage is not extensive, the larva may begin to feed, but it reaches the second instar at most. After the first moult, during the interstadial interval the green tissue surrounding the mine becomes mortified and, consequently, the larva is unable to take up feeding after the break.

The female carefully inspects the upper surface of the leaf selected, feeling it with the antennae and with the ovipositor region of body in order to find a suitable place for laying eggs. Then it incises the upper epidermis with the ovipositor, inserts the ovipositor under the epidermis, separating it in this manner from the palisade layer over some area. In so prepared a pocket the female lays an egg. During the formation of the pocket the movement of the ovipositor is always the same. It passes sideways from the back towards the front of the body, on its left or right side. During the formation of the pocket the sawing sheath of the ovipositor (valves I and II — Fig. 11 and Pl. XLII fig. 2A, B), sunk under the epidermis for the whole length, moves throughout nearly 180° relative to the main body-axis. The pocket being incised, the ovipositor returns freely the same way but in the opposite direction, that is, from the anterior position backwards. It looks as if the insect checked the execution of the pocket. Next, valves I and II, joined together, move to the front throughout nearly 90° to stop right in the middle of the pocket, in which an egg is deposited at this moment. After laying the egg the female removes the ovipositor from the pocket and retracts it into the sheath (valvifer II and valve I — Fig. 10).

It takes the female on the average 30—45 seconds to perform a pocket and lay an egg. While forming the pocket, the female assumes a characteristic posture, with its legs set strongly on the surface of the leaf, the abdomen bent into the form of a bow, and the whole body leant to the side on which the ovipositor is positioned. The sawing motion of the ovipositor is communicated to the whole body and brings about its vibration. After laying an egg, the insect always rests for a while and almost always cleans its legs and antennae.

The pocket is often too shallow and the egg deposited is only partly hidden in it or even it lies whole on the surface of the leaf outside the pocket (Pl. XLIII, fig. 4). Among some scores of eggs laid by a female there are a few placed outside the pockets. Occasionally the ratio is even as 1:1. The eggs laid improperly usually become mouldy and the larvae only seldom hatch from them. These larvae perish, being unable to gnaw into the green tissue of the leaf. The number of eggs laid by one female is various, depending on the size and vigour of the insects. The number of eggs laid by some of the females in the laboratory are as follows: 12, 18, 21, 22, 23, 27, 30, 36, 41, 47, 53, 57, 61, 62, 65, 69, 71, 76, 86, 88, 91, 98, 114, 186.

Under natural conditions, in one leaf there is usually one egg, more rarely several and only exceptionally 10—15 eggs (September 1961, Krzemionki in Kraków). When the number of eggs deposited in one leaf is large, they are disposed in groups of a few eggs lying near each other, at intervals of several millimetres.

In the laboratory, where the female is offered only a few leaves, the number of eggs per leaf may amount up to 28, 30, 42 and even 70 (Pl. XLIII, fig. 2 A, B).

The distribution of eggs in the leaf is various. Under normal conditions the eggs are never deposited in the close neighbourhood of the main vein or its branches of the first order.

The Size and Appearance of Eggs

New-laid eggs are colourless, transparent, and oval in shape (Pl. XLIII, fig. 3). Immediately after oviposition the measurements of eggs range from 553 to 615 μ in length and from 246 to 344 μ in width. These differences are due to the differences in size between the females laying the eggs, though it often happens that some of the eggs laid by the same female in the same period differ in size by scores of microns.

Embryonic Development

Three to five days after oviposition the embryo can be seen in the egg under a magnification of roughly 100 times. It is situated on the semifluid deutoplasm, which fills the egg. When several days old, the embryo is glassy and white, elongate in shape, with the head hardly distinguishable from the rest of the body, and the segmentation slightly marked; every now and then it evidently changes its position. At that time the egg-shell is well visible as a very thin transparent membrane.

About 6 days after egg-laying the embryo occupies half the content of the egg and at 9—10 days it fills the whole egg tightly. At this stage of development the larva in the egg shell corresponds to the feeding larva in the first instar in appearance.

The shape of the egg changes in the course of embryonic development. It becomes bigger and its width:length ratio decreases. For example, an egg 553 μ long and 307 μ wide when newly laid, was 639 μ long and 430 μ wide after 10 days, when the embryo filled tightly its inside. In this stage the egg is well seen with the naked eye on the surface of the leaf (Pl. XLIII, fig. 2A).

THE LARVAL PERIOD

Structure of the Larva

This general description will include only the characters that all the instars of the larva have in common. The changes occurring in the structure of the body, as the larva develops, will be presented in the descriptions of particular instars.

The body of larval *H. vagans* FALL. consists of the head and 13 segments, the first three of which form the thorax and the remaining ones the abdomen (Fig. 15). The flattened head is prognathous. The thoracic segments are more flattened and much wider than the abdominal ones, which are rather oval in cross-section and, with the exception of the last two segments, divided transversely into two annulations each. This character is especially distinct in the later instars (Fig. 25). The abdomen tapers caudad. The head is yellow-brown, the thorax and abdomen whitish, with a dark brown pattern. Tuberculiform abdominal feet are located on the ventral side of the abdomen, near to the median line, on segments II—VIII and X.

Head

The head, which is the most flattened part of the body, is elliptical in outline (Fig. 16). The head-capsule is divided into 3 parts by the short epicranial suture, which further splits into two frontal sutures. The oval frons, bounded by the frontal sutures, occupies the central part of the head, with an epicranial area on either side. The head-capsule is strongly sclerotized and more or less uniformly yellow-brown; only the sutures are somewhat darker. The back of the head, up to the place where the epicranial suture branches, is usually covered by thoracic segment I. A single lateral ocellus is situated in the anterior part of either epicranial area; it has the shape of a telescope (Fig. 17) and is arranged obliquely, with its lens directed towards the front of the head. The setting of the ocellus and its pigment are dark brown, the lens is convex and colourless.

Inferior to the ocellus, near the base of the mandible, is the 3-jointed antenna (Fig. 17). In the first instar the antenna is almost flat, in the later instars it is conical. On the surface of the antenna there are gland-like accumulations of sense organs. The antenna is set in a circular area covered with small and large warts (Fig. 28).

In the lower part of the epicranial area there are 6 long setae, 5 between the ocellus and the base of the mandible and one at the back, above the ocellus

(Fig. 16). The frons is devoid of setae, it bears a few warts only. Small numbers of similar warts are also present on the epicranial area.

The clypeus, composed of two parts, the pre- and postclypeus, is separated from the frons by the slightly marked epistomal suture. Both parts of the clypeus bear warts, which are disposed symmetrically, two in each part (Fig. 16). The labrum is an elongate rounded plate (Fig. 18A). Its posterior margin is connected with the clypeus by two processes, and the lower margin bears a median sinusoidal indentation, in the middle of which there is a small well-defined area in the shape of the letter „U“ with about 5 shallow grooves. Up to 16 big warts are located on the external side of the labrum. The epipharynx, ending in two arcuate rows of stout fringy processes, adjoins the internal side of the labrum (from the side of the mouth cavity). These processes, about 10 in each row,

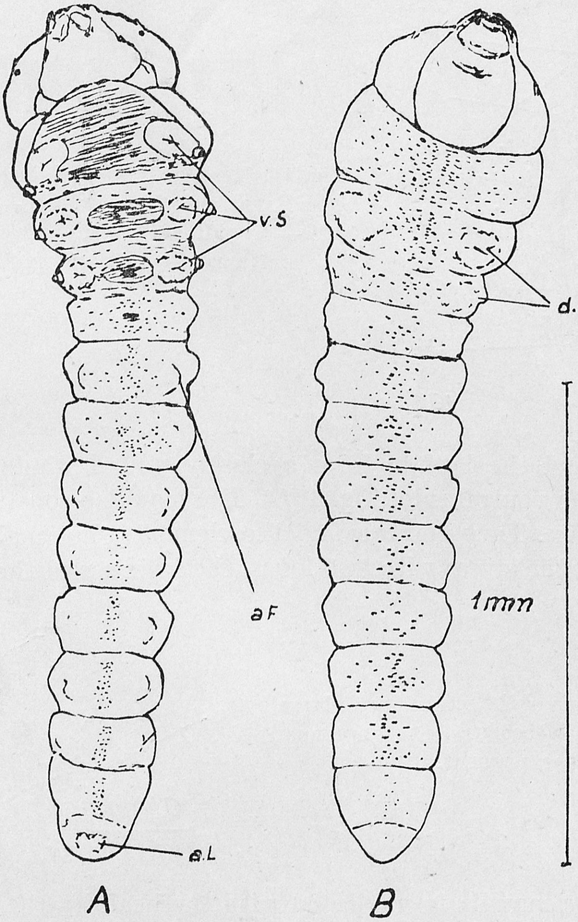


Fig. 15. The first-instar larva of *H. vagans* Fall. A. Ventral view; v. S — ventral suckers, a. F — abdominal feet, a. L — anal legs. B. Dorsal view; d. S — dorsal suckers.

project beyond the margin of the labrum. Towards the pharynx the surface of the epipharynx is furnished with small barbs.

The mandibles are irregular tetrahedra, heavily sclerotized and dark brown in colour (Fig. 18 B). The incisor area bears 4 blunt teeth, which differ in size. The last tooth on the external side has its surface shaped into fine ribs. Externally, there is one seta in the region of the posterior articular process.

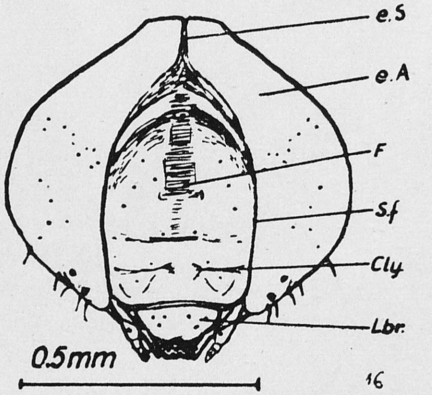
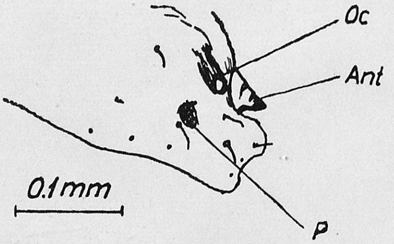


Fig. 16. Head of the fourth-instar larva of *H. vagans* Fall., anterior view. e. S — epicranial suture, f. S — frontal suture, F — frons, e. A — epicranial area, Cly — clypeus, Lbr — labrum.

The maxillae and the labium form a closely united whole, bounding the mouth cavity on the ventral side (Fig. 18 C). The maxillae constitute the lateral parts of the complex. They comprise all the elements that make up a typical maxilla: the cardo, the stipes with two lobes, the lacinia and the galea, and the maxillary palp. The maxilla is connected with the head by the cardo and it is grown together with the labium for the whole length of the internal margin of the stipes. The cardo is relatively poorly developed and forms a bent narrow plate embracing the basal portion of the stipes. The stipes, the largest element of the maxilla, widens towards the base and bears 2 setae on the external surface. Apically it has 2 lobes — the lacinia and the galea — on the internal side and the palp on the external side. The lacinia is hard to notice, as it is covered by the labium; the whole of the structure cannot be seen until the maxilla has been separated from the labium (Fig. 19 B). The lacinia is a very elongate delicate plate with about 3 rows of fringy processes on its distal end. Three of the processes, neighbouring upon the galea, are remarkably thicker and bigger than the others (Fig. 19 C).

Fig. 17. Eye and antenna of the second-instar larva of *H. vagans* Fall. Oc — ocellus, Ant — antenna, P — eye pigment.



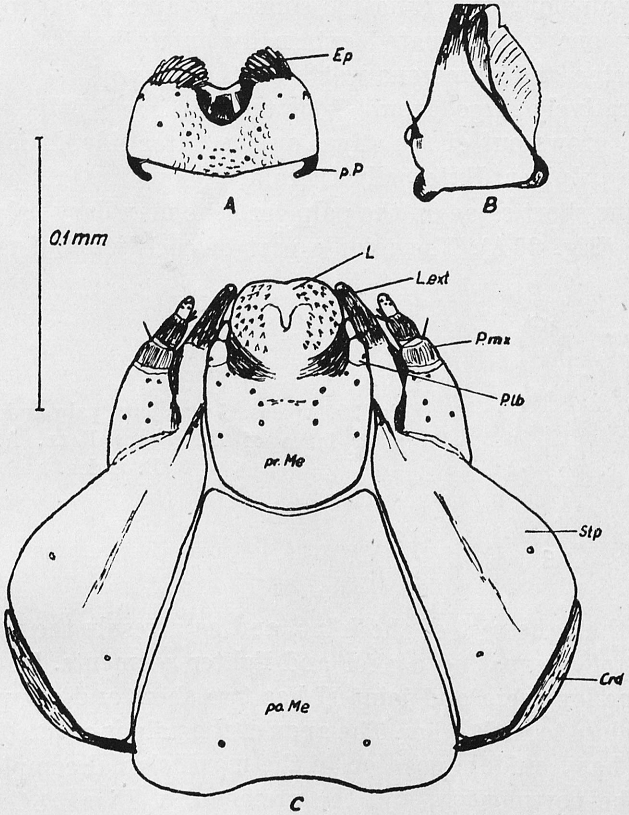


Fig. 18. Mouth-parts of the first-instar larva of *H. vagans* FALL. A. Labrum. Ep — epipharynx, p. P — posterior process. B. Mandible. C. Maxillolabial complex. Crd — cardo, Stp — stipes, P. mx — maxillary palp, L. ext — galea, po Me — postmentum, pr Me — prementum, P. lb — labial palp, L — ligula.

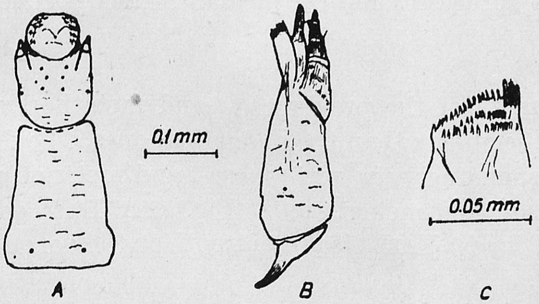


Fig. 19. Dissected maxillolabial complex of the fourth-instar larva of *H. vagans* FALL. A. Labium. B. Right maxilla of 1st pair, lateral view. C. Terminal part of lacinia.

The galea is an elongated truncated conus. Its apex seems to form a distinct part with only one seta, situated externally on its border. There are about 6 short stout setae and numerous warts on the apex of the galea (Fig. 20 B).

The comparatively large, stout, 3-jointed maxillary palp, subequal to the galea in length, grows out of the stipes on the outer side. It is set in a sturdy basal joint, the palpiger. Externally there are about 5 warts and, in the later instars, also some short setae on the palpiger. The maxillary palp is a truncated conus in shape (Fig. 20 A). The middle part of each joint of the palp is dark brown, darker than the rest of the joint, and as a result the whole palp looks as if composed of alternating darker and lighter segments. The outer edge of joint I bears one long seta and joint II has two short and comparatively stout setae, situated close to each other. The apex of the palp is covered by 8 fine setae.

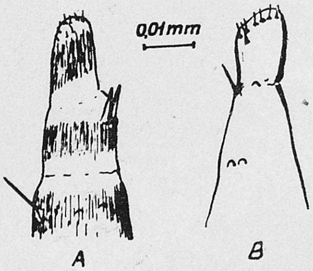


Fig. 20. Apices of maxillary palp and galea of the first-instar larva of *H. vagans* FALL. A. Maxillary palp. B. Galea.

The labium has a middle position in the maxillolabial complex and consists of two parts, the postmentum and the prementum (Figs. 18 C and 19 A). The postmentum is a large trapeziform plate with two warts disposed symmetrically in its lower corners. The prementum is considerably smaller, rounded distally, and has about 12 warts, in the later instars also setae, on its external surface. The small 3-jointed labial palps grow out on both sides, more or less in the middle of the prementum. The paraglossae and glossae are wanting; instead, the ligula with the opening of the spinning gland on it has developed in their place. The hypopharynx adjoins the labium internally. Its external edge usually carries fringy fleshy processes and the median surface is covered with numerous short spines.

Thorax

The thorax consists of the pre-, meso-, and metathorax, which are larger and more flattened segments than the abdominal ones. The dorsal parts of these segments are correspondingly the pro-, meso-, and metanotum, and the ventral ones: the pro-, meso-, and metasternum (Fig. 21 A, B). A dark brown pattern, characteristic of *H. vagans* FALL., is present both on the dorsal and on the ventral side of the thorax.

The prothorax is the largest of the thoracic segments. It covers the base of the head both dorsally and ventrally. The central part of the pronotum is occupied by a heavily sclerotized brown shield, divided medially by a light-coloured unpigmented line (moulting line).

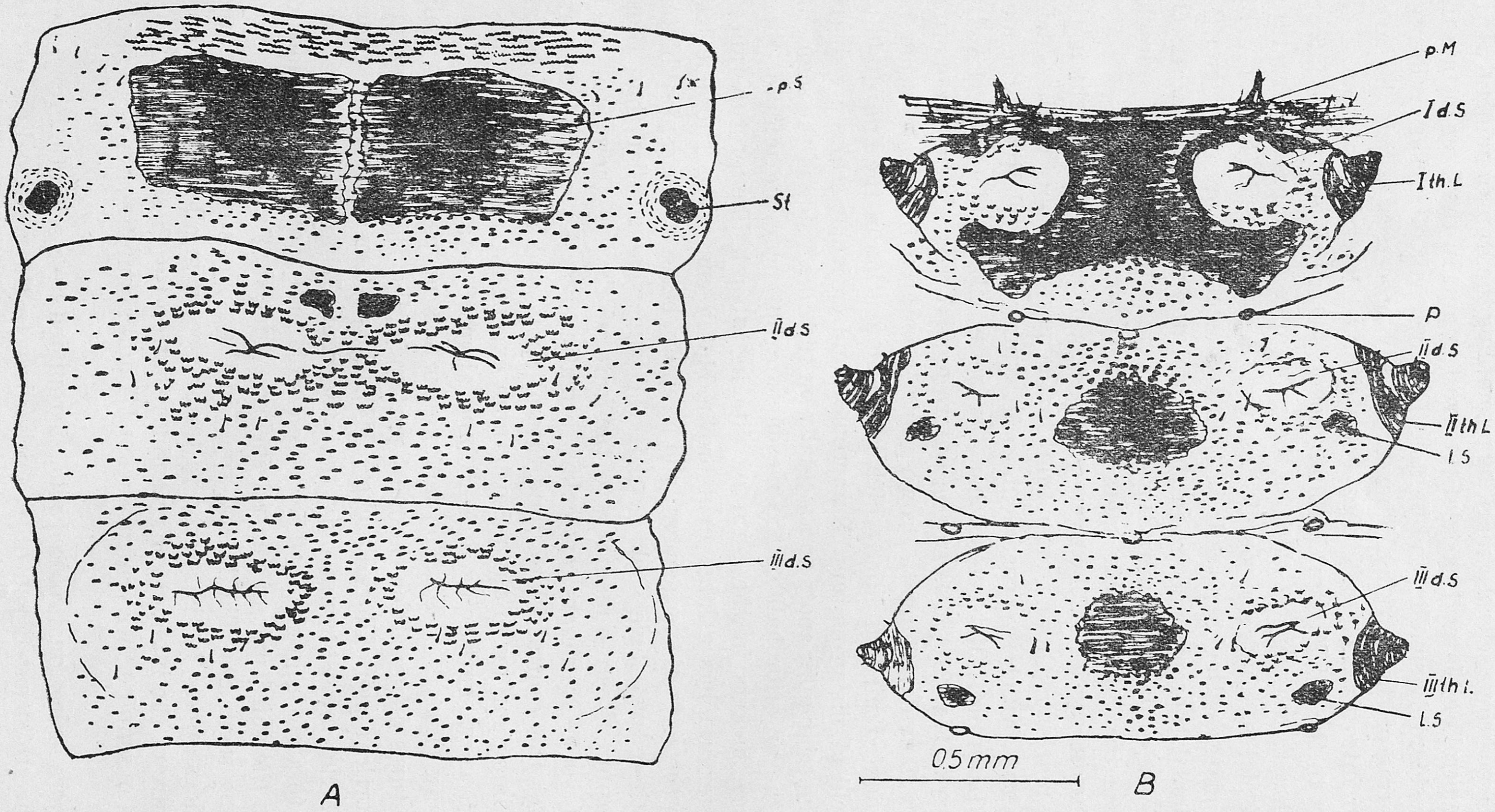


Fig. 21. A. Dorsal view of the body-wall of the fifth-instar larva of *H. vagans* Fall. p. S. — pronotal shield, St — spiracles, II d. S — dorsal sucker II, III d. S — dorsal sucker III. B. Ventral view of the body-wall of the fifth-instar larva of *H. vagans* Fall. p. M — prosternal marking, I d. S, II d. S, III d. S — dorsal suckers of first, second and third pair, I th. L, II th. L, III th. L — thoracic legs I, II and III, P — pit, l. S — lateral spot.

There is a large brown sclerotic marking resembling the Roman numeral „I“ in shape in the central and lateral parts of the prosternum. In the later instars the marking is considerably smaller and lighter. The first pair of suckers is located between the arms of the marking. They are fleshy processes, which the larva can expand or introvert. Thoracic legs I are situated laterally to them.

In addition to the shield, marking and suckers described above, the integument of the dorsal and ventral sides of the prothorax bears brown structures in the form of plates, which are rounded or furnished with teeth (Fig. 21A, B). The cuticular plates with sharp teeth on their free edges are present round the ventral and dorsal thoracic suckers in the second and subsequent instars. On either side of the prothorax, near the posterior margin, there is a spiracle, located between two semicircular spots (Fig. 21A).

The prosternum carries on the average 10 setae, of which 2 are right in the middle of the marking. On the pronotum, in the posterior part of the shield, 8 setae form a row, which is perpendicular and symmetrical relative to the long axis of body. Laterally, this segment has 4 setae on either side (Fig. 21A, B).

Mesothorax (Fig. 21A, B). In the antero-medial part of the mesonotum there are two triangular elongate brown spots, separated from each other by a light unpigmented median line, which is a prolongation of the line dividing the dorsal shield of the pronotum. Numerous round cuticular scales are distributed round the triangular spots and medially on the dorsal side of the segment. Laterally, in the anterior half of the mesonotum but near the middle, there are single large suckers in the form of slits in tubercle-like protuberances.

The mesosternum has a large oval brown blotch centrally. Thoracic legs II grow out on the sides of the segment, and laterally, between the central blotch and the legs there are single suckers (pair II), somewhat smaller than those on the prosternum. Postero-medially to the base of the leg there is a small brown lateral spot. Numerous cuticular formations, scales and plates, are scattered round the central blotch and lateral spots and round the legs, all over the remaining surface of the mesosternum except the suckers. The mesothorax bears 8 very short setae dorsally and about 6 setae ventrally.

Metathorax (Fig. 21A, B). The metanotum has no pattern except scaly cuticular structures disposed for the most part medially. Like the mesonotum, this segment carries a pair of dorsal suckers (III). The pattern of the metasternum is like that of the mesosternum only that the central blotch is smaller and approximates to a circle in shape. There are also lateral spots in the regions of legs as well as the third pair of ventral suckers, somewhat smaller than those of the preceding segments. The lateral spots in the regions of the second and third pairs of legs appear in the second instar and occur in all the later instars.

The sculpture of the integument resembles that on the mesosternum. There are about 3 setae round either ventral sucker III and about 4 posterior to dorsal suckers III.

Distinct, more or less oval, paired pits, surrounded by a sclerotic brown ring of cuticle each, are situated ventrally, fairly close to the median line, on the borders of thoracic segments I and II, II and III, and III and abdominal segment I (Fig. 21B—P). The function of these pits is unknown.

The thoracic legs are short, conical, set on the sides of the thoracic sternites and composed of three joints (Fig. 22). The joints of the leg are brown and the articulations colourless; as a result, the leg looks as if it were striated. The second of the joints is the longest and the third the shortest, and resembles a minute promontory in shape. Externally joint I bears 3 fairly long setae arranged close to each other in a line. Joint II has about 5 setae, and a short thick curved claw is located in the proximity of the base of joint III.

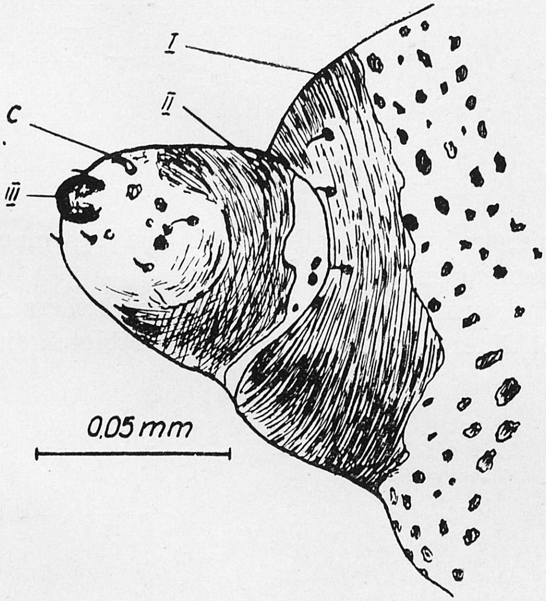


Fig. 22. Left thoracic leg I of the fourth-instar larva of *H. vagans* FALL. I, II, III — leg segments I, II and III, C — claw.

Abdomen

The abdomen consists of 10 segments; it is less flattened than the thorax, almost oval in cross-section (Fig. 15). As has already been mentioned, the abdominal segments except the last two are divided into two annulets each; the anterior annulet is broader than the posterior. This division is very well seen in the older larvae.

The dorsal side of the abdomen is devoid of any patterns, there are only characteristic scale-like cuticular structures, more or less brown, disposed along the median line for the whole length of the abdomen. Ventrally, segments II—VIII and X have abdominal feet in the form of big tubercles, round in outline and with oblique slit-like depresions on the tip (Figs. 15A, 23). The first 7 abdominal feet are arranged in pairs on the sides of the sternites. The last pair, on segment X, forms the so-called anal legs, which have grown together into a median tubercle (Fig. 24). The anal legs are surrounded anteriorly by a strongly sclerotized brown crescent with about 7 blunt teeth on the margin. There are up to 10 short setae round the anal legs. Posterior to them, behind the anus, 10 setae are located almost at the edge of the last segment; two of them, situated in the middle, are exceptionally long and stout. In addition, there are very numerous brown small scales in the integument round the anal legs and the surrounding crescent.

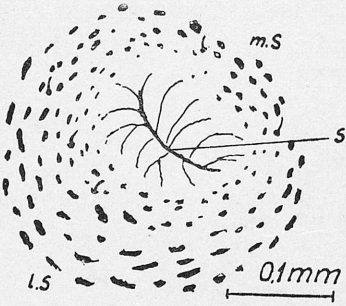


Fig. 23. Abdominal feet II (left) of the fifth-instar larva of *H. vagans* FALL. Sl — slit, m. S — medial side, l. S — lateral side.

Centrally, on the sternite of abdominal segment I there is an almost round brown spot, several times smaller than the similar blotch on the metasternum (Fig. 15A). Also segments II, III, and even IV have often a central spot ventrally. These spots decrease gradually in size, from the largest on segment I to the smallest on segments III and IV.

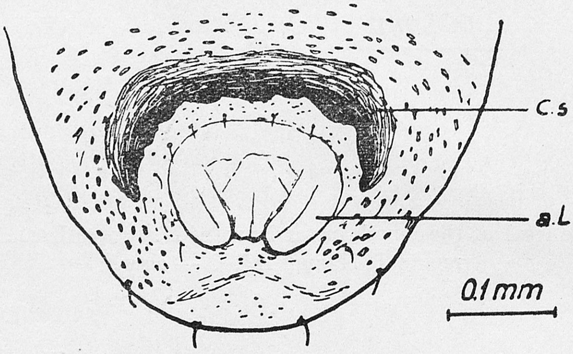
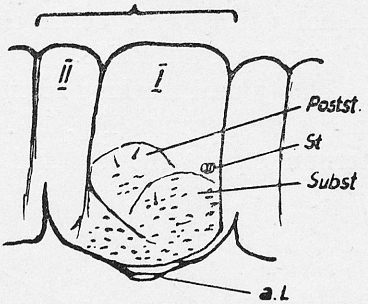


Fig. 24. Anal legs of the fourth-instar larva of *H. vagans* FALL. a. L — anal legs, Cs — crescent surrounding anal legs.

Spiracles are present on both sides of segments I—VIII. They are evidently smaller than the thoracic spiracles and displaced towards the dorsal side. The spiracles are situated in the broader portion of the segment, close to the furrow separating it from the adjacent segment (Fig. 25). All the abdominal spiracles, like those on the thorax, have two semicircular plates surrounding the aperture.

On the sides of the abdominal segments there are fleshy lobes (Fig. 25). The more or less bifid substigmal lobe, with 2 setae on it, is located below the spiracle and the poststigmal lobe, also with 2 setae, behind it.

Fig. 25. Schematic drawing of lateral lobes in an abdominal segment of the fourth-instar larva of *H. vagans* FALL. I — anterior part of segment, II — posterior part of segment, Subst — substigmal lobe, Postst — poststigmal lobe, St — spiracle, a. L — anal leg.



Larval Stadia

During the active period of life or during the period of feeding and growth, which lasts from the hatching from the egg to the withdrawal into the cocoon, the larva goes through the successive stadia, casting its skin off 5 or 6 times. The time of growth and development of the larva which ends feeding with the fifth ecdysis or reaching its sixth instar averages 20 days (18—24) and, in the larva ending the feeding period after the sixth ecdysis, i. e., reaching its seventh instar, 25 days (22—30).

The male larvae of both the first (summer) and the second (autumn) generation and the female larvae of the first generation cease feeding after the fifth moult and most of the female larvae of the second generation after the sixth moult.

Instar I

The first stadium of larval growth, from the eclosion of the larva from the egg to the first ecdysis, lasts on the average 5 days.

Mean body-length of larva: 1·2 mm

Mean width of head: 0·36 mm

Mean width of thoracic segment I: 0·39 mm

Mean width of abdominal segment IX: 0·18 mm

The larva in the first instar is relatively short, with a big head and broad thoracic segment I (Fig. 15). The body is strongly flattened and yellow-white in colour, the head being pale amber. The sutures of the head, part of the genae, and mandibles are darker. The antennae, different from those in the later instars, are almost flat (Fig. 26). The antennal socket abounds in sensory elements in the form of rings varying in size.

The pattern of the body is light brown. The structure of the mouth-parts does not deviate from the general type (Fig. 18).

Besides the differences in body measurements, the first-instar larva differs essentially from those in the later instars in the development of the body pattern. The pattern is wanting on the dorsal side (Fig. 15B). The dorsal suckers on segment II and III are comparatively poorly developed. A light median line runs across the pronotum and half-way across the mesonotum along the long axis of body. On the dorsal side of the thorax and abdomen, mainly in their medial parts, there occur characteristic cuticular structures in the form of pale brown oval scales.

The typical marking resembling the Roman numeral „I" in shape is present on the prosternum (Fig. 15). It occupies nearly the whole surface of the prosternum except the legs and the suckers, which are located in the vicinity of the legs. The suckers of all the three ventral pairs are distinct (Fig. 27). Centrally the meso- and metasternum have a large oval blotch, which spreads over the nearly whole width of the segment (Fig. 27). The blotch on segment III is much smaller than that on segment II, whereas the central spot on abdominal segment I is still smaller or, often, wanting at all. The lateral spots at the side of the thoracic legs of the second and third pair are also wanting.

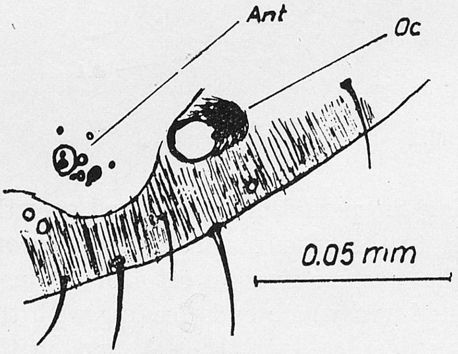


Fig. 26. Ocellus and antenna of the first instar larva of *H. vagans* Fall. Ant — antenna, Oc — ocellus.

Instead of the brown ring crescent round the anal legs there is a colourless fold of skin resembling in shape the ring which appears in the later instars. The sculpture of the integument is like that on the dorsal side.

Instar II

Mean body-length of larva: 2·2 mm
Mean width of head: 0·42 mm
Mean width of thoracic segment I: 0·53 mm
Mean width of abdominal segment IX: 0·27 mm
Mean duration of stadium: 3—4 days

As compared with instar I, the body proportions are more regular owing to the great elongation of the thorax and abdomen. The flattening of the body is also less remarkable. The antennae are typically conical (Fig. 17). The larva is darker in colour, the head pale brown and the pattern of the body dark brown. The pattern of the body is complete, like that in the later instars, i.e., ventrally, there is one small spot on either side, in the neibourhood of each leg of the second and third pair, and where the spot is lacking, the cuticle is furnished with structures in the form of dense accumulations of dark-coloured scales. The anal legs are surrounded by a dark brown ring.

Dorsally, on the pronotum there is a dark brown shield occupying the very centre of the segment and divided by a pale line longitudinally. The mesonotum has two triangular spots separated from each other, located in the middle of the anterior margin of the segment.

The sternite of abdominal segment I is marked with an oval or round central spot, the sternites of segments II and III have often similar but smaller spots.

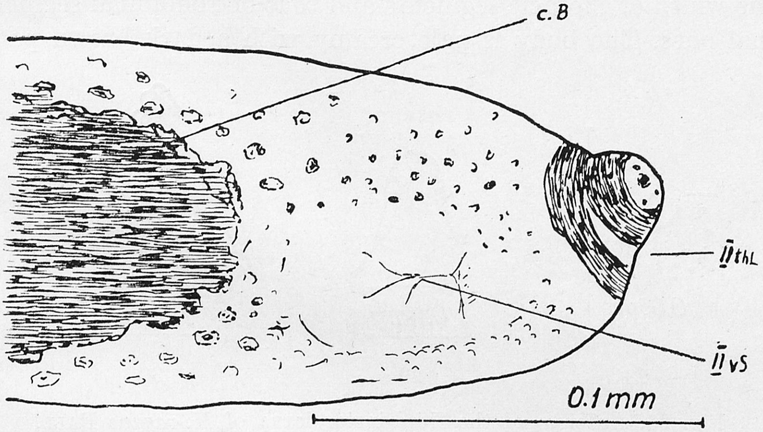


Fig. 27. Half of mesosternum of the first-instar larva of *H. vagans* FALL. c. B — central blotch, II th. L — thoracic leg II, II v. S — ventral sucker II.

In the integument round the second and third pair of both dorsal and ventral suckers there are plates, sparsely disposed and furnished with 1 or 2 teeth on the margin. The remaining parts of the body are sculptured as in stadium I.

Instar III

Mean body-length of larva: 3·2 mm

Mean width of head: 0·54 mm

Mean width of thoracic segment I: 0·67 mm

Mean width of abdominal segment IX: 0·35 mm

Mean duration of stadium: 3 days

The body is dirty yellow with a black-brown pattern, the head pale brown.

Except for the essential variance concerning the size of body, the larva of the third instar little differs from that of the second instar. The pattern on the dorsal and ventral sides of the body is almost the same, only the central shield on the pronotum is larger and occupies nearly the whole tergite. There are central spots on the ventral side of the abdominal segments, at least on segments I and II but often also on segments III and IV.

The antennae are evidently conical (Fig. 28). The mouth-parts, as in the larva in the second instar, conform in structure to the general type.

The sculpture of cuticle occurs in the form of rounded scales varying in size and, in the region of the dorsal and ventral suckers, also in the form of crenated plates.

Instar IV

Mean body-length of larva: 4·2 mm

Mean width of head: 0·72 mm

Mean duration of stadium: 2—4 days

The larva is less flattened as compared with the previous instars, especially the abdomen is more rounded in cross-section. There are no major differences between the width of thoracic segments and that of abdominal segments except the terminal ones. The body is pale creamy with a dark brown pattern. The pattern is practically typical. The shield on the pronotum is somewhat smaller than in the larva of the third instar, it occupies only its central portion. The pattern on the ventral side the same as in the third-instar larva. The number of central spots on the sternites of abdominal segments I—III is variable.

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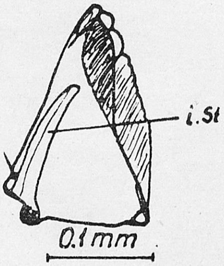

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Fig. 28. Antenna of the third-instar larva of *H. vagans* Fall.
Fig. 29. Mandible of the fourth-instar larva of *H. vagans* Fall.
Fig. 30. Mandible of the fifth-instar larva of *H. vagans* Fall. i. St — internal stylet.

The mandibles have undergone a change; they have no teeth now but two sharp, serrated and broad incisor areas running lengthwise. The external incisor area is broader than the internal one (Fig. 29).

The segments of the thoracic legs have brown rings unequal in width. The rings are evidently wider on the outer side of the legs (Fig. 22). The second segment of thoracic legs has grown in length considerably.

The sculpture of the integument is the same as in stadium III.

Instar V

Mean body length of larva: 7 mm

Mean width of head: 0·86 mm

Mean duration of stadium: 5 days (4—7)

The cylindrical body is yellow-brown in colour. This colour is for the most part due to the food seen through the translucent skin. The head is brown, the pattern of the body darker than the head, typical and distinct both on the dorsal and on the ventral side (Fig. 21 A, B).

The conical antennae are visibly 3-jointed and they project beyond the head surface remarkably.

Further changes have taken place in the mandible, inside which a small stylet, similar to the mandibles of the larva after the last ecdysis, has developed (Fig. 30). After tearing off the mandible, it is easy to take the stylet out of its inside.

In addition to the typical scales and plates constituting the sculpture of the integument, the cuticle is densely folded in the anterior portion of the pronotum, in front of the shield. The ridges of these folds are strongly sclerotized, brown, and finely crenated. The edges of the folds are parallel to each other and square to the main axis of body (Fig. 21A).

Instar VI

Most of the larvae of the autumn generation go through stadium VI, which lasts on the average 7 days.

Mean body-length of larva: 9·7 mm

Mean width of head: 0·98 mm

The larva in the sixth instar is very much like that in the fifth instar. Of all parts of the body only the head is strongly flattened. It is positioned obliquely in relation to the main body-axis and sticks remarkably out of the prothorax so that its basal part is well visible. The head is brown with the darker genae, the pigment being irregularly distributed in larger and smaller accumulations.

The mandible is like that in stadium V only that the inner stylet is bigger.

The body is yellow-brown in colour, with a dark brown pattern. The shield of the pronotum is situated in its antero-medial part. The posterior portion of the shield is marked by its intense brown colour and a higher degree of sclerotization. The setae on the pronotum are considerably smaller than those in the previous instars. The mesonotum has two small brown spots on the anterior margin; these spots are often absent.

The suckers in the antero-medial part of the mesonotum are very large and often look like a single sucker extending transversely throughout the mesonotum.

The marking on the prosternum is smaller and less typical than in the previous instars and irregularly coloured. Only the middle and lateral portions of the marking are brown. The three pairs of the ventral suckers are well developed, their slits being more or less three-branched. The central blotches on the meso- and metasternum are smaller. The central spot on abdominal sternite I is very small; there are no spots on the next segments.

THE PUPAL STADIA

Having finished feeding and constructed cocoon after the last – fifth or sixth — moult, the larva of *H. vagans* Fall. enters upon the resting stage. This stage may be divided into three stadia: two prepupal stadia (eonympha and pronympha) and a pupal stadium (Lorenz and Kraus, 1957). The resting stage lasts on the average 15 days in the summer generation and 6—10 months in the autumn generation.

Immediately after the last moult and before withdrawing into the cocoon the larva changes its colour and becomes uniformly aquamarine-yellow and devoid of any patterns.

Prepupa I (eonympha)

Mean body-length: 6·85 mm

Mean width of head: 0·95 mm

The prepupal stadium begins after the larva has constructed the cocoon (Lorenz and Kraus, 1957) and lasts for 8—10 days (summer generation) or about 8 months (autumn generation). The body of prepupa I is flattened dorsoventrally and shortened remarkably, the head of the ortho-prognathous type is retracted into the thorax for half its length (Fig. 31).

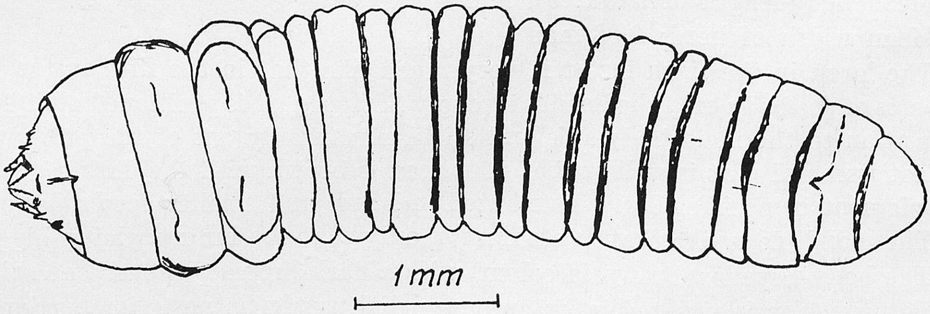


Fig. 31. Dorsal view of prepupa I (eonympha) of *H. vagans* Fall.

The head-capsule is poorly sclerotized and pale yellow, only the genal parts are darker. The sutures of the head are quite pale and thickened. There is a stout seta at either side near the epistomal suture and, besides, 3 short setae laterally in the middle part of the frons. The clypeus bears 2 setae and six long setae are disposed in the anterior part of the gena, as in the larval instars (Fig. 32).

The antenna is longer than that in the larva and set in the well-defined and somewhat bulging antennal socket (Fig. 33). The external parts of the antennal joints are pale brown.

The mouth-parts (Fig. 34) have undergone great changes. The mandibles have the form of stylets with massive basal parts. They are dark brown in colour (Fig. 34C). Turned to each other at rest, the mandibular stylets are positioned just under the labrum and their tips reach to its anterior margin. The shape of the labrum is more or less like that in the larval instars (Fig. 34B). The surface of the labrum is furnished with about 12 light warts. The epipharynx is in a vestigial state; the fringy processes are replaced by structures that seem to be narrow short tubes, 10 in a line, on either side of the anterior margin of the labrum.

The maxillolabial complex (Fig. 34 A) is largely shortened and makes a compact whole difficult to dissect. A big fleshy spinning papilla is located anteriorly in the medial part of the complex (Fig. 32).

The cardo and stipes show no major changes. The palpifer is short and stout, with 2 setae and a wart on the external surface. The maxillary palp is no longer 3-jointed but 4-jointed. It is a conus with light brown joints. On the external side of joints I and II there are two big warts disposed symmetrically. Two short blunt spines are situated on the border of joints III and IV. The apical surface of joint IV is covered with numerous warts.

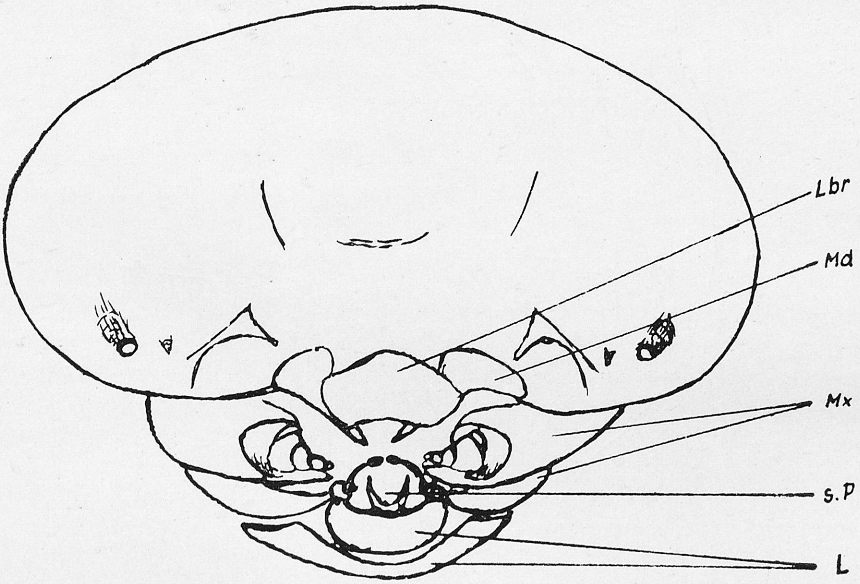


Fig. 32. A diagram of the head of prepupa I (eonympa) of *H. vagans* FALL., viewed from in front. Lbr — labrum, Md — mandible, Mx — maxilla of 1st pair, s.P — spinning papilla, L — labium.

The galea is shorter than the palp and bent to the inside. The galea bears 4 big warts in the middle part of the external surface and many far smaller warts on the apex. The lacinia is not a plate, as in the larval instars, but more massive and, like the galea, conical. There are 2 spine-like processes on the external side, situated inferiorly to the apex.

The labial palps have undergone a marked shortening and the hypopharynx and ligula have grown together into a kind of short tube opened to the outside. In the opening of the tube there is a spinning papilla with the orifice of the labial spinning glands (Fig. 35 A, B, C). The ventral part of the tube is formed by the hypopharynx, which has been greatly transformed. It is possible to distinguish an anterior plate in it, more or less corresponding in size to the ligula (Fig. 35 C). Behind the anterior plate there is a strong sclerotic ring, coalesced with the ligula at the sides and connecting the hypopharynx with

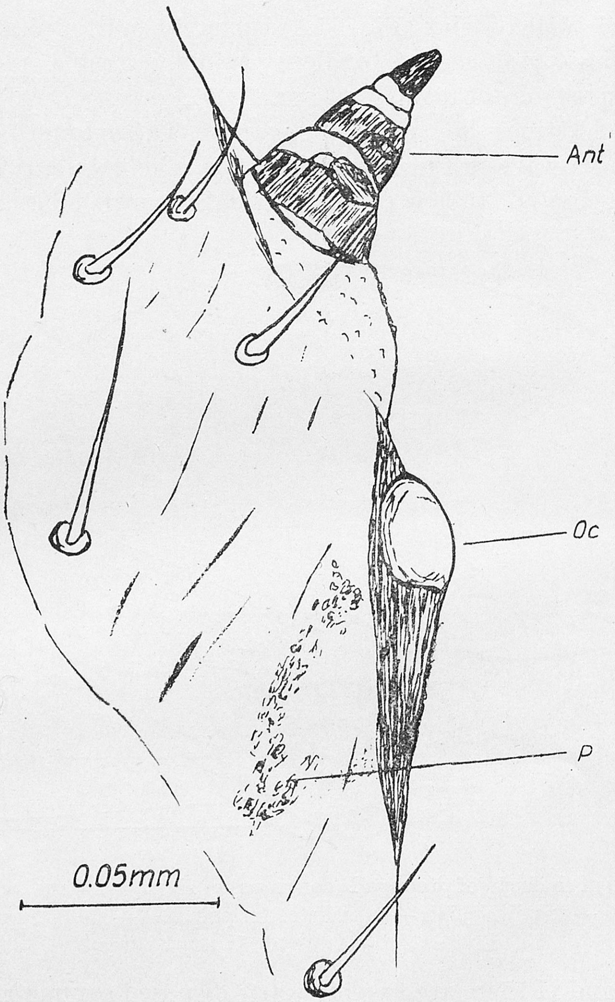


Fig. 33. Antenna and ocellus of prepupa I (eonympha) of *H. vagans* Fall. Ant — antenna, Oc — ocellus, P — eye pigment.

the labium. From the ring towards the pharynx the hypopharynx passes into a thin elongate bifid plate. The ligula with a sinusoidally indented external margin makes the dorsal part of the tube (Fig. 35 A). Centrally, in the tube there is an elongate sclerotic fork (Fig. 35 B), the prongs of which point at the pharynx.

The prementum carries 4 small warts and 4 short setae. The labial palp is short, 3-jointed.

The body of prepupa I is uniformly aquamarine in colour, without a sign of pattern or at most with its faint outlines in the form of stronger sclerotizations of cuticle on the dorsal and ventral sides of the prothorax. The meso- and metathorax are evidently broader and more convex dorsally than the prothorax (Fig. 31). A slightly marked pale-yellow shield divided medially

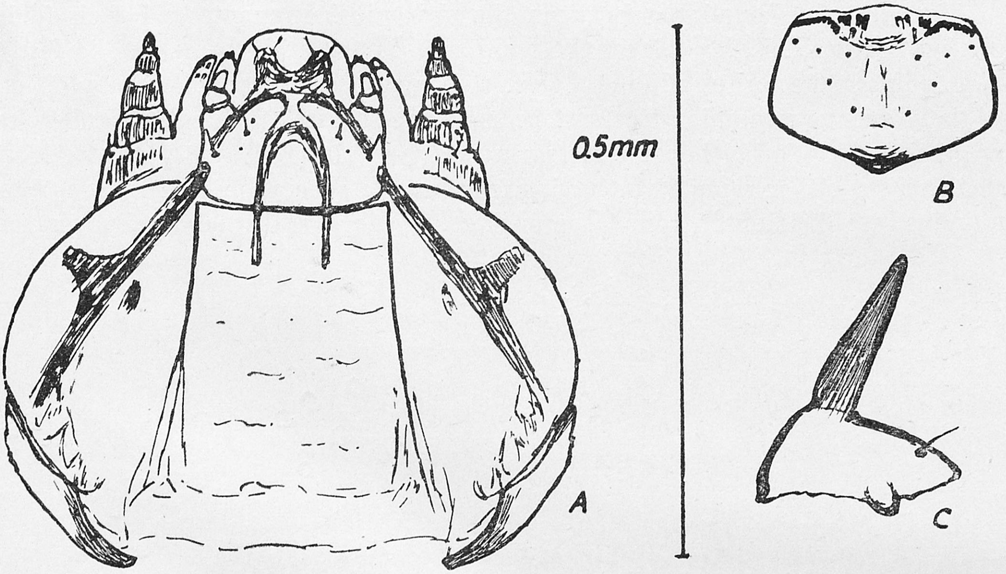


Fig. 34. Mouth-parts of prepupa I (eonympha) of *H. vagans* FALL. A. Maxillolabial complex. B. Labrum. D. Mandible.

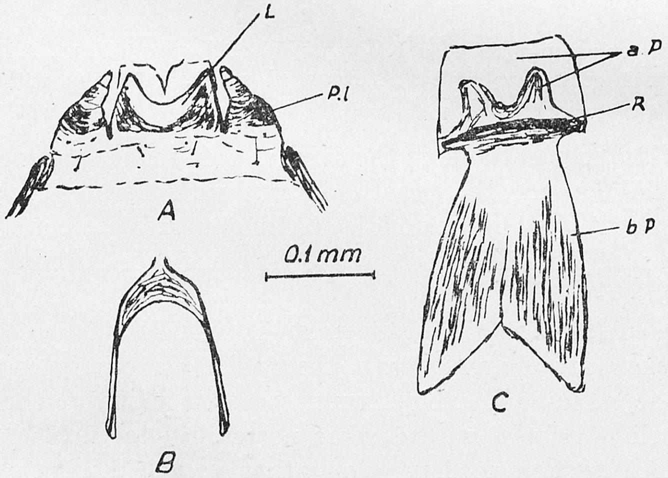


Fig. 35. Apex of labium and hypopharynx of prepupa I (eonympha) of *H. vagans* FALL. A. Apex of labium. L — ligula, P. l — labial palp. B. Fork. C. Hypopharynx. a. P — anterior plate, R — ring, b. P — bifid plate.

by an irregular groove is present on the pronotum. The setae approximate in arrangement to those in the larval instars, but they are much smaller.

The suckers on the meso- and metanotum are well developed, the integument below each of the suckers is smooth and lightly sclerotized. The first-pair suckers are oval, the second-pair ones round; there are 6 setae on the integument below each sucker of the first pair and 5 below those of the second pair.

Dorsally, the boundaries between the abdominal segments and their folds are light brown. In these places the sculpture of cuticle is represented by fairly large polygonal sclerites adjoining closely to each other (Fig. 36 A). In addition to them, on the remaining free surface there are sclerites with central tubercles projecting remarkably beyond the surface of the skin (Fig. 36 B_1, B_2). Besides, small scales, either rounded or having from one to several sharp teeth on their margins, are distributed round the suckers. Toothed scales occur all over the surface of the last segment and on the sides of the broader portions of the other segments, round the smooth sclerotized areas with 4 setae each.

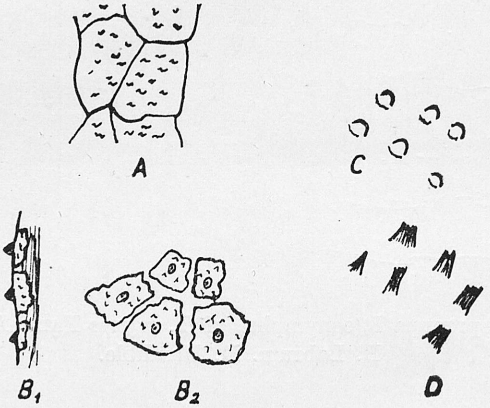


Fig. 36. Cuticular sculpture of prepupa I (eonympha) of *H. vagans* Fall. A Polygonal plates. B_1, B_2. Plates with central tubercles. C. Rounded scales. D. Scales with toothed edges.

The spiracles, situated in the middle of a bulging area each, are concentrically surrounded by plates of different types, which constitute the cuticular sculpture of these places.

There is no pattern on the prosternum, its cuticle is smooth with 6 short setae. The suckers are big and fleshy, the cuticle posteriorly to the suckers is sclerotized. The meso- and metasternum bear no signs of the pattern, the suckers are well developed with 2 setae posteriorly to each.

The thoracic legs show no changes only that segment III has elongated, they are light brown in colour.

The cuticular sculpture on the ventral side of the thorax — below the suckers — consists of smooth and oval plates or those with central tubercles. As in the larvae, there are 3 pairs of intersegmental pits of unknown function.

The abdominal feet and their chaetotaxy as in the larva; externally they are surrounded with a crescent formed of sclerotized cuticle.

The cuticular sculpture of the middle part of the abdomen, especially on the borders of the segments, consists of plates, which are smooth or with central tubercles and adjoining to each other. In the other parts there are loosely disposed rounded scale-like plates.

The shape of the crescent and the number of setae round the anal legs as in feeding larvae only that the crescent is light brown.

Prepupa II (pronympha)

Mean body-length: 10 mm

Mean width of head: 0·95 mm

The change of prepupa I into prepupa II is not accompanied by moulting, nevertheless after LORENZ and KRAUS (1957) the second prepupal stadium has been distinguished on account of certain morphological changes occurring in the prepupa in this period of life. Prepupal stadium II lasts on the average 2 days and precedes transformation into the pupa. The essential differences lie in that the body of prepupa II is cylindrical and more elongate owing to the expansion of the segments, the head is completely thrust out of the prothorax and prognathous, and the buds of the compound eyes are seen through the translucent head-capsule as dark lateral spots. The body is light in colour, the head and thorax yellowish and the abdomen aquamarine.

The labial palps are longer than in prepupa I and equal to the maxillary palps in length. The thoracic legs are also much longer.

The other parts of the body as well as the cuticular sculpture are the same as in prepupa I.

As the time preceding the moulting and formation of the pupa goes by, the entrails of prepupa II, enclosed in the integument, shrink gradually. As a result, the skin is entirely detached from the body and at its end about 3 mm of the integument is left empty (Pl. XLIV, fig. 2).

Pupa (pupa libera)

After ecdysis prepupa II enters upon the pupal stadium, which lasts 4—7 days. The body-length of the pupa is 4—6 mm, the coloration changes by degrees from light green-aquamarine to yellow-brown-black, and the shape of the body approximates to that of the imago.

The pupal body is wrapped up in a very thin and transparent membranous case enclosing the head, thorax and abdomen. There are separate membranous cases for each antenna, for the mouth-parts, of which the maxillary palps are enclosed apart, and for each thoracic leg and wing.

The very young pupa is uniformly aquamarine except for the spots marking the compound eyes and the contours of the ocelli, which are pale brown. At the beginning no facets can be seen in the compound eye; instead, there is a number of small dark dots disposed regularly on the light surface. There is no distinct segmentation of the antennae, mouth-parts, and limbs. All the external organs are, as a rule, like those in the imago, at least in respect of size.

There are male and female pupae (Pl. XLIV, figs. 3, 4), their genitalia being at the same stage of development as in the imagines.

After about 24 hours the antennae, mouth-parts, legs, wings, and genitalia become almost translucent, whitish, the eyes and ocelli dark brown, and the rest of the body remains aquamarine. Next, evident changes can be seen 3 days after the formation of the pupa. The compound eyes are almost black and the particular facets are visible. The head and thorax are colourless and almost translucent, whereas the abdomen except the genitalia is aquamarine.

In the further course of life the body of the pupa becomes darker, the head and thorax change from light brown to brown-black, and the abdomen from aquamarine to translucent orange. In brief, the coloration becomes like that of the imago. As the process of maturation advances, the mobility of the pupa increases; at first it is able to move only its abdomen and in the final phase there are also movements of the antennae, mouth-parts, and limbs.

After the emergence of the imago from the pupa, a very thin pupal case of transparent membrane is left in the cocoon.

LIFE OF THE LARVA IN THE MINE

When the embryonic development is concluded, the larva, still in the egg shell, begins to move its mandibles. The mandibles operate in the horizontal plane; they open and close like pincers, their movements being very slow. As a result, a tear is made in the egg shell. Continuing the movements of the mandibles, the larva makes its way out through the aperture thus accomplished and reaches the palisade tissue of the leaf. The teeth of the mandibles catch on the palisade tissue and tear pieces out of it. In the first phase of feeding only the head of the larva protrudes outside, the rest of the body, bent in the shape of a horseshoe, is still within the egg shell. As the larva eats the palisade tissue out, it crawls gradually out of the egg shell. In the further description the space limited by the egg shell lying under the upper epidermis of the leaf will be termed the incubation vesicle (vesicula incubatoria, DZIURZYŃSKI, 1948).

When the larva begins feeding, it is already completely shaped and turned with its ventral side to the upper surface of the leaf. It keeps this position throughout the feeding period. During the observations carried out for a few years only one larva was found to feed in the opposite position; having finished feeding it constructed a cocoon. At the very beginning of the feeding stage the body of the larva is transparent, only the head-capsule and the pattern of the body are pale yellow. The mandibles are sclerotic and brown.

The palisade tissue torn out with the mandibles gets into the mouth and pharynx and passes through the oesophagus to the mid-intestine. The alimentary canal is filled gradually with food and after about 30 minutes the larva discharges the first pellet of frass. At first the larva feeds very slowly, with frequent breaks, which last from a few to more than ten minutes; it does not take food during defecation.

In the abandoned part of the incubation vesicle the larva deposits its frass, which it rams tight with the end of the abdomen. Consequently, when the larva has left the incubation vesicle completely, it is tightly packed with small brown pellets of frass. The incubation vesicle filled with frass lies on the palisade tissue immediately under the upper epidermis of the leaf, higher than the mine formed in this tissue by the feeding larva. As a result, on the surface of the leaf there is an evident, though very small, protuberance — equal to the incubation vesicle in size — indicating the beginning of the mine.

The remarkable flattening of the head enables the larva to reach the palisade tissue in the narrow space between the upper epidermis and the spongy parenchyma. The dorsal and ventral thoracic suckers as well as the thoracic legs make it possible for the larva to keep its position and to move in the mine.

Owing to the prognathism of the head the larva can move it, especially to the sides. When feeding, the larva swings its head from side to side, twisting the whole body at the same time and crawling forward. These movements result in the formation of a circular mine.

The mine of larval *H. vagans* FALL., produced by eating out the palisade layer, is superficial and of the chamber type. The formation of the chamber is due to the swinging movements of the larva.

The metabolism of the larva causes the accumulation of gases in the mine. They are responsible for the distention of the mine, especially in the more advanced stadia of development. The mines are not transparent, because the upper epidermis of the leaf is very thick and the tissues which bound the space eaten out in the palisade layer are blackened.

The manner of eating out the tissue and the direction in which the larva advances, as well as the constant depositing of frass in the first, i.e., the oldest, part of the mine cause the eccentric shape of the mine (Pl. XLIV, fig. 5) and considerably less frequently, when the larva eats out the palisade tissue round the incubation vesicle, the concentric shape (Fig. 38 and Pl. XLIV, fig. 6).

The mines in young leaves or in not very fresh ones are quite different. They are irregular, in the shape of a broad gallery, with frass dropped everywhere in a disorderly manner; they do not resemble a typical mine formed in the normal way, especially in the first phase. Such specimens may be found in the laboratory, if a female has laid eggs in an unsuitable leaf offered to it.

Normally only one larva feeds in the mine, but often a few larvae can be seen in a single mine, and under laboratory conditions even more than ten (Pl. XLV, fig. 1). This happens when the eggs are deposited in the leaf at small distances from each other. Then, owing to the simultaneous enlargement the mines fuse into one whole. The larvae living in one mine are quite indifferent to each other. If a large number of larvae feed in one leaf, the palisade tissue may run out before the larvae complete their development. In such cases the larvae, if they are already in the fifth instar, undergo moulting and construct cocoons, often prematurely, whereas those in the earlier instars either perish or leave the mine and get outside. However, after leaving the mine, even though the larva manages to find a suitable leaf, it cannot reach the palisade layer and begin feeding.

If such a larva is transferred to another leaf of alder with a ready mine produced by a member of another hymenopteran species, e.g., *Fenusa dohrni* TSCHB., it begins feeding almost at once, even if it is a second-instar larva. The larvae transferred to other leaves with mines of *F. dohrni* Tschb. (Fig. 37a, b) continue their development to the end and form cocoons.

Some larvae of *H. vagans* Fall. were also transferred to empty two-sided mines of a butterfly of the genus *Lithocolletis* in another alder leaf. They were placed in the mine at the natural opening on the lower surface of the leaf. The larva began feeding almost immediately, devouring the lower spongy layer of the mesophyll. It was able to feed even in the case when only the head and thorax stuck in the mine and the rest of the body protruded outside because of the small size of the mine. In these experiments, however, the larvae left the mine or died in a short time.

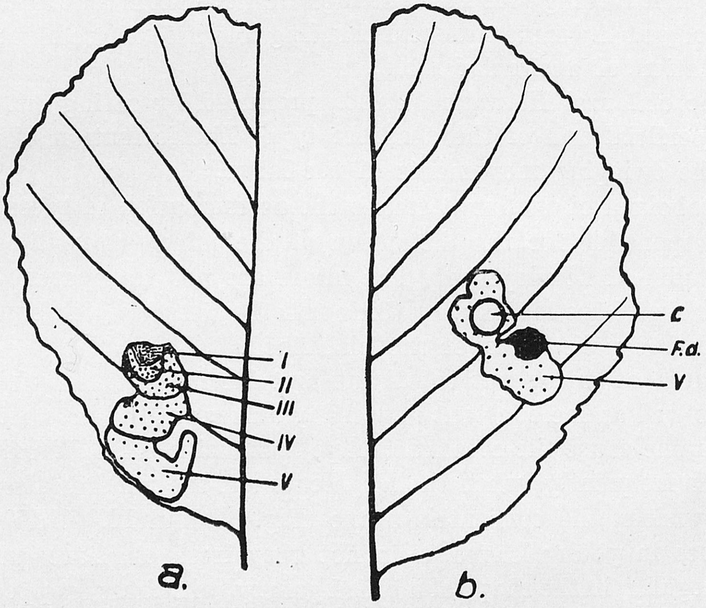


Fig. 37. Mines of the same larva of *H. vagans* Fall. in two leaves; a. leaf I, mine areas after stadia I, II, III, IV and partly V; b. leaf II; F. d. — mine of *Fenusa dohrni* Tschb. V — extension of the mine by the fifth-instar larva of *H. vagans* Fall., C — cocoon of the larva of *H. vagans* Fall. (life-size).

The larvae of *H. vagans* Fall. transferred to the mines in leaves of other plants perish or, if suitably advanced in development, form cocoons.

The abandonment of mines or the early formation of cocoons takes place also when the leaf becomes dry or mouldy. It is in the withering leaf and only then that the larva was found to feed on the spongy parenchyma.

The rate of feeding of the larva in instars I—IV is low and, consequently, the area of the mine is small up to the fourth stadium (Pl. XLV, fig. 2); it does not usually go beyond the space between two branch veins of the first order. Within the particular stadia of larval life the rate of feeding also varies, being

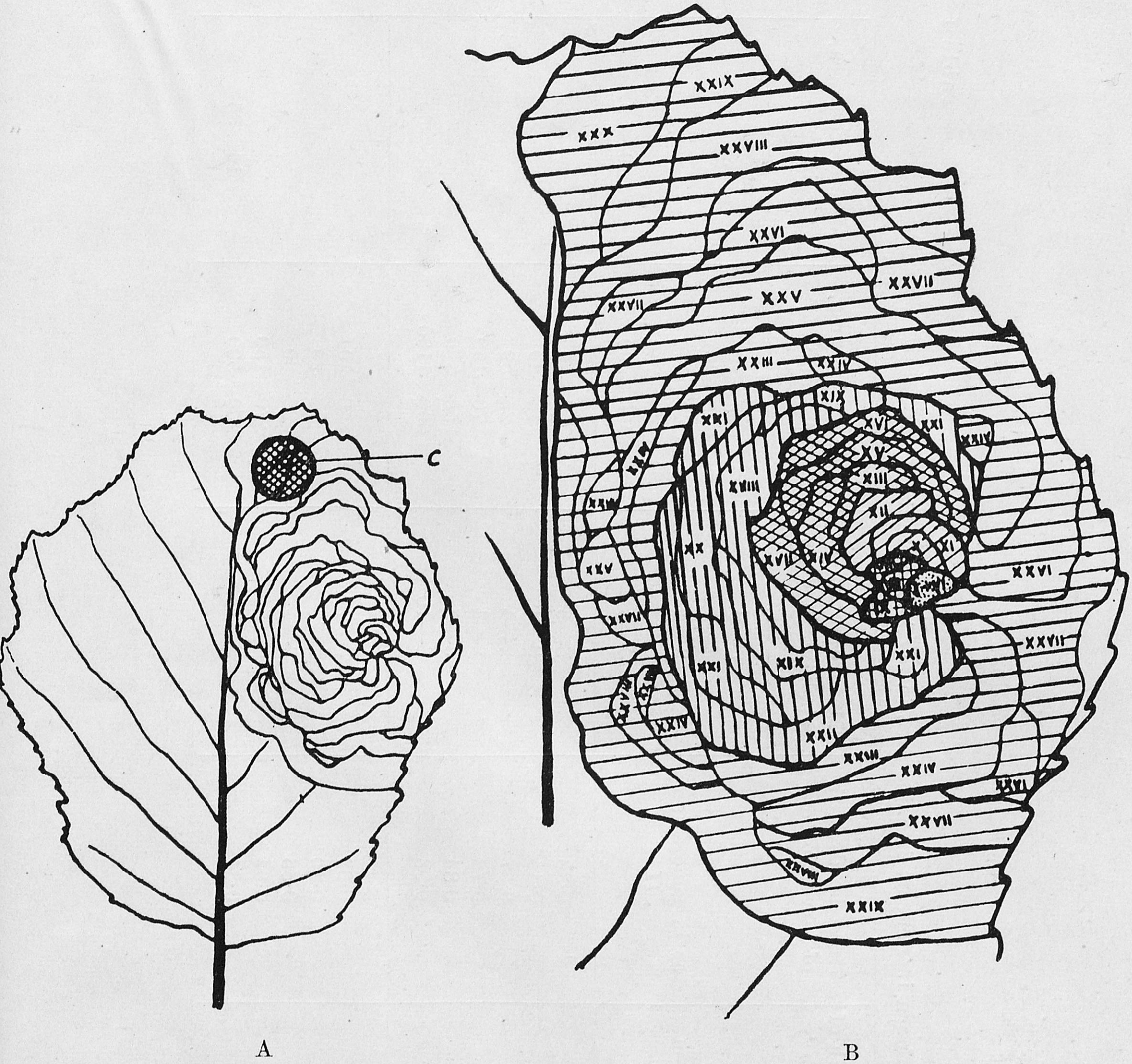


Fig. 38. A. A leaf of the black alder (*Alnus glutinosa* L.) with a mine of the larva „N" (life-size). The lines mark out the successive daily increments in area of the mine. C — cocoon. Fig. 38. B. The mine of the larva „N", to a larger scale. Successive daily increments in area of the mine are marked I—XXX (the boundary lines of increments from I to VI during stadium I are lacking). The mine areas formed during the successive stadia are shown by different types of hatching.

the highest in the middle period of each stadium. Larval *H. vagans* FALL. feeds only in the day-time.

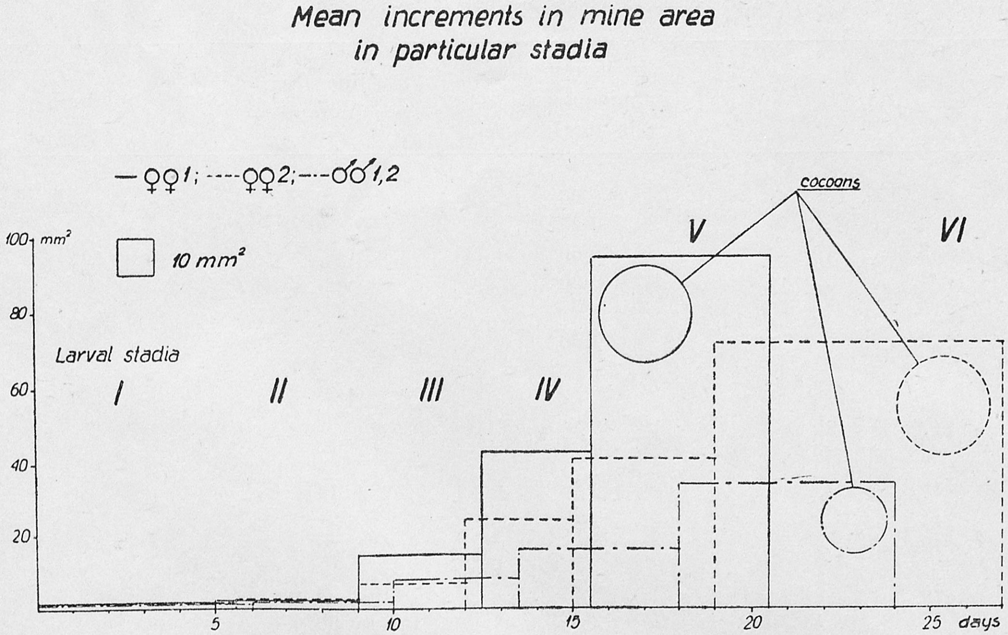
The period of the most intense feeding occurs in the last stadium or in the last two stadia of larval development and then the mine increases rapidly in area, expanding in the leaf irrespective of its venation. The surface area of the mines at the end of successive stadia depends on the leaf thickness, the sex of the larva, and its individual characters, such as the size of body and that of mandibles.

Table I

Mean incremenst in mine area in particular stadia

	Larval stadium	Mean body-length of larva, in mm	Mean head-width of larva, in mm	Mean duration of stadium, in days	Mean mine area, in mm^2	Mean cocon area, in mm^2
Female generation I	I	as in generation II	as in generation II	4—6	5—10	
	II			4	15—20	
	III			3—4	40—100	
	IV			3	150—250	
	V			4—6	450—900	40—60
Female generation II	I	1·21	0·36	5—6	5—10	
	II	2·23	0·44	3—4	13—20	
	III	3·17	0·57	2—4	25—50	
	IV	4·20	0·72	2—4	70—150	
	V	6·96	0·86	3—5	250—300	
	VI	9·72	0·98	6—10	600—1100	40—60
Male generations I and II	I	0·83	0·33	5—7	6—10	
	II	1·92	0·40	4	13—20	
	III	2·98	0·55	3—4	30—60	
	IV	4·11	0·64	4—5	70—150	
	V	5·25	0·84	5—7	250—500	14—35

Table II



The mean values of the mine areas at the end of each particular larval stadium are presented in Table I and II (p. 540, 541). The table comprises the data for female larvae of the first generation (5 stadia), female larvae of the second generation (6 stadia), and male larvae of both generations (5 stadia), separately. Both male and female larvae of *H. vagans* FALL. of the first (summer) generation as well as male larvae of the second generation go through 5 developmental stadia, whereas most of the female larvae of the second generation have 6 stadia. Male larvae of both generations produce smaller mines than the female larvae do, even in the case of the same number of stadia.

The data obtained by measuring the increments in the mine area during its expansion for a female larva „N“ of the second generation show that this larva consumed the palisade tissue from an area of

4 mm^2 in stadium I	63 mm^2 in stadium IV
10 mm^2 in stadium II	180 mm^2 in stadium V
14 mm^2 in stadium III	751 mm^2 in stadium VI

The larva „N“ fed for 30 days and the daily increments in the mine area caused by its feeding are shown in Tables III and IV (p. 542, 543) and Fig. 38 A, B. The final area of the mine of this larva was 1022 mm^2 and the surface area of the cocoon 54 mm^2.

More or less up to stadium V, and so as long as the area occupied by the mine is relatively small, the larva gathers the frass, ramming it tight in the initial portion of the mine, which results in the formation of a kind of frass plug. In this way the larva maintains isolation from its excreta. In the final

Table III

Daily increments in mine area of the larwa "N,,

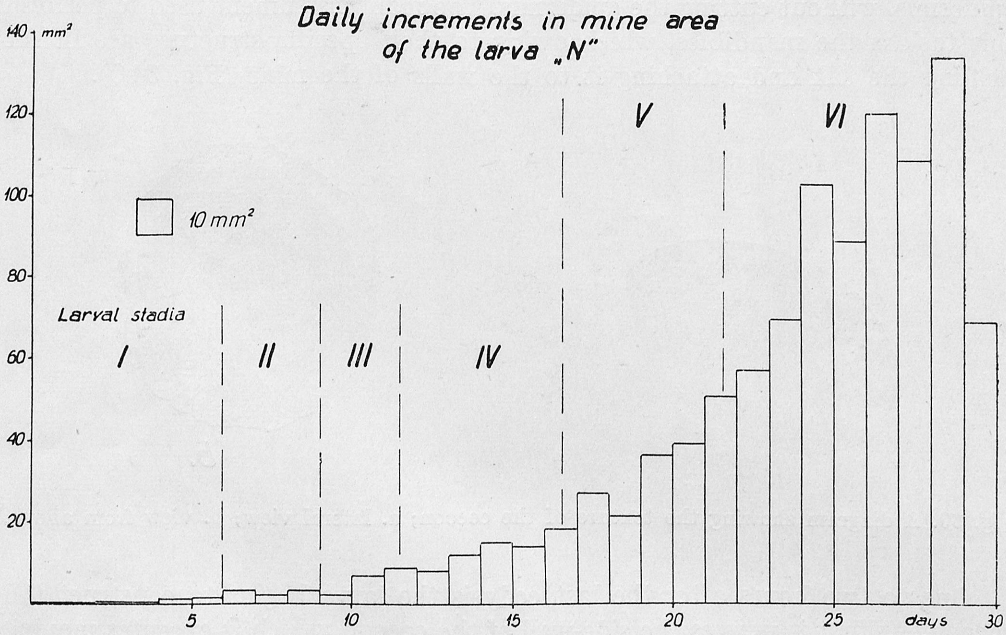
Date	Daily increment in mine area, in mm²	Mine area, in mm²	Stadium
1. IX. 1963	0·25	0·25	I
2. ,, ,,	0·25	0·50	
3. ,, ,,	0·50	1	
4. ,, ,,	0·50	1·50	
5. ,, ,,	1	2·50	
6. ,, ,,	1·50	4	
7. ,, ,,	3	7	II
8. ,, ,,	2	9	
9. ,, ,,	3	12	
10. ,, ,,	2	14	III
11. ,, ,,	7	21	
12. ,, ,,	9	30	
13. ,, ,,	8	38	IV
14. ,, ,,	12	50	
15. ,, ,,	15	65	
16. ,, ,,	14	79	
17. ,, ,,	18	97	
18. ,, ,,	27	124	V
19. ,, ,,	21	145	
20. ,, ,,	36	181	
21. ,, ,,	39	220	
22. ,, ,,	51	271	
23. ,, ,,	57	328	VI
24. ,, ,,	70	398	
25. ,, ,,	103	501	
26. ,, ,,	89	590	
27. ,, ,,	120	710	
28. ,, ,,	109	819	
29. ,, ,,	134	953	
30. ,, ,,	69	1022	

larval stadia, when the area of the mine is very large, thick and elongate pellets of frass, often joined together, are disposed loosely throughout the mine, mainly in its central part (Pl. XLIV, fig. 6).

Together with frass the larva drops its successive exuviae.

The larva ceases feeding about an hour and a half before each moulting, withdraws towards the middle of the mine, and remains still, assuming an outstretched posture with its abdomen directed to the accumulation of frass. After the lapse of this time the old skin ruptures along the median line (running on the dorsal side of thoracic segment I and half-way across thoracic segment II), the so-called moulting line, where the cuticle is poorly sclerotized. Some time later the larva puts its head through the cleft and performing vermicular movements of the body works the slough slowly backwards (Pl. XLV, fig. 3).

Table IV



The very process of moulting lasts on the average from 15 to 30 minutes. The slough is passed backwards by stages and after each stage the larva rests from a few to some dozen minutes. Directly after moulting the larva remains straightened and quiescent in the same place, its skin being colourless and devoid of the pattern. Approximately 30—90 minutes later the integument becomes harder and darker and the pattern on it becomes gradually more visible. When the pattern on the body is not yet very clear, the larva crawls up to the palisade tissue and begins to feed (Pl. XLV, fig. 4). It is not, however, feeding in the full sense of the word, the larva plucks several portions of tissue and next rests for a fairly long time. More or less at that time it performs some swinging movements with its body to push the discarded slough into the accumulation of frass. Feeding alternating with long breaks for rest is continued till the complete hardening of the skin, which is marked by the appearance of the distinct and well-developed pattern.

The interstadial interval, i.e. the period from the moment when the larva gives up feeding through moulting to the resumption of normal feeding averages 4—6 hours.

LIFE IN THE COCOON

The larva of *H. vagans* FALL. undergoes pupation inside the cocoon formed in the leaf, in the youngest portion of the mine, entirely free from frass. The larva builds the cocoon, utilizing the silk thread produced by the spinning papillae, so as to join two identical circles: one of the upper epidermis of the leaf, the other of the floor of the mine, i.e., of the spongy parenchyma and the lower epidermis, without cutting the epidermis. The main instrument used to perform this task is the mandibles, which owing to their specific structure are fit for holding the silk and attaching it to the walls of the mine (Fig. 34C).

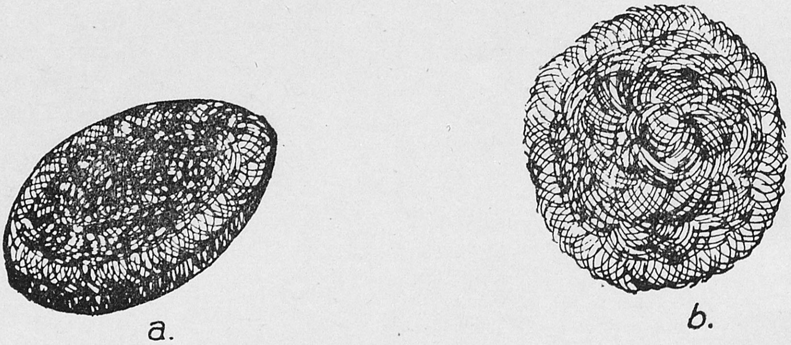


Fig. 39. A diagram showing the texture of the cocoon; a. lateral view; b. view from above.

One to two hours after the last ecdysis the larva begins to construct the cocoon. At first it weaves the side-wall of the cocoon, which it executes moving its head vertically and fastening together the upper epidermis and the lower portion of the leaf. At the same time it performs rotary motion, turning round till the ring constituting the side-wall of the cocoon has been closed (Pl. XLVI, fig. 1). Silk freshly produced by the gland is very sticky, comparatively thick and transparent. Owing to its glueyness it sticks readily to the leaf and its property of rapid solidification prevents particular threads from sticking together or adhering to the larval body. As the originally colourless thread hardens, it becomes brown and its strength increases.

After constructing the ring which separates the space of the cocoon from the rest of the mine, the larva lines its inside. First it secures the edges of the upper and lower walls (Fig. 39a, b). Moving forward round the ring formed previously, the larva performs swinging movements of the head to the sides, leading the silk thread right and left so that it forms arcuate lines attached to the leaf at both ends. Simultaneously with these swinging movements of the head the larva bends its prothorax and mesothorax to the sides, whereas the rest of the body is motionless. After several to some dozen such movements with the simultaneous spinning of silk and attaching it to the leaf the larva moves forward a bit and again „draws“ a few lines with silk, then moves on, etc. As a result, a network of short arched threads directed towards the centre is formed on the edges of the upper and lower walls.

Having secured the edges, the larva lines the middle part of the cocoon wall in the same way as previously only that the circles are smaller and smaller till they cover the whole surface of the upper and lower walls. The silk threads are laid in several layers so that they cross each other and after hardening the inside surface of the cocoon looks as if it were covered with a coat of paint using a brush with thick hair. The structure of the network lining the cocoon is always the same, made up of short arcuate sections of thread arranged concentrically.

When constructing the cocoon, the larva often rests, but for a short time, and its movements are slow. At that time the body of the larva is somewhat shortened and the head is ortho-prognathous, partly retracted into the thorax. The time it takes to make the cocoon ranges from 8 to 14 hours.

The newly made cocoon may be easily ruptured, as the silk thread has not yet completely solidified and, consequently, it is weak. However, as the thread hardens, the structure of the cocoon becomes stronger and its crushing and rupturing strength increases incomparably. The cocoon walls are leather-like and, on the inside, shiny as if polished. The lower wall is flat and the upper one convex (Pl. XLVI, fig. 2). As the leaf with a mine dries up and crumbles, the cocoon is not damaged but falls out of it. In addition, the properties of the silk thread make the cocoon waterproof but pervious to air. The surface area of a cocoon depends on the size of the larva. It amounts on the average to 40—60 mm^2 for female larvae and 14—35 mm^2 for males (Tables I and II).

A few days after its withdrawal into the cocoon the larva shrinks very much, bulges dorso-ventrally and still more retracts its head into the prothorax (Fig. 31), its body becomes intensely aquamarine in colour, and thus it transforms into typical prepupa I (eonympha). In the cocoon prepupa I assumes a straight or bent position, and it is hardly active, though, when touched through the medium of the cocoon wall, it moves rapidly. It is able to turn round its axis; one can often find a prepupa turned with its back to the upper wall of the cocoon, but the opposite position is the commonest.

If necessary, prepupa I is capable of re-forming the cocoon. It retains this capability nearly till the end of this stadium. If the cocoon has been completely destroyed, the prepupa builds a new one; if it has been damaged, the insect mends it by stitching the damaged place with silk.

The cocoon provides a shelter successively for prepupa I (eonympha), prepupa II (pronympha), the pupa, and the adult insect. In the cocoon prepupa II, during its transformation into the pupa, and the pupa, at the emergence of the imago, cast off their skins and, consequently, in the empty cocoon, abandoned by the insect, there are 2 sloughs, of which the pupal one is a very thin white pellicle.

Prepupa I inhabits the cocoon for the longest time, on the average 15 days or about 8 months, prepupa II for the shortest time, about 2 days. The pupa and imago stay in it 4—7 days each. Both the pupa and the imago rest in the cocoon, for the most part, turned with their ventral side towards the upper wall. In connection with this position the insect gets out of the cocoon through an opening cut out in its upper wall (Pl. XLVI, fig. 3 A, B). The opening is always circular in shape, 1—2 mm in diameter; the size of diameter depends on the size of the insect. A disc, resembling a lid, cut out of the cocoon will be left at the side of the opening. Occasionally the insect leaves the cocoon at an opening in the lower wall. In addition, in the upper and lower walls of the cocoon there are sometimes a few openings, which the insect abandoned unfinished.

DISCUSSION

It has been mentioned at the beginning of the present paper that different authors disagree as to the number of generations of *H. vagans* FALL. It may be stated on the basis of my observations that there is a spring generation (I), relatively not very abundant, from May to July, and a considerably more abundant autumn generation (II), from mid-August to October.

A small number of mines is observed in spring, because at that time only few prepupae of generation II continue their development. Nevertheless, the females that emerge then lay eggs, from which the larvae and, finally, the mature insects develop to give rise to generation II in the same year.

A sound argument supporting the opinion that each year there are two generations is that the spring larvae differ from most of the autumn ones in their biology; their developmental period is shortened, they go only through 5 stadia and have a very short diapause.

The mass occurrence of mines in autumn is due to the fact that July and the second half of August are the emergence season of a large number of insects of generation II of the previous year and generation I of the current year. These insects are responsible for the abundance of autumn mines.

In the area of Krzemionki in Kraków generation I of *H. vagans* FALL. was very scarce in 1960—1964. I hardly managed to find a few leaves with mines in a large group of alders. On the other hand, the autumn generation in the same area and in the same years was as a rule very abundant. In the autumn of 1961 there was at least one mine in almost every leaf of all the young alder-trees. Out of Kraków, in the Niepołomice Forest, Kostrze, Radziechowy, and Rajcza-Nickulina, from where my control material was derived, generation I was considerably more numerous than at Krzemionki.

In the laboratory, imagines rather often emerged from the pupae of generation II of the same year late in the autumn, which was probably due to the artificially created favourable conditions. If this had occurred under natural conditions, which however was not ascertained, the emerging insects would not have been able to originate generation III, because at that time most alder leaves were already withered and falling.

Leaves with mines of *H. vagans* FALL. occur in the lower portions of trees or in young shrubby alders, which is probably connected with the weak and low flight of these insects, characteristic of sawflies (BERLAND, 1951).

Both males and females show great variation in body size and coloration. The males, however, are generally smaller and darker. There is, in addition, some correlation between the size of an insect and its coloration, irrespective of sex: the smaller the insect, the darker its coloration. Variation was also found in the number of antennal joints and the venation of wings.

Since arrenotokous parthenogenesis was observed in laboratory breeding, it may be supposed that it also takes place under natural conditions and that males are produced in this way. If this is true, it might be inferred from the small number of males that parthenogenesis is a rare phenomenon in *H. vagans* FALL. or only few females are not fertilized. On the other hand, we should have to assume, just because of the small number of males as compared with females, that one male fertilizes several females.

The following fact and reasoning may provide some evidence for the occurrence of arrenotokous parthenogenesis in *H. vagans* FALL. under natural conditions: Only one female usually deposits eggs in one leaf, the opposite case being hardly probable under natural conditions. It was next found that males emerged from all the cocoons collected in an area. Consequently, it may be supposed that the eggs were laid by unfertilized females.

It was ascertained that the development of males, both from the unfertilized eggs obtained in the laboratory and from the eggs collected in the field, is always the same; in both cases the larvae go through 5 developmental stadia.

The female larvae of generation I have also only 5 stadia, whereas in most of the female larvae of generation II the number of stadia amounts to 6.

Females instinctively avoid depositing eggs in the proximity of the main vein and its branches of the first order. This is probably connected with the weak mouth-parts of the young larva, which are unfit for gnawing thick veins. Neither do the females lay eggs in still growing young leaves, very sensitive to slightest injuries, which cause the mortification of the leaf tissue.

The body structure of larval *H. vagans* FALL. exhibits evident adaptations to its ways of life. These adaptations are the prognathism of the head and its remarkable flattening, the partial flattening of the thorax, the strong development of the lobi, and the development of new organs, such as the dorsal and ventral thoracic suckers. DZIURZYŃSKI (1948, 1958) observed similar adaptations in the leaf-mining caterpillars of the *Tineoidea*.

The flattening of the head and its prognathism, as well as the partial flattening of the thorax, make it possible for the larva to gnaw into the palisade layer in the cramped space between the upper epidermis and the spongy layer and to eat out the food, which is more or less at the level of its body.

In the light of the results obtained by DZIURZYŃSKI (1948) and me the thoracic suckers enable the larva to maintain its position in the mine and allow the temporary immobilization of its body in the place of feeding. However, since the larva of *H. vagans* FALL. has the thoracic legs and 8 pairs of abdominal feet, its suckers are of lesser importance than those in the leaf-mining caterpillars of the *Tineoidea*, in which they serve to perform progressive motion. The action of the suckers is complemented by a small number of setae arranged round them. The larvae in more advanced stadia, when the mine chamber is large and it is difficult for them to keep steady during feeding, have their thoracic suckers particularly well developed.

As regards the maintenance of the uniform position of larval *H. vagans* FALL. during feeding, i.e., with its back turned towards the lower epidermis of the leaf, we may agree with DZIURZYŃSKI'S opinion (1948) that this position in the caterpillars of *Antispila stachjanella* DZ. is connected with the disposition of stomata in the lower epidermis of the leaf and the occurrence of spiracles on the flanks of the dorsal side of larval body. The same explanation may be adopted for the position assumed by the prepupae, pupa and imago in the cocoon.

Differences in area between the mines of larvae in the same instar result, on the one hand, from individual characters of the larvae, that is, their size and vitality and, on the other hand, from the thickness of the leaves in which they feed. With the same amount of consumed leaf tissue the area of mine in thinner leaves is proportionally larger than in thicker ones.

The way in which the larva distributes frass both in the first and in the later stadia is to isolate the larva from its own excreta as well as possible. In the first period, when the area of mine is small, the larva gathers its frass together into a compact pellet, which it places at the beginning of the mine; later, when the mine is spacious, it scatters frass so as to further its drying. Frass, especially when moist, is a great danger to the larva, for it favours the development of fungi and infectious diseases.

As far as the spinning gland is concerned, it may be assumed that, as in *Pontania salicis* (PFLUGFELDER, 1934), in the larval stadia its secretion is a liquid resembling saliva in density and it is not until after the last ecdysis that this secretion thickens into an unsoluble silky substance, used to construct cocoons.

It will be seen from the experiment, in which a cocoon was damaged repeatedly on purpose and each time mended by prepupa I, that the spinning gland is still capable of producing silk. Prepupa I retains this capability till the end of the stadium.

According to SEIDEL (1926), the large „strong“ larvae of *H. vagans* FALL. are able to form their cocoons anew three times, whereas the small „weak“ larvae fail to rebuild their cocoons once.

The complete change of the structure of the mandibles after the last larval moulting may be explained by the now quite different function of the mandibles. They become the main instrument used for constructing the cocoon. The terminal part of the mandible, shaped like a stylet, enables the larva to hold the silk thread produced by the gland. The movements of the mandibles have also been modified. Owing to the change in the structure of the basal portion, the replacement of the condyle from the side to the middle and the suitable musculature, the movements performed by the mandible are based on the principle of the single-arm lever (SZWANWICZ, 1956). This property combined with slight movements of the head allows the larva to draw out short arched sections of thread and to attach them to the walls of the mine.

The transformation of the mandibles proceeds by degrees, for as early as the fifth instar a small stylet develops inside the mandible and it constitutes the bud of the future terminal part of the mandible after the last moult.

The type of the head, which has changed from prognathous to ortho-prognathous after the last larval moulting, is of great importance for the formation of the cocoon. Joining together the two halves of the cocoon, the larva leads the thread from the upper wall to the lower one and back, performing movements of the head in the vertical plane.

The assumption of two prepupal stadia seems to be just, though there is no moulting separating them from each other, because fairly distinct differences may be seen between the appearance of the prepupa just after it has retired into the cocoon and that a few day before moulting and transformation into the pupa.

The survival of prepupae in cocoons depends on temperature and humidity. For example, in the period of winter diapause prepupae I stood low temperatures of about 30°C below zero, when subjected to them in the laboratory. In natural conditions the cocoons enclosing prepupae do not lie beneath the ground, but in a thin layer of litter, among fallen leaves, and are exposed to the action of cold weather.

The prepupa is able to endure hard winter conditions thanks to its state of torpor. Besides, at that time its body is shrunk very much, the body area is very small, and its inside is filled abundantly with fat materials, which constitute a natural isolation.

Lack of moisture seems to have a greater effect on the survival rate of the prepupae, since it has been found many a time that they died in large numbers during a prolonged lack of moisture under laboratory conditions.

SUMMARY

The results of my experiments and observations carried out on the biology and morphology of *Heterarthrus vagans* FALL. may be summarized as follows:

1. There are two generations of *H. vagans* FALL. in a year: a generally scarce spring generation (I) from May to July and a considerably more numerous autumn generation (II) from mid-August to October.
2. Both male and female larvae of generation I go through 5 developmental stadia and have a reduced diapause.
3. Male larvae of generations I and II have 5 stadia.
4. Female larvae of generation II go through 5 or 6 stadia.
5. Pupal instars include two prepupae, I (eonympha) and II (pronympha), and a pupa (pupa libera).

6. Part of prepupae of generation II of the previous year conclude their development and undergo transformation into imagines in the spring of the next year, the others transform into adult insects as late as summer, giving rise to generation II.

7. Arrenotokous parthenogenesis occurs and presumably it is the only way in which males are produced.

8. Females are larger and lighter in colour than males.

9. Females are much more numerous. The ratio of males to females is as 1:4.

10. The size and coloration of insects, the number of antennal segments, and the venation of wings are very variable.

11. The larvae of *H. vagans* FALL. are monophagous, feed exclusively in the leaves of alder *(Alnus)*, and the mines formed by them are superficial mines of the chamber type, usually eccentrical, more rarely centrical.

12. The main characters differentiating the particular larval stadia are the breadth of head-capsule, the length of body, and the pattern on the body.

13. The structure of larval body exhibits adaptations to its ways of life: the prognathism, the flattening of the body, and the development of dorsal and ventral thoracic suckers.

14. The mine area depends upon the individual characters of the larva and the thickness of leaf.

15. The changes in the mandibles after the last larval moulting are caused by a change in their function. After modification they are used by the larva to construct the cocoon.

16. During the diapause, prepupal survival rate depends on humidity; the lack of moisture is the commonest cause of their high mortality.

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STRESZCZENIE

W oparciu o przeprowadzone badania i obserwacje nad biologią i morfologią *Heterarthrus vagans* Fall. można podać następujące ogólne wyniki:

1. Występują dwa pokolenia: na ogół nieliczne I — wiosenne, od maja do lipca i znacznie liczniejsze II — jesienne, od połowy sierpnia do października.

2. Larwy I pokolenia, zarówno samcze jak i samicze przechodzą 5 stadiów rozwojowych oraz posiadają skróconą diapauzę.

3. Larwy samcze I i II pokolenia posiadają 5 stadiów rozwojowych.

4. Larwy samicze II pokolenia przechodzą 5 lub 6 stadiów rozwojowych.

5. W stadiach poczwarkowych występują dwie przedpoczwarki — I eonympha, II — pronympha oraz poczwarka — pupa libera.

6. Część przedpoczwarek II pokolenia roku ubiegłego, kończy swój rozwój przekształcając się w owady dojrzałe na wiosnę roku następnego, pozostała część przeobraża się dopiero w lecie, dając początek II pokoleniu.

7. Występuje partenogeneza arrenotokiczna, która przypuszczalnie stanowi jedyną drogę rozwoju samców.

8. Samice są większe i jaśniej ubarwione niż samce.

9. Samice są znacznie liczniejsze. Ilościowy stosunek samców do samic przedstawia się jak 1:4.

10. Wielkość i ubarwienie ciała owadów, ilość członków czułków oraz wykształcenie użyłkowania skrzydeł podlegają dużej zmienności.

11. Larwy są monofagami, żerują tylko w liściach olszy (*Alnus* MILL.); miny powstałe skutkiem ich żeru są minami wierzchnimi typu komorowego, zwykle ekscentryczne, rzadziej centryczne.

12. Zasadniczymi cechami pozwalającymi rozróżnić poszczególne stadia larwalne są: szerokość puszki głowowej, długość ciała oraz wykształcenie rysunku na ciele larwy.

13. Występują przystosowania w budowie ciała larwy do jej trybu życia: prognatyzm głowy, spłaszczenie ciała, wykształcenie grzbietowych i brzusznych przylg tułowiowych.

14. Powierzchnia miny zależy od indywidualnych cech larwy i grubości liścia.

15. Przekształcenia żuwaczek po ostatnim linieniu larwy są spowodowane zmianą ich dotychczasowej funkcji. Przekształcone, są pomocne larwie przy budowaniu kokonu.

16. Przeżywalność przedpoczwarek w okresie ich diapauzy zależy głównie od wilgotności; — jej brak jest najczęstszą przyczyną ich wymierania.

РЕЗЮМЕ

Опираясь на результатах исследований и наблюдений над биологией и морфологией *Heterarthrus vagans* FALL. можно сделать следующие общие выводы:

1. Выступают два поколения: в общем немногочисленные, I — весеннее, от мая до июля и более многочисленное II — осеннее, от половины августа до октября.

2. Личинки I поколения как самцов так и самок проходят пять стадий развития и их диапаза сокращена.

3. Личинки I-го и II-го поколения самцов имеют пять стадий развития.

4. Личинки самцов II-го поколения проходят пять либо шесть стадий развития.

5. В стадиях куколок выступают две предкуколки — I-я, eonympha, II-я pronympha, а также куколка — pupa libera.

6. Часть предкуколок II-го поколения прошлого года кончают цикл своего развития превращаясь во взрослых насекомых весной следующего года, остальная часть превращается летом и даёт начало II-му поколению.

7. Выступает арренотокичный партеногенез, который вероятно является единственным путём развития самцов.

8. Самки больше самцов и их окраска светлее, чем окраска самцов.

9. Самки более многочисленны. Количественное соотношение самцов и самок равняется 1:4.

10. Величина и окраска тела насекомых, количество члеников усиков, а также рисунок жилок крыльев подвергаются изменениям.

11. Личинки являются монофагами и откармливаются на листьях ольхи (*Alnus* Mill.); мины, возникшие в результате их откорма являются минами верхними, камерного типа, обычно они бывают эксцентричны, реже центричны.

12. Основными признаками, позволяющими отличать отдельные личиночные стадии является: ширина головной коробки, длина тела, а также форма рисунка на теле личинки.

13. В строении тела личинки выступают приспособления, связанные с её образом жизни, а именно: прогнатизм головы, уплощение тела, формирование позвоночных и брюшных туловищных пульвилл.

14. Поверхность мины зависит от индивидуальных свойств личинок и толщины листьев.

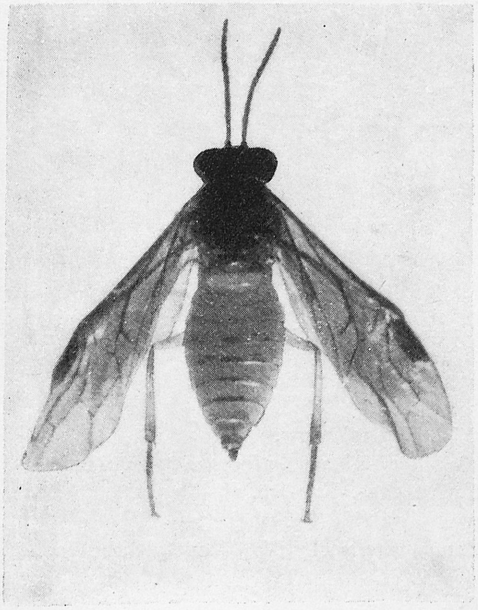
15. Преобразование жвал после последней линьки личинки вызвано изменением их первоначальной функции. Такие преобразованные жвала помогают личинке в строении кокона.

16. Живучесть предкуколок в период их диапазы зависит в основном от влажности; — отсутствие влажности является чаще всего причиной их вымерания.

Plate XLII

Fig. 1. Female of *H. vagans* FALL. A. Dorsal view, B. Ventral view.

Fig. 2. A. Terminal part of valve I, (microphotograph). B. Terminal part of valve II, (microphotograph).



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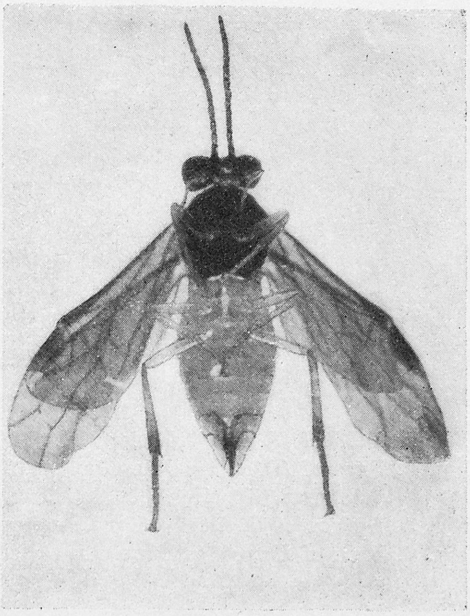

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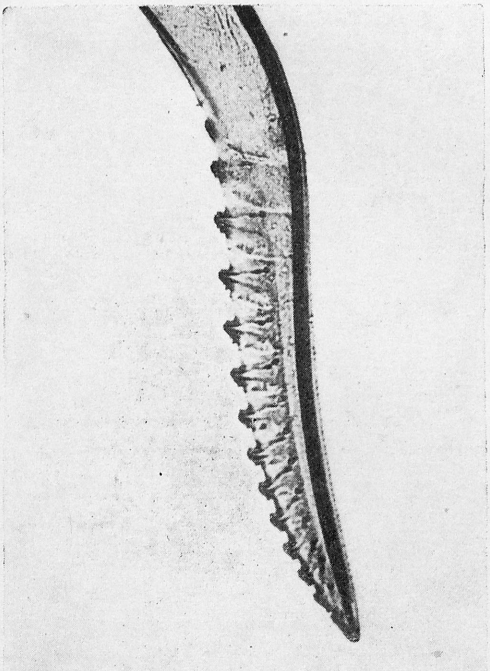

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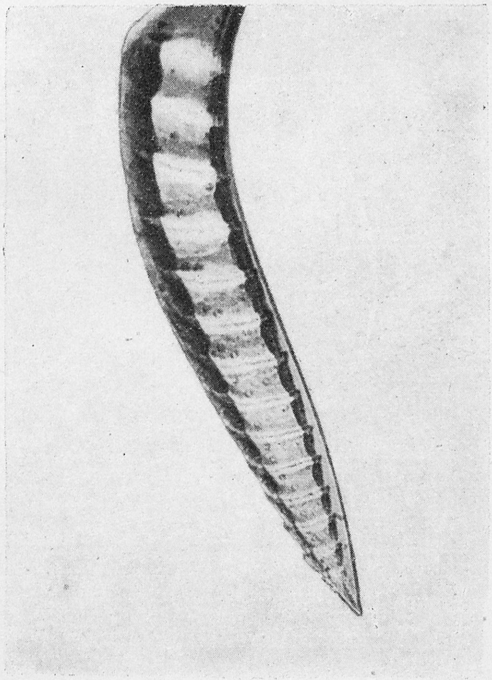

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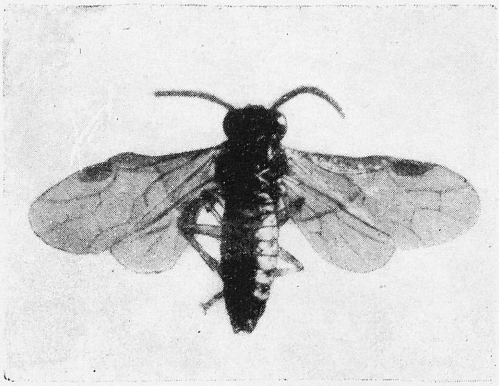
Plate XLIII

Fig. 1. Male of *H. vagans* Fall. A. Dorsal view, B. Ventral view.

Fig. 2. Eggs of *H. vagans* Fall. in a leaf of black alder (*Alnus glutinosa* L.). A. whole leaf with eggs (life-size); B. Fragment of leaf with eggs. X c. 15. E — eggs.

Fig. 3. An egg of *H. vagans* Fall., several hours old, outside the pocket.

Fig. 4. Eggs of *H. vagans* Fall. A — partly hidden in the pocket, B — outside the pocket.



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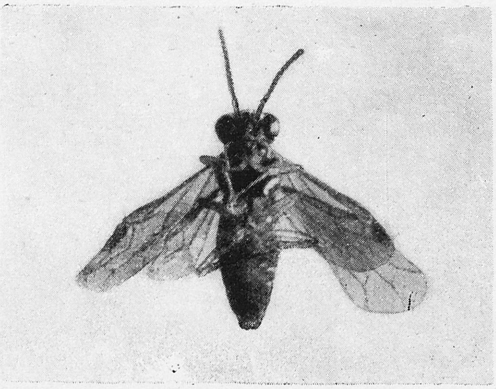

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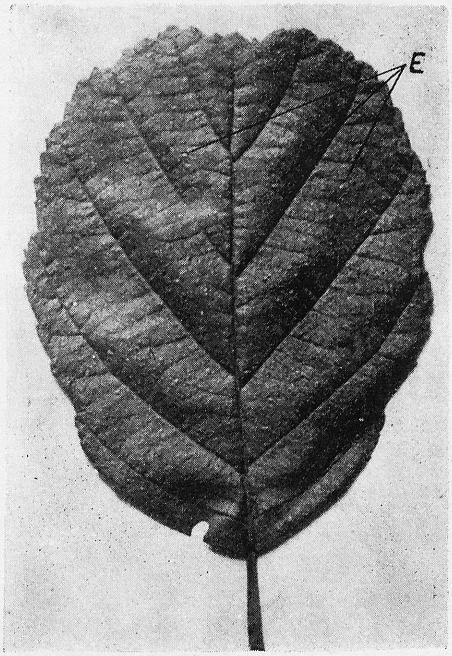

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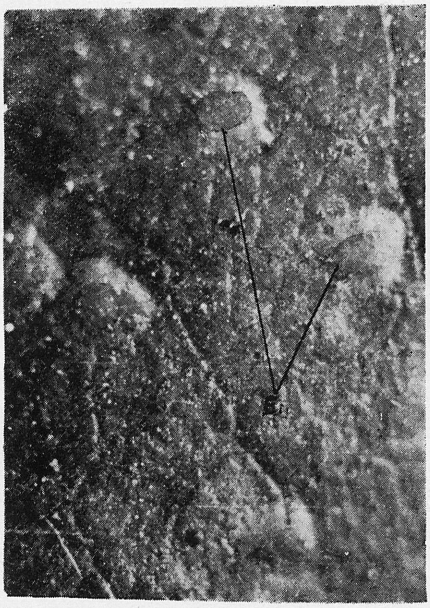

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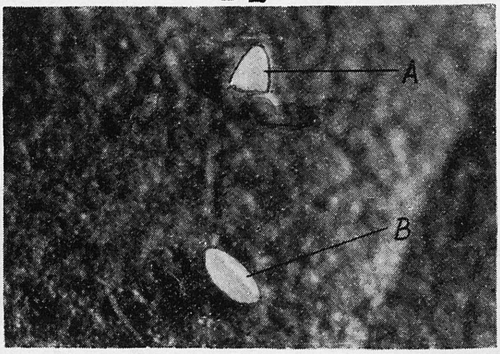

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Plate XLIV

Fig. 1. An egg of *H. vagans* FALL. in the pocket. X c. 30.

Fig. 2. Lateral view of prepupa II (pronympha) of *H. vagans* FALL. in the final period of development. e. C — empty cuticle.

Fig. 3. Female pupa of *H. vagans* FALL. Ventral view.

Fig. 4. Male pupa of *H. vagans* FALL. Ventral view.

Fig. 5. Eccentrical mine with a fourth-instar larva of *H. vagans* FALL. Mine area — about 50 mm^2 (from parthenogenetic breeding, June, 1963).

Fig. 6. Concentrical mine with a fifth-instar larva of *H. vagans* FALL. Mine area — about 270 mm^2 (from Krzemionki, Sept. 29, 1963).

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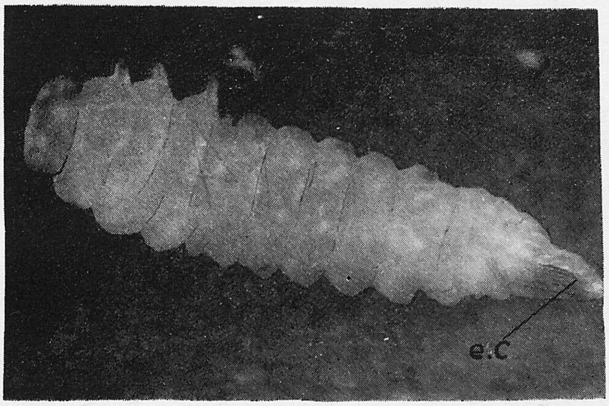

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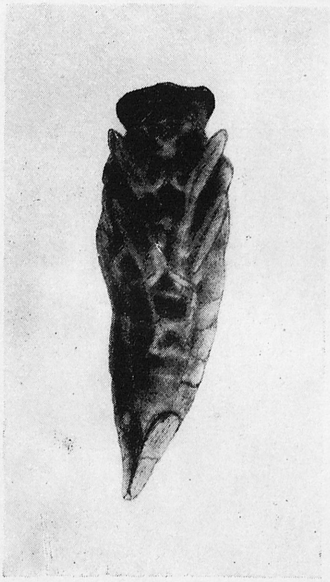

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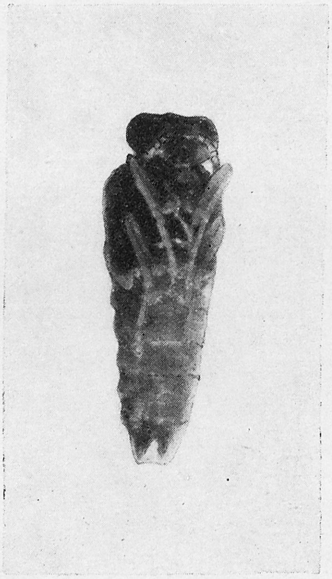

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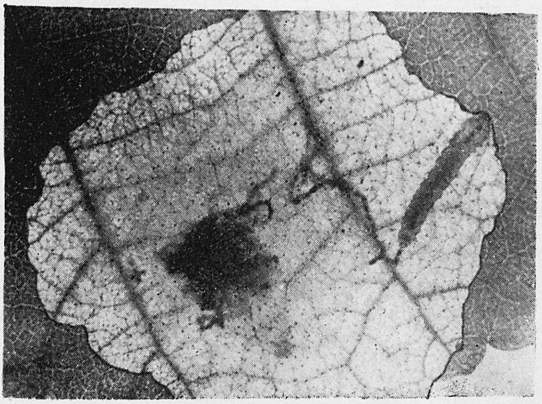

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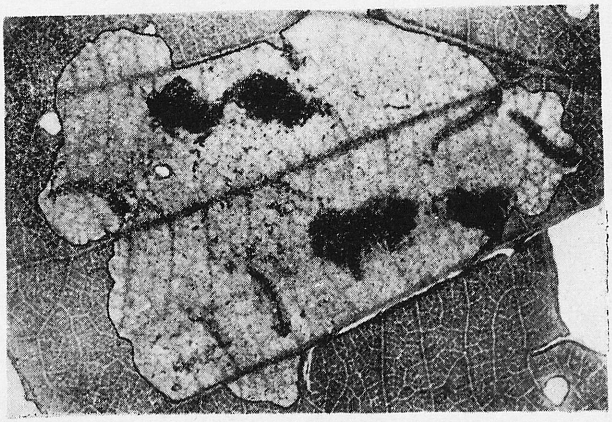
Plate XLV

Fig. 1. Mine with four feeding fourth-instar larvae of *H. vagans* FALL. (from Krzemionki, Sept. 21, 1963).

Fig. 2. Mine with a first-instar larva of *H. vagans* FALL. Mine area — about 8 mm² (from parthenogenetic breeding, May 21, 1963).

Fig. 3. A larva of *H. vagans* FALL. during the 5th moulting, ventral view. c. S — cast-off skin.

Fig. 4. A larva of *H. vagans*., which begins to feed after the 4th moulting. Mine area — about 130 mm². c. S — cast-off skin.



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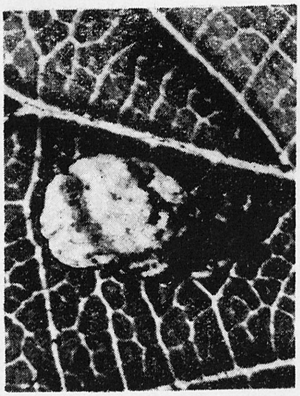

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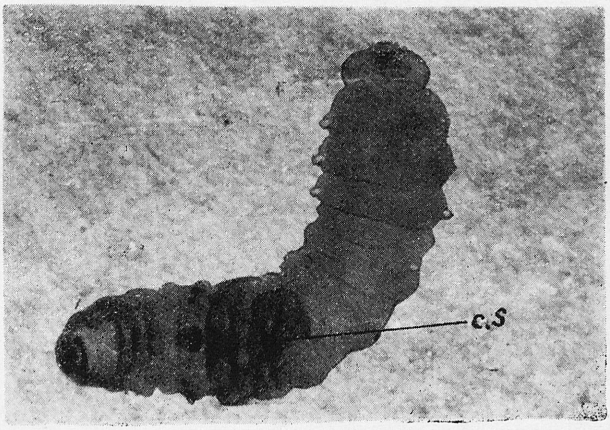

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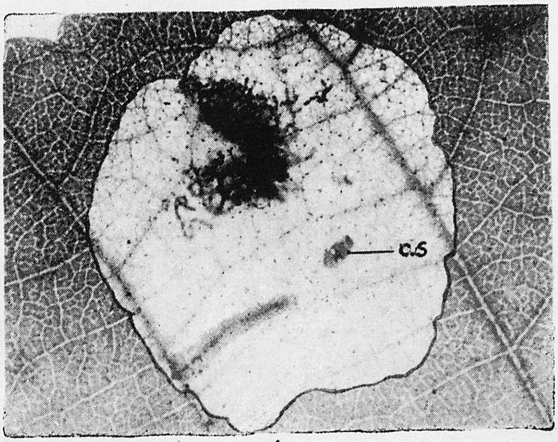

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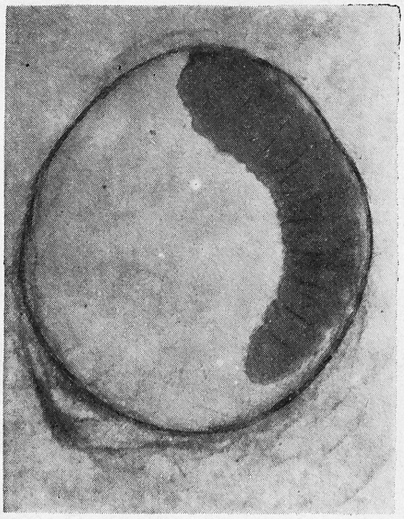
Plate XLVI

Fig. 1. A larva of *H. vagans* FALL. in the cellophane cocoon after forming its side wall, dorsal view.

Fig. 2. A cocoon of *H. vagans* FALL. in a dry alder leaf. Cocoon area — about 34 mm^2.

Fig. 3. An empty cocoon of *H. vagans* FALL. after the emergence of the insect. A. The whole cocoon with an opening cut out in it; C — cocoon, O — opening, L — lid. Cocoon area — about 45 mm^2. B. The opening cut out in the cocoon, highly magnified.



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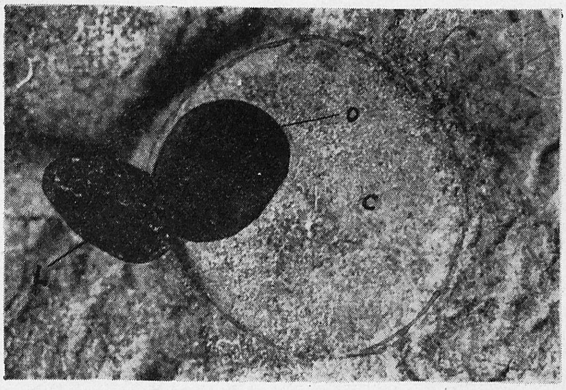

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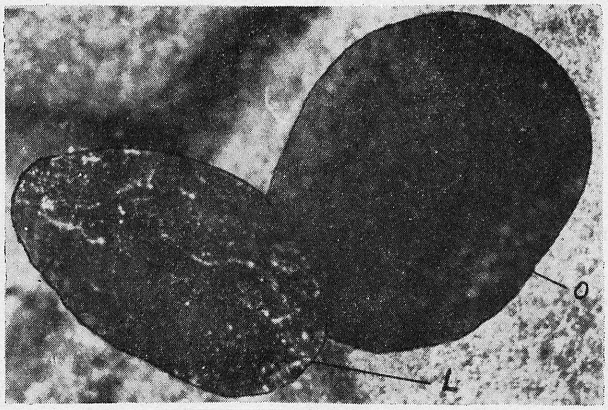

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