THE HOLLY LEAF-MINER (PHYTOMYZA ILICIS, CURT.) AND ITS PARASITES, - A STUDY IN NATURAL CONTROL

BY

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D E C L A R A T I O N

I HEREBY DECLARE -

i. That the research on the Holly Leaf-miner and its parasites, etc., described in the following pages is a record of my own work,

and

ii. that the Thesis has been composed by myself.

Confirmed by:

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INTRODUCTION

In British Columbia, where the mild humid climate is particularly favourable to its growth, European Holly - Ilex aquifolium, L. - is rather extensively cultivated. Because it cannot be grown successfully in other parts of North America, an important industry has sprung up in this region, and the sales of cut holly from the Pacific North-West, which area includes West Washington and North-west Oregon in the United States, amount to several hundred thousand dollars annually. For planting as an ornamental tree in public parks and private estates it is also in good demand, and many fine specimens are to be found in this part of the world, especially in the city of Vancouver. The only 'fly in the ointment' so far as the growing of this tree is concerned, is literally a fly - Phytomyza ilicis, Curt., or the Holly Leaf-miner, an insect whose larvae burrow in the mesophyll and produce, in course of time, large unsightly blotches or mines on the surface of the leaves. As many as 75 to 80 per cent of the latter may be disfigured annually in this way, and as a consequence, the cut foliage, from a commercial point of view, is considerably reduced in value. The trees themselves are also rendered less ornamental and attractive, and although the effect is not very apparent, it is quite possible that they suffer somewhat in health by the wholesale removal of such a large mass of chemically active cells.

Like its host, the Holly Leaf-miner is a native of North-west Europe and the phenomenal success which it has attained in British Columbia is said to be due to the absence of its parasites from this area. Since these natural enemies apparently failed to accompany the fly when the latter was accidentally introduced into Canada, the Dominion authorities decided to make good this deficiency in the fauna and asked the Imperial Institute of Entomology to secure the necessary parasites. When the great difficulties involved in chemical control, - such as for example, the invulnerability of the larvae in their secure situation underneath the protecting cuticle, and the leaf-shedding reaction of the tree to strong sprays - are realised, the fact that, at the outset, natural control offered the best, if not the only prospects of success, will be better appreciated. As a preliminary to the work of collection and export, the present writer undertook a general study of the fly and its parasites in England, in order to obtain a good working knowledge of the latter, and to find out what part they play in the control of the pest in this country. The results of this investigation are set down in the following pages.

The paper opens with a general account of the systematics, morphology, biology and distribution of the fly itself. This introductory section is followed by the largest division of the work, which deals with the various parasites reared from English material. Keys to the adult and later developmental stages of these insects precede the comprehensive account of the systematics, distribution, host relationship, biology and general morphology of the six most important species. Other mortality factors, such as the predatory Blue Tit, bacterial disease, etc., are discussed in some detail, while the final section is concerned with the natural control of the fly in England, and touches briefly on such points as population density and oscillations therein, parasite efficiency, reaction of parasites on each other, the interrelationship of biological and chemical forms of control, and the use of immune varieties of holly.

Twenty-one figures illustrating, for the most part, various developmental stages of the different parasites, one plate dealing with holly, and two graphs in connection with the section on natural control, complete the thesis.

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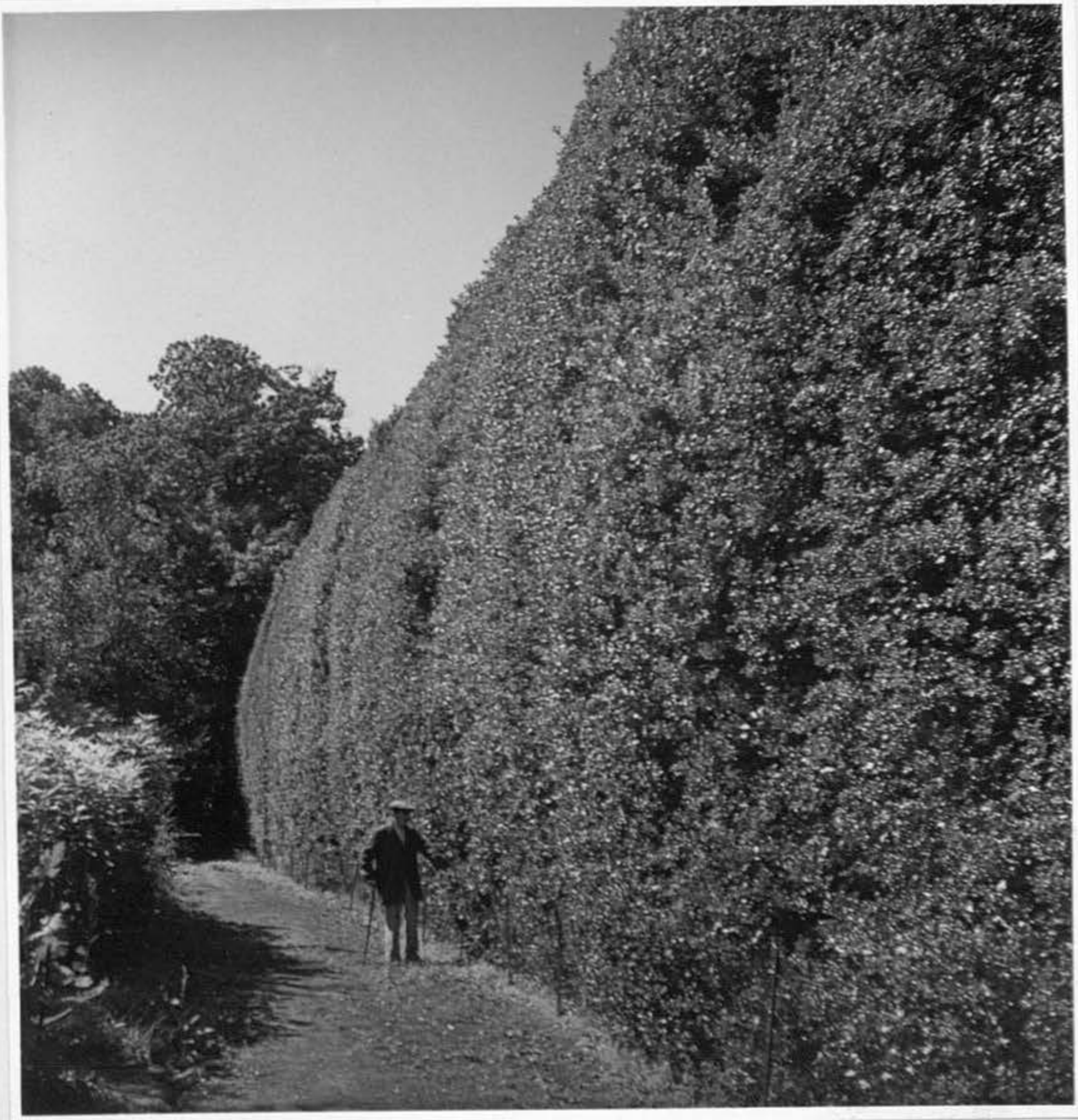


PLATE 1. This holly hedge growing at Bagshot, Surrey, is over 40 feet in height, and is supposed to be the highest and finest of its kind in England, if not in the world.

I. SYSTEMATICS AND BIOLOGY OF PHYTOMYZA ILICIS.

i. SYSTEMATIC POSITION, SYNONYMY AND DESCRIPTION OF ADULT.

Phytomyza ilicis belongs to the Family AGROMYZIDAE (DIPTERA), a family of small flies, the larvae of which are usually leaf-miners. According to Imms (1934), a characteristic feature of these larvae, with the exception of Cryptochaetum and Leucopis, which are carnivorous in habit, is the presence of sphaeroidal concretions of calcium carbonate in the Malpighian tubes. Deposits of this nature have been observed in all three larval stages of the Holly Leaf-miner.

On reading through the literature dealing with Phytomyza it was discovered that the synonymy and exact identity of the dipterous flies whose larvae mine the leaves of holly, was in a state of some confusion. Reference was made to the published works of Curtis (1846); Goureau (1851), Frost (1923), Hering (1927), Hendel (1918), and Löew (1863 and 1872), and the conclusion was reached that although many different names have been applied to these flies, in reality there are only two recognisable species - (1) Phytomyza ilicis, Curt., and (2) P. ilicicola, Löew. In his monograph on the leaf-mining Diptera of North America, Frost (1923) also reduced the number of species to two - (1) Phytomyza aquifolii, Goureau, which he believed to be conspecific with P. ilicis, Kalt., and (2) P. ilicis, Curt., synonymous with Chromatomyia ilicis, Curt., Phytomyza obscurella, Weyenb., P. ilicicola, Löew, and P. obscurella var. ilicicola, Melander. So far as aquifolii, Goureau is concerned, it is quite clear from the latter's description of this fly, - which, incidentally, is extremely short and inadequate, - that he was dealing with ilicis, Curt. The mine of aquifolii, which he figures, is also exactly similar to that of ilicis. In addition, both Hering (1927) and Hendel (1918) agree that Goureau in 1851 was dealing with the same species which Curtis had described five years previously, so that it is perfectly evident that aquifolii is a misnomer, and ilicis, Curt., having the prior claim, must be regarded as the valid name for this species. P. ilicis, Curt., is the only species, so far as I am aware, that exists in Europe, and it must therefore be taken to be the insect which, having been introduced into Canada, forms the subject of the present investigation. It is obvious, however, from his descriptions that Frost actually observed two different species of flies, and since we have shown that one of these is the European species ilicis, Curt., the other, which he calls P. ilicis, Curt., with its numerous synonyms, can only be ilicicola, Löew, which was described from North America in 1863. This species is distinct from ilicis, and the difference between the two is most clearly brought out in Figure 1, where the mines of both are portrayed - that of ilicis taking the form of a broad blotch, while that of ilicicola is linear and serpentine. When he discovered this new species, Löew called it P. ilicis, Löew, but nine years later (1872), he realised that this name had already been appropriated by Curtis for the European species, so he altered it to ilicicola. The correct identity and synonymy of these flies is therefore as follows :

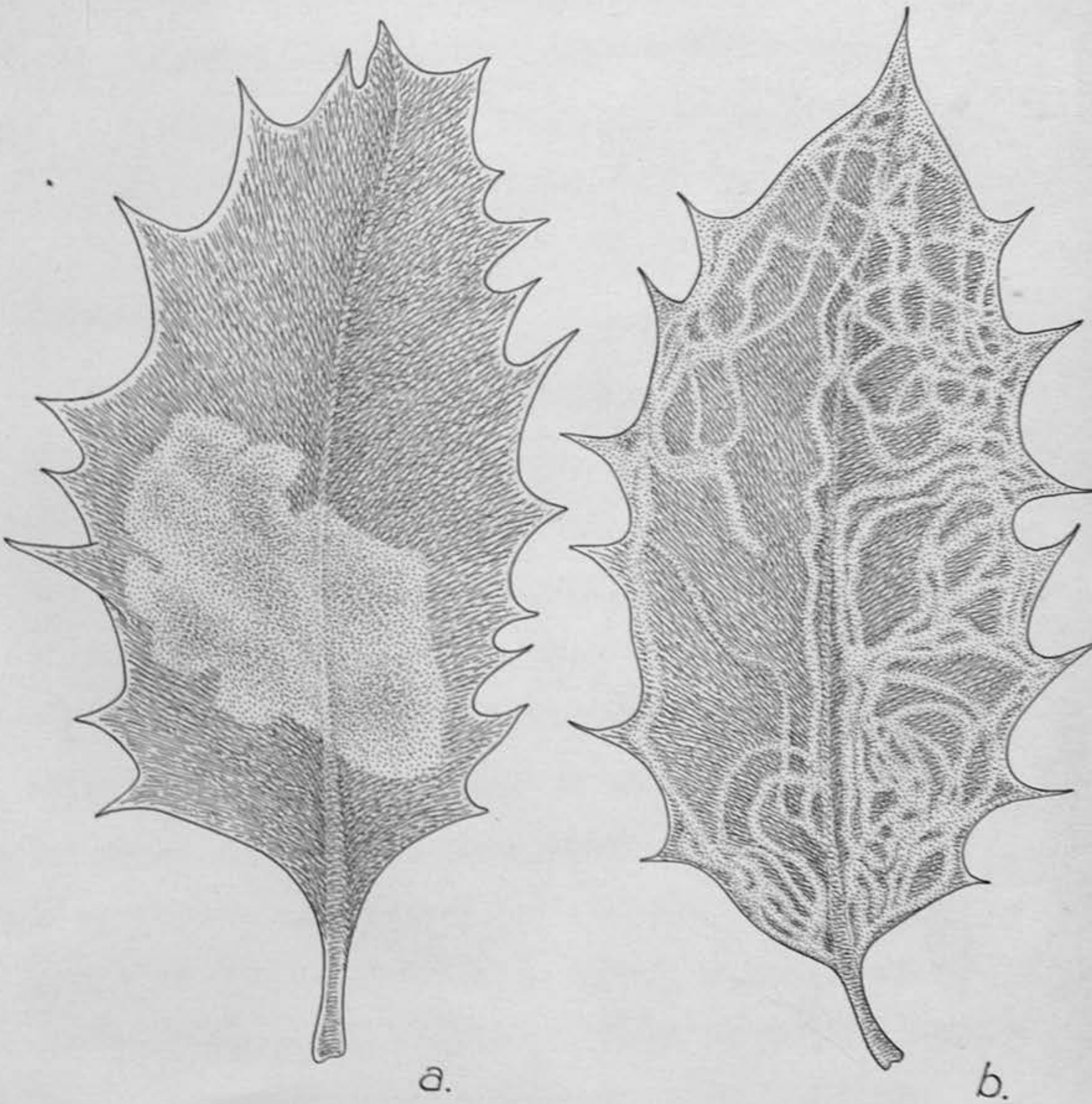


FIGURE 1. Holly leaves mined by (a) *Phytomyza ilicis*; (b) *P. ilicicola*. ((b) redrawn from Essig) (x 1.5)

1. Phytomyza ilicis, Curtis, synonymous with Chromatomyia ilicis, Curt., and P. aquifolii, Goureau.
2. Phytomyza ilicicola, Löew, synonymous with Frost's P. ilicis, Curt., and with P. obscurella, Weyenb., and P. obscurella, var. ilicicola, Melander.

Description of Adult (Fig. 2)

Average length :- Male 2.4 to 2.5 mm., Female 2.9 to 3. mm.

General colour :- Black with grey tinge. Thorax and abdomen with covering of small black hairs; head and thorax with a number of strong, stout, black bristles.

Head :- Eyes large, almost circular in outline and widely separated, chestnut-brown in colour; frons, except for two narrow, pale coloured areas between the orbits and the ocellar triangle, dark-brown to black; face straw-coloured; cheeks pale brown, subtriangular; ocellar triangle black and continuous in colouring with black orbits and occiput; ocelli - on top of head - dark yellow in colour; palpi dark brown; proboscis pale yellow. The bristles on the head are arranged as follows :- Fronto-orbitals, four pairs large, and one pair small, (on the orbits next to the eye margin there is a row of small setae); Ocellar, one pair in ocellar triangle; Verticals, two pairs on the occiput, one on each side near the eye margin; Post-verticals, one pair behind the ocellar triangle; Post-orbitals, a row of smaller bristles near the posterior margin of the eye extending down to the posterior margin of the cheek; Vibrissae, a row on either side of the epistoma.

Antennae :- Black, three-segmented, with arista on segment 3. Arista three times as long as last antennal segment, slightly pubescent.

Thorax :- Mesonotum black, lightly dusted with grey and covered with a number of small hairs and strong bristles. The latter are arranged in the following order :- Humeral, one pair; Notopleural two pairs; Pre-sutural, two pairs; supra-alar, one pair; Intra-alar, two pairs; Dorso-central, four pairs; Scutellar, two pairs. In addition to these the central area of the mesonotum is covered with a number of small hairs or bristles, which might be defined as acrostichals, but these are so indefinite that any attempt to enumerate them would be valueless.

Pleural sutures narrowly yellow. Metanotum, sub-shiny, black, and smooth.

Wings :- Hyaline and iridescent, with a close covering of small setae. There are eight longitudinal, dark-brown nervures, including the costa, sub-costa, and a short basal one between numbers six and eight. The costa, sub-costa, and two following nervures are strong and well-defined, but the others are less distinct. Cross veins are present between the costa and sub-costa, 4 and 5, 5 and 6, 6 and 7, 7 and 8, all near the wing base, while 2, 3, and 4 have a common basal part. Costa strongly ciliated and prolonged round the edge of the wings almost to the tip. Nervures 3 and 4 join on to the costa near its distal end above the wing tip, while 5 and 6 touch the wing edge below the tip, and 7 and 8 do not come to the wing edge at all. Calypteres dark-brown to black, halteres pale-yellow.

Legs :- Dark-brown to black, and clothed with dark hairs, tarsi 5-jointed; claws very small.

Abdomen :- Black, shiny, covered with bristles; that of female fusiform, tapering off rather quickly from broadest part of segment 2 to truncated end containing genital apparatus with the retractile ovipositor; that of the male narrower and somewhat cylindrical. The shape of the abdomen together with size, is the most useful characteristic for separating the sexes.

The main points of difference between ilicis and

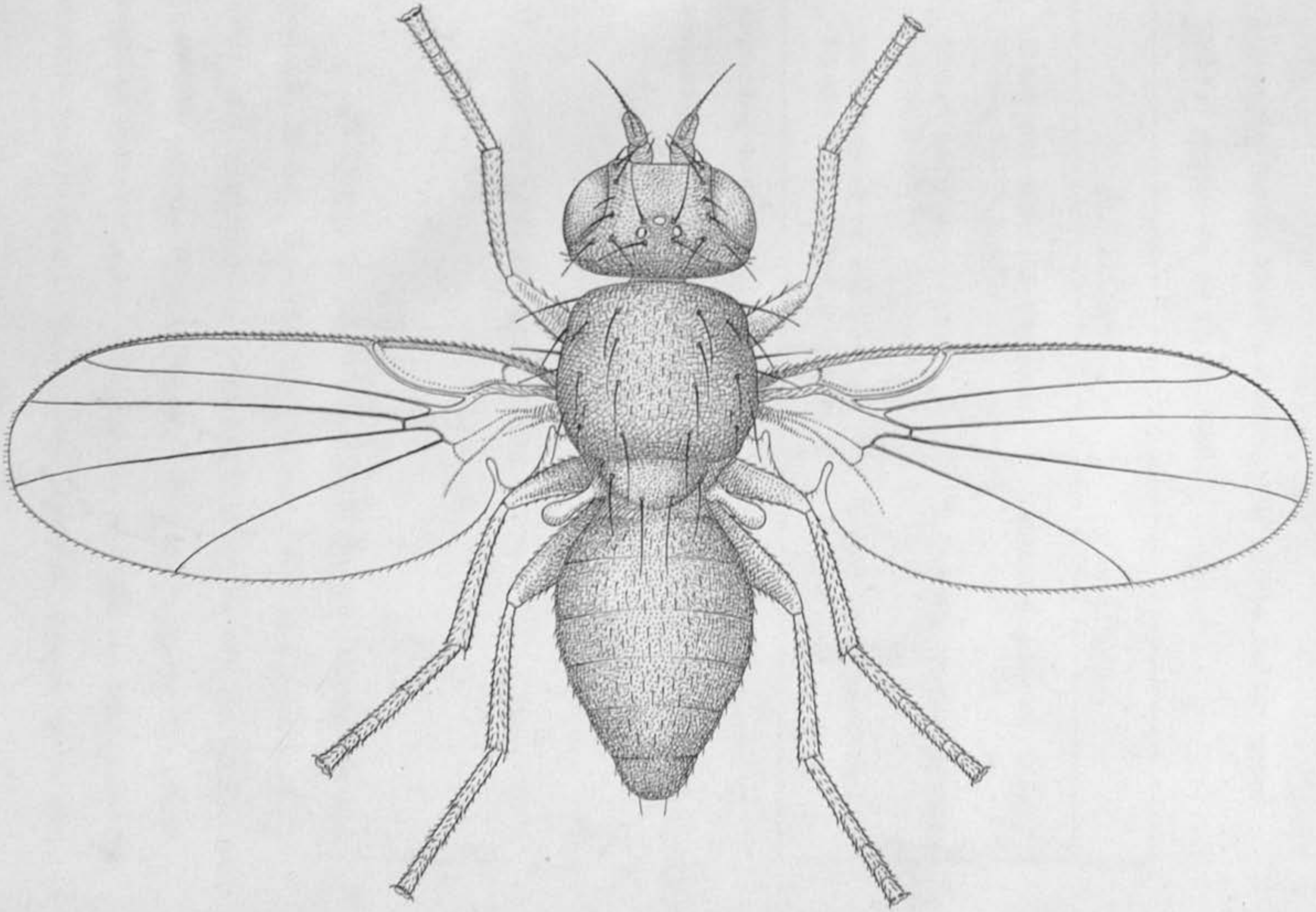


FIGURE 2. *Phytomyza ilicis*, adult female. (x 33)

ilicicola (using Frost's description of the latter under ilicis) appear to be as follows :

ilicicola.	ilicis.
First two antennal segments brown, third black.	Antennae entirely black.
Thorax and femora more strongly dusted with grey.	Thorax and femora darker.
Last segment of abdomen in female with yellow incisure.	Yellow incisure absent.

According to Frost there are 5 - 9 slits in the posterior stigmata of the larva of ilicis, and twenty in that of ilicicola.

ii. DISTRIBUTION AND HOST PLANTS.

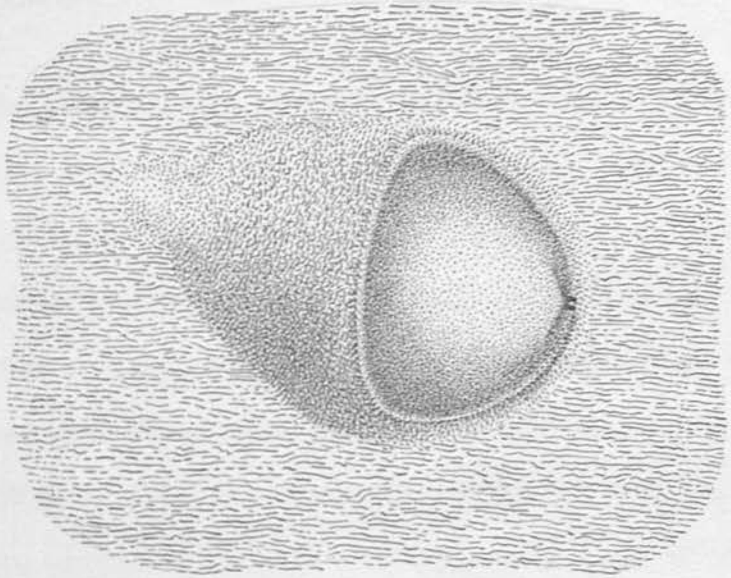
P. ilicis is fairly common in Europe, especially in England, France, Germany, and Holland, and as a result of accidental introduction it is now present in the New World, both in Canada and the United States. P. ilicicola, on the other hand, is indigenous to North America and has not been recorded outside that country. This latter species, according to Essig

(1929), attacks both European (Ilex aquifolium) and American holly (I. opaca), while ilicis appears to be confined to the European species, with its numerous varieties.

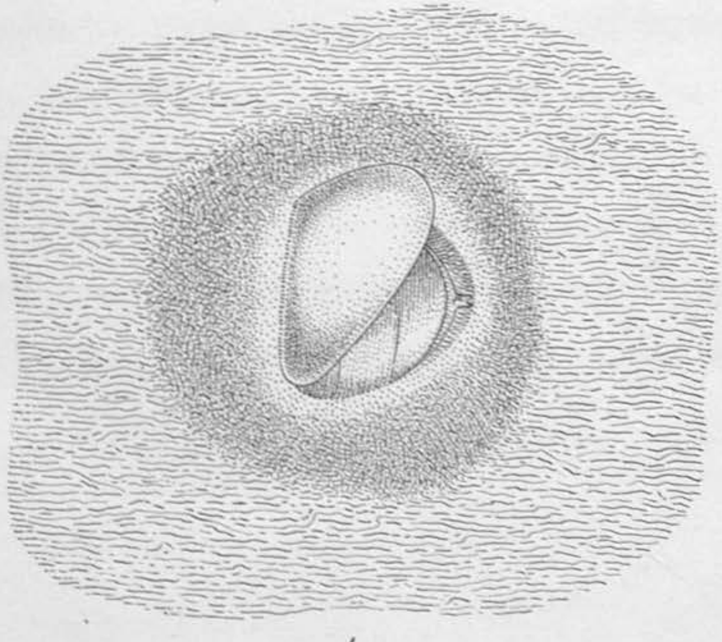
iii. LIFE-HISTORY.

Two separate accounts of the life-history of the Holly Leaf-miner have already been published, one in England, by Miall and Taylor (1907), dealing chiefly with the anatomical structure of the fly and its various developmental stages, and the other in Canada by Downes (1931) concerned more with chemical measures of control. The following short description is compounded from these two papers, and is confirmed by my own observations.

The imago emerges from the puparium towards the end of May, and flies may be found fairly plentifully on the holly trees throughout June. Soon after fertilization the female proceeds to lay her eggs in the small young leaves of the current year's growth. This foliage, being quite soft, is easily penetrated by the ovipositor. The site selected for oviposition is located near the base of the mid-rib on the under side of the leaf. Here the female fly bores a vertical shaft which, on reaching the vessels of the leaf, bends at right angles and continues horizontally along the mid-rib. In this horizontal section of the tunnel the egg, which is white in colour and .383 mm. long by .160 mm. broad, is deposited. The latter soon hatches, but for several months afterwards the small first-stage larva gives no indication of its presence in the leaf. During this period it remains hidden in the mid-rib, making its way slowly forward until in September, October or November, it leaves the central vessels and enters the soft green outer tissues. Here it gradually eats away the parenchyma below the epidermis until a large irregular blotch with a distinctly disfiguring effect, is formed. This blotch, or mine, which reaches its maximum size in March, may occupy a considerable area beneath either the upper or lower epidermis, but it is usually confined to the former, although occasionally it extends to both surfaces. Between July and March the larva moults twice and passes through three larval stages, the first lasting from July to December, the second from December to January, and the third from February until the formation of the puparium about the end of March. Some little time before



a.



b.

FIGURE 3. Puparium of *Phytomyza ilicis*, '*in situ*' on holly leaf; (a) before emergence of fly, - note protruding anterior spiracles; (b) after emergence, - note raised triangular flap.

(x 33)

pupating, the mature larva prepares a thin triangular area on the cuticle of the leaf, against which a hinged emergence plate of similar size, on the puparium, will abut, so that when the fly has matured, its escape may be easily accomplished. While feeding on the tissues, the larva lies on its side, but before entering the pupal stage it turns over on its back so that its ventral surface is pressed against the epidermis and its anterior spiracles are projected through the attenuated area of cuticle. The imago makes its escape from the leaf by pressing with the ptilinum against the hinged emergence plate on the puparium, which in turn breaks through the thin cuticle above it. (Fig. 3).

In British Columbia the life-history of the fly is substantially the same as it is in England, except that the emergence of the adults takes place about a fortnight earlier than in this country, and the other stages are correspondingly advanced.

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II. PARASITES OF P. ILICIS

a. PARASITES REARED.

Although an extensive search was made through the literature no reference to any parasite of the Holly Leaf-miner in Palaearctic regions could be found. It may therefore be taken that the following species reared by the writer in the course of the present investigation, are now recorded, from this host, for the first time.

CHALCIDOIDEA :

EULOPHIDAE : 1. *Chrysocharis gemma*, (Curt.) Walk.

2. *Chrysocharis syma*, Walk.

3. Pleurotropis amyntas, Walk.

4. Closterocerus trifasciatus, Walk.

5. Tetracampe sp. (near nemocera, Masi)

PTEROMALIDAE :

6. Sphegigaster flavicornis, Walk.

7. Cyrtogaster vulgaris, Walk.

ICHNEUMONOIDEA :

BRACONIDAE :

Opiinae : 8. Opius ilicis, sp.nov.

The forementioned parasites emerged from material collected in the South-east of England, more particularly in the counties of Buckinghamshire and Surrey, and also from the New Forest in Hampshire, and the Forest of Dean in Gloucestershire. The order of their abundance is as follows : (1) Chrysocharis gemma, which is by far the most common species; (2) Sphegigaster flavicornis; (3) Chrysocharis syma (which comes fairly close to Sphegigaster); (4) Cyrtogaster vulgaris; (5) Pleurotropis amyntas; (6) Opius ilicis; and lastly, Closterocerus trifasciatus and Tetracampe sp., which are extremely rare. All of them, with the exception of C. gemma, which completes its life-history on the larva, are parasites of the pupa, and all except P. amyntas are primary in habit.

The latter species was found acting in the dual capacity of a primary on the fly pupa, and a secondary on the larva and pupa of Sphegigaster flavicornis and other pupal parasites.

This section, which comprises the main bulk of the paper, contains identification keys to the adults and mature larvae of the various parasites, and a fairly comprehensive account of the systematics, host relationship, distribution, biology and morphology of the five chief species, which are all Chalcids. It will be found that the latter fall into two main groups, one consisting of Chrysocharis gemma, C. syma, and Pleurotropis amyntas, all endoparasitic in habit and all members of the Family EULOPHIDAE, and the other of Sphegigaster flavicornis and Cyrtogaster vulgaris, both ectoparasites and both typical Pteromalids. It is interesting to observe, however, that although very striking differences have been discovered in the larvae of these parasites, differences which, in this particular instance, enable one to place these larvae in the same sub-families as the imagos, yet these distinguishing characteristics being related only to the endo- or ecto-parasitic habit, cannot serve as a basis for a general classification of Chalcid larvae, which will coincide with the system already in use for the adults. It is possible, however, that (even if some exceptions do occur) they may be found generally useful for determining, with some degree of accuracy, whether a particular Chalcid larva is an internal or external feeder. This would be useful, especially in the case of advanced larvae which have destroyed their host, and with it all obvious indication to their mode of life. Chrysocharis gemma and Sphegigaster flavicornis have each been made representative of the group to which they belong, the first to the endoparasitic Eulophids, and the second to the ectoparasitic Pteromalids, and these two species are therefore described in greater detail than any of the others.

The Braconid, Opius ilicis, although not a common parasite of the Holly Leaf-miner, is also treated in some detail and the most important developmental stages are described.

b. KEYS TO ADULT AND DEVELOPMENTAL STAGES.

Adults :

1. Antennae elbowed, wing venation simple, Chalcid type. 2

Antennae not elbowed, wing venation complex, forewing with only one recurrent nervure, Braconid type . . . . . . Opius ilicis.

2. Fore tibiae with one large curved spine, marginal nerve shorter than the subcosta, radius usually long. Tarsi five-jointed. 3

Fore tibiae with one short, thin, straight spine, marginal nerve mostly long, often longer but not shorter than the subcosta, radius and post-marginal usually short. Tarsi four-jointed (except female of Tetracampe with 5) 4

3. Petiole longer than the hindmost coxae. Legs medium brown . . Sphegigaster flavicornis.

Petiole shorter than the hindmost coxae. Legs almost black. . Cyrtogaster vulgaris.

4. Wings with dark cross bands . . Closterocerus sp.

Wings without cross bands 5

5. Abdomen petiolated. 6

Abdomen sub-sessile 7

6. Antenna 10-segmented, tarsi with four joints, light coloured, rest of leg dark . . . . Pleurotropis amyntas.

Antenna 12-segmented, tarsi of female with 5 joints, of male 4, dark coloured like rest of leg. . . . . Tetracampe sp.

7. Femora pale straw-coloured. Dorsum of female light green, of male burnished gold and green mixture, scape of male yellow. Dark circular area on forewings, sometimes lighter in colour . . Chrysocharis gemma.

Femora black, except for pale straw-coloured extremity. Dorsum of female metallic green, of male dark bronze-green. Scape of female black. Dark circular area on forewings absent. . . <u>Chrysocharis</u> <u>syma</u>.

<u>Mature larvae</u> :

1. Skin smooth 2

Skin shagreened . . . . <u>Opius</u> <u>ilicis</u>.

2. Strong rectangular tentorium present in cephalic skeleton (Fig. 17, page 86); atrium of spiracle large, diameter not less than 20 µ, rings below atrium 3 - 6 in number, valvular apparatus below rings conspicuous (Fig. 18, page 88); endoparasitic type 3

Strong tentorium absent (Fig. 8, page 42). Atrium of spiracle less than 20 µ in diameter. Rings below atrium 10-17 or more in number, valvular apparatus not apparent (Fig. 9, Page 47) 4

3. (The two species in this group are practically identical in the larval stage and the mature larvae should therefore be left for a few days until they have pupated, when identification becomes relatively easy)

Early pupa white in colour; internal angle of antenna very obtuse (Fig. 19d, page 93) . . <u>Sphegigaster</u> <u>flavicornis</u>.

	Early pupa white with black markings on venter of abdomen (Fig. 19b, page 93); angle of antenna almost a right angle.	. Cyrtogaster vulgaris.
4.	Larva or larval skin lying free in mine without any evidence of a puparium	. Chrysocharis gemma.
	Larva contained in host puparium . . .	5
5.	Sensory papilla in region of inferior mandibular articulation vertical-oval in shape. Small, rather slender larva about 1.6 mm. in length. Hibernates mostly in larval stage and is usually hyperparasitic in habit	. Pleurotropis amyntas.
	Sensory papilla more or less circular in outline. Larger larva, rather rotund about 2.14 mm. in length. Does not hibernate as a larva and is primary in habit	. Chrysocharis syma.

1. Chrysocharis gemma, (Curt.) Walk.

This species is the commonest and most important parasite of the Holly Leaf-miner in the South of England, over which area it was found to be generally distributed. It was most abundant in 1938, when the highest attack obtained was 71 per cent at Burnham Beeches in Bucks. In 1937 the maximum

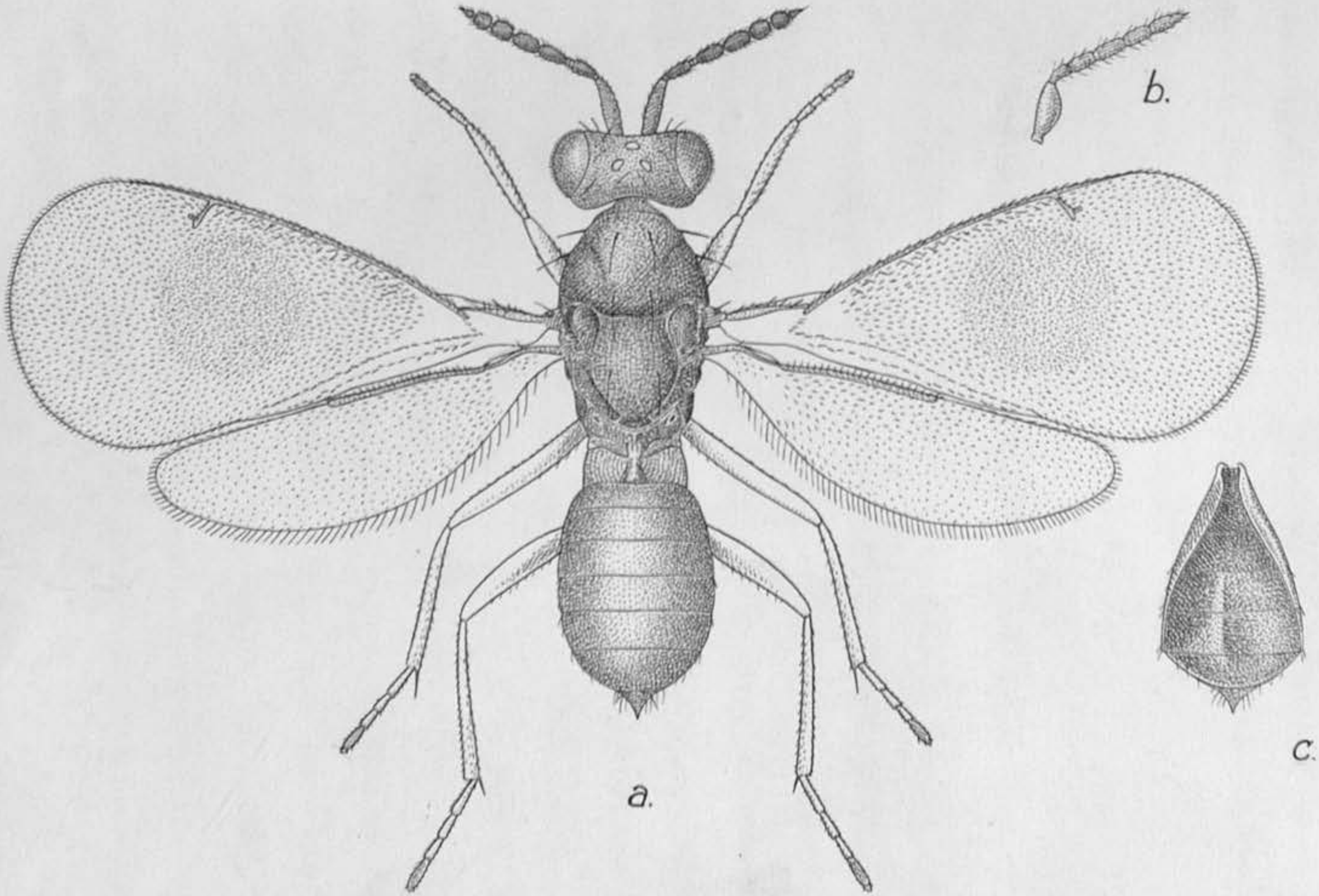

FIGURE 4. Chrysocharis gemma, (a) adult female; (b) antenna of male; (c) shrunk abdomen of pinned female.

(all circa x 37)

parasitism was 55 per cent at Sunninghill, Berks., while in most other districts as many as 30 - 35 per cent of the host larvae were usually parasitized by this species.

i. Systematic Position and Description of Adult.

C. gemma belongs to the Family EULOPHIDAE, tribe Entedonini, and sub-tribe Omphalina. According to Ashmead (1904), the Omphalina can be distinguished from the other sub-tribes of the Entedonini by the antennae, which are never more than ten-jointed, the abdomen which is sessile or sub-sessile, and the parapsidal furrows which are quite distinct. The genus Chrysocharis itself, which was erected by Forster in 1856, can be identified by the nine-jointed antennae (with one ring joint), the distinct malar space, and the eyes, which do not extend to the base of the mandibles. There are twenty-one species of Chrysocharis listed in the "GENERA INSECTORUM", but since that was published fourteen additional members of the genus have been described, so that the total number up to date is thirty-five.

Curiously enough this species, unlike the other Chalcid parasites of P. ilicis has no synonyms.

Description of Adult (Fig. 4).

Average length : Female 2.15 mm., male 1.5 - 1.6 mm.

General colour : Male, Burnished golden-green; female bright green, with petiole and middle part of abdomen black, propodeum black with golden tinge.

Head : Female green, male golden-green, shiny, reticulated, with a number of strong projecting hairs, eyes large, chestnut colour, pubescent, three ocelli on top of head.

Antennae : Inserted low down on face, scape of female smoky-brown, of male orange-yellow and rather swollen, pedicel of female black, of male orange, flagellum of female black, of male dark-brown; three annelli in both sexes, distal one in female much larger than other two; five-jointed flagellum, the terminal joint prolonged as a stout proboscis-like spine, which may in the female have several projecting spines half way along its length, and in the male a further terminal spine attached to the end. The whole antenna is covered with strong, spiny hairs, but the flagellum has, in addition, a number of strong, incurved, almost adpressed spines with rather peculiar broad bases (in the male these may have some orange pigment), there are also a number of stalked globular papillae scattered over the flagellum.

<u>Thorax</u> : Green in female, burnished golden-green in male, strongly reticulated, shiny, number of strong, backwardly projecting hairs on dorsum, notauli well marked, propodeon with a number of strong median ridges and a pair of large spiracles, post-scutellum small but well marked. Large parapsidal furrows.

<u>Wings</u> : Both fore and hind wings covered with hairs except for small area at base, forewing of female with slightly infuscated, circular, central area; marginal nervure much longer than sub-costa, post-marginal only slightly longer than radius. Tegulae yellow.

<u>Legs</u> : Very pale straw-coloured in the female, except for coxae, which are black with a green tinge, the tarsi of the first pair of legs, part of the anterior tibiae, and the last one or two tarsal joints of the middle and hind legs, which are slightly darkened. In the male the anterior and middle legs are hyaline, and the posterior ones straw-coloured, while the last tarsal joint of each pair may be slightly darkened.

<u>Abdomen</u> : Petiole short, much wrinkled, abdomen pear-shaped, the surface reticulated, segments, 3, 4, and 5 in

female dark brown, remainder green; abdomen of male burnished golden-green in colour, 7 segments visible from above in both sexes.

The sexual dimorphism may be tabulated thus :

Characteristics.	Male	Female
Average length.	1.5 - 1.6 mm.	2.15 mm.
General colour.	Burnished golden green.	Bright green, propodeon black with golden tinge, segments 3, 4, and 5 of abdomen dark brown.
Antennae.	Scape orange-yellow, rather swollen and prominent, pedicel orange.	Scape smoky brown, pedicel black.
Forewings.	Without clouded area centrally.	Central clouded area.
Legs.	First two pairs glassy, posterior pair glassy to pale straw colour.	Pale straw colour, coxae black-green, tarsi of anterior legs and last one or two tarsal joints of middle and hind legs darkened.
Abdomen.	Burnished golden green.	Segments 3, 4, and 5 dark brown, remainder green.

ii. <u>Distribution and host records.</u>

The genus <u>Chrysocharis</u> is very widely distributed. It occurs in four out of the five continents of the world and has been recorded from the following countries :

1. Europe - England, Germany, Austria, Spain, Sweden, and Russia.
2. Africa - Kenya, Uganda, and Tanganyika.
3. America - North and South America and Hawaii.
4. Australasia - New Zealand.

<u>C</u>. <u>gemma</u> itself has not been reared before but has been taken in Great Britain by Walker, who named the species.

The host relationship of the genus, as revealed in the following list, which includes the four most important Orders of insects, is rather interesting.

1. <u>Diptera</u> : Mainly <u>Phytomyza</u> spp., also <u>Scaptomyza</u> and <u>Cerodonta</u> spp.
2. <u>Lepidoptera</u> : Mainly <u>Lithocolletis</u> spp., <u>Coleophora</u> spp., <u>Leucoptera</u> spp., and <u>Lyonetia</u> spp. (all Tineina).

3. Hymenoptera : (1) Fenusa sp., and Phyllotoma sp. (Tenthredinidae).

4. Coleoptera : Rhynchaenus spp. (Curculionidae).

Ashmead, the North American Chalcid expert, who was partly aware of this diversity of hosts, thought that many of the records were wrong and believed that most of the species would be found to be parasitic only on Diptera, since "where the records conflict", he says, "Diptera are usually associated with the Lepidoptera or Coleoptera either as parasites or as co-habitants on the same plant". The present writer, however, does not agree with this hypothesis because (1) most of the forty records examined appear to be perfectly genuine; (2) the diversity of hosts is too great to be accounted for by mistakes in rearing, and (3) most important of all, because all these hosts, although widely separated systematically are all closely linked ecologically. The larvae of all of them are leaf-miners, and being small and enclosed within the tissues of the leaf on

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(1) Chrysocharis sp. has been recorded from the Ichneumonid, Angitia sp. and the Braconid, Microgaster sp. by Voukasovitch from Serbia, but in view of the fact that in all other records this genus is stated to be primary, it seems to me that these two instances of hyperparasitism are somewhat doubtful, and should be received with suspicion until further confirmation of them is forthcoming. It is quite possible that the real host, some inconspicuous leaf-miner, on the same plant which harboured the host of this Ichneumonid and Braconid, had been overlooked.

which they feed, they present a more or less similar general appearance to the parasites which prey upon them.

iii. General Biology of C. gemma.

The females of this species in common with some of the other parasites of P. ilicis, have the rather unusual habit of overwintering in the adult stage. At first it was thought that they hibernated in some alternative host, but when they were found ovipositing in the mines as early as the end of February and the beginning of March, doubts were entertained on this point. It was therefore decided that holly trees in the neighbourhood of the Laboratory should be swept at regular intervals throughout the winter months, especially on fine sunny days. As a result females were taken from October onwards. Egg laying begins towards the end of February and continues throughout March, while a few females may still be sttempting to oviposit early in April, although few host larvae are available during that month. It is quite possible that some eggs may be deposited early in February, or still earlier, if the weather is warm and the mines are beginning to show up, but the numbers laid before the end of February must be very small indeed. The act of oviposition lasts about three minutes or less, a single egg being deposited through the cuticle of the leaf into the body cavity of the larva. Occasionally a certain amount of superparasitism occurs, and two or more eggs may be found. In 1937, at Sunninghill, Berks, where this parasite was fairly abundant, eggs and first-stage larvae were quite common in the host about the middle of March, and in 1938, owing to the advanced spring season, they were plentiful at the beginning of this month. Larvae which have been attacked by C. gemma, even although they contain only the egg of the parasite, are quite different in appearance from healthy unparasitized hosts. In contrast to the latter, which are rather turgid and of a bright, shiny lemon-yellow colour, they are flaccid and of a pale, dirty-yellow hue. The incubation period lasts about a week to ten days, depending on the temperature, after which a very characteristic first-stage larva makes its appearance. The most striking peculiarity of this larva is the presence of backwardly projecting spines on the dorsum of the posterior segments, which are absent in the second stage, but these and other morphological characteristics will be discussed in the succeeding section. From emergence to maturity, a period of about sixteen to twenty days elapses, during which time the larva moults twice and passes through at least three distinct stages. (The difficulty of ascertaining with any

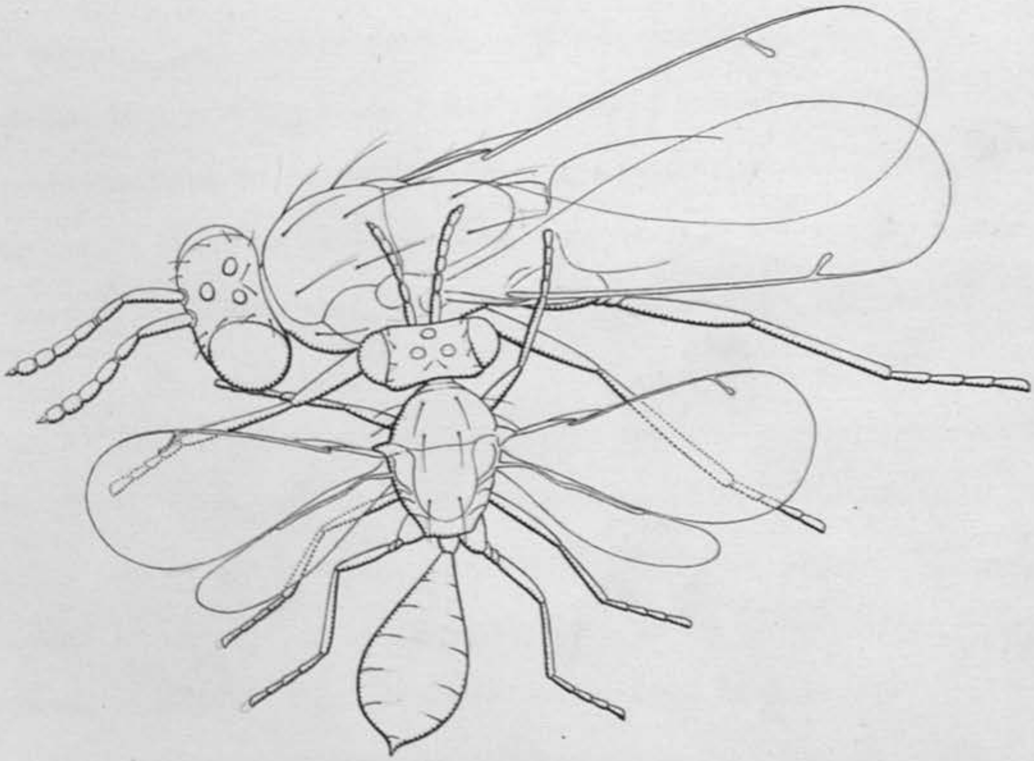


FIGURE 5. *Chrysocharis gemma*, mating position.

(x 40)

degree of exactitude the number of moults which an internal parasite undergoes in the course of its larval life, can easily be appreciated). After feeding has been completed, the larva remains in a resting stage for a further eight to ten days before changing to a prepupa, so that altogether, the length of the larval stage is about a month. After this the insect spends a further four days as a prepupa, and thirty-eight days as a pupa.

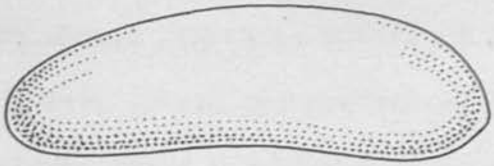
There is such a long period of egg-laying that eggs and all larval stages can be found throughout March and part of April. Pupae can be found from the 12th of April onwards (or earlier if the spring is warm like that of 1938) and this instar becomes plentiful from about the second week in May. The imagos begin to make their appearance early in June, the peak of emergence being reached about the middle of the month. Thus the total length of time occupied by metamorphosis, from the deposition of the egg to the emergence of the perfect insect, is roughly eighty-two days. As a rule the males emerge about five or six days before the females and the sex ratio is .5 or two females to one male.

The courtship of this species, being rather unusual, is worthy of special notice. When the male becomes aware of the presence of the female he pursues her with wings fully extended, and antennae held straight out in front, both wings and antennae vibrating rapidly. On catching up with her he grips her on the dorsum of the hinder part of the thorax, or on the wing with one of the front pair of legs, his body meanwhile being held in a curved position at right angles to that of his partner (Fig. 5). In this position he keeps up the rapid vibration of wings and antennae, whilst his body quivers and the grasping leg is occasionally released. The female does not appear to be much affected by this performance, but carries on with the task of cleaning her abdomen with the hind pair of legs, and in moving her antennae slowly up and down. The manoeuvres of the male lasting for about two or more minutes are evidently in the nature of a preliminary courtship intended to make the female receptive. She, however, remains rather frigid and walks away with the male hanging on to her by one leg, and still holding his body in its unusual position. Although the movements of several pairs were watched for some time, actual copulation was not observed in the laboratory, so that C. gemma may be included with the many other species of insects which refuse to mate in captivity.

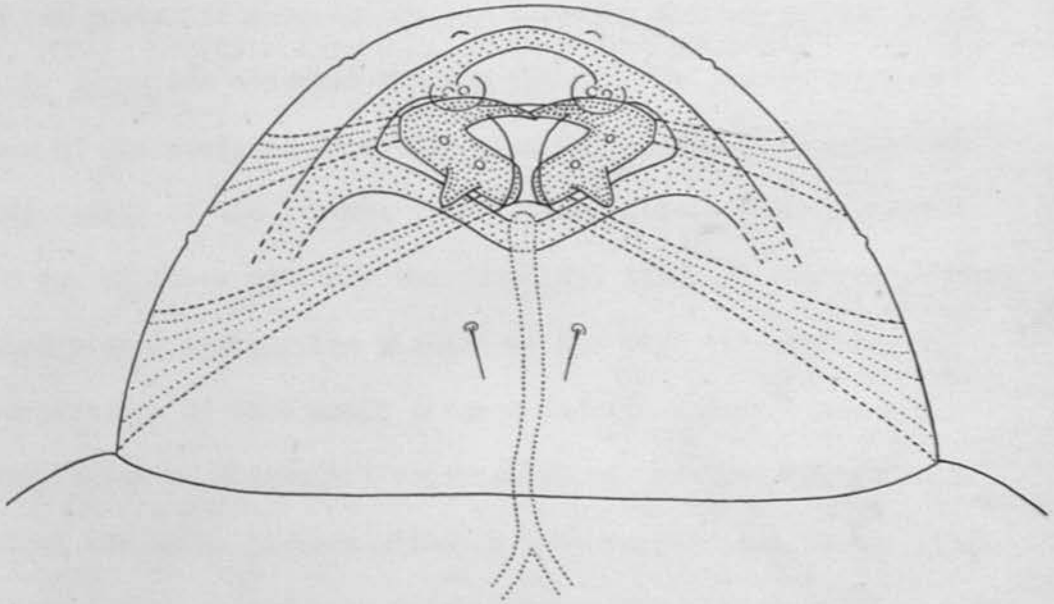
iv. Detailed Description of Developmental Stages.

The Egg : The egg (Fig. 6a) is greyish-white in colour, smooth and somewhat kidney-shaped. It is slightly broader at the micropylar end than at the other, and measures .28 mm. in length by .084 mm. in maximum breadth.

First Stage Larva : The first stage larva (Fig. 6c) consists of a head and thirteen well-marked body segments. It is somewhat fusiform in shape and the skin is more or less transparent. When newly hatched it measures .29 mm. - .31 mm. in length by .o84 mm. in maximum breadth, the breadth of the head being .063 mm. The shape of the latter is somewhat like that of a thimble and bears quite a good general resemblance to that of the first stage larva of an internal Ichneumonid parasite. The mandibles are very distinct and in side view the pharynx is clearly discernible. A distinct lobe is present on the ventral side of the head, some little distance behind the mouth. The armature on the skin is rather unusual. It consists of a row of small dorsal spines on the anterior margins of segments 4 - 12 (Fig. 6c), which are not particularly easy to see except under good magnification. They measure about 2. to 2.5 μ in length and are separated from each other by a similar distance,



a.



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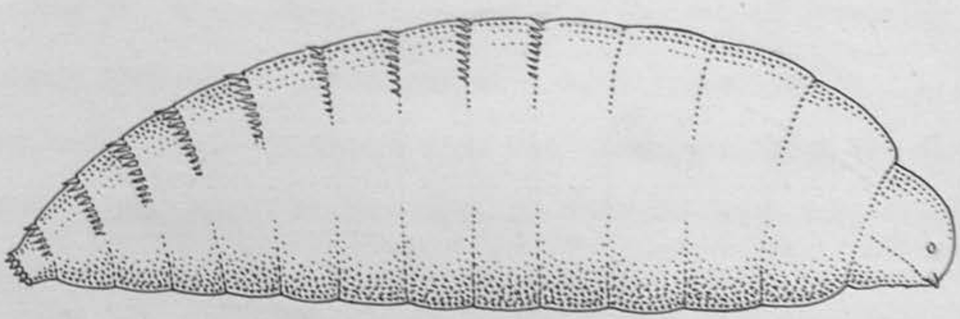


c.

FIGURE 6. Chrysocharis gemma, (a) egg (x 225); (b) head of first stage larva showing cephalic skeleton and mandibular muscles (x 1200); (c) first stage larva. Note spines on posterior segments. (x 350).

although they are not always regularly spaced in a row. On segments 8 - 12 inclusive, spines are present on the pleurae as well as on the dorsum, while the last segment, which is truncated is characterized by a circular ring of strong spines on its posterior margin. On one occasion a first instar larva of C. gamma was observed through the more or less transparent skin of its host, to be moving along quite rapidly inside the body cavity of the latter. The method of propulsion involved the use of these spines - the truncated spiny thirteenth segment being placed against the tissues of the host and the body of the parasite by this means given a forward thrust. Perhaps some degree of discomfort experienced in the dissecting fluid caused the larva to move along in this manner, but at any rate the fact that it can move freely inside its host when necessary was clearly demonstrated. It seems, however, that the main function of the spines is connected with the act of effecting eclosion from the egg, a supposition which appears to be confirmed when one considers that they disappear after the first ecdysis. The layout of the cephalic skeleton (Fig. 6b), or system of chitinized rods situated round the mouth, is very similar to that of the mature larva, so that a detailed description of it here will be unnecessary.

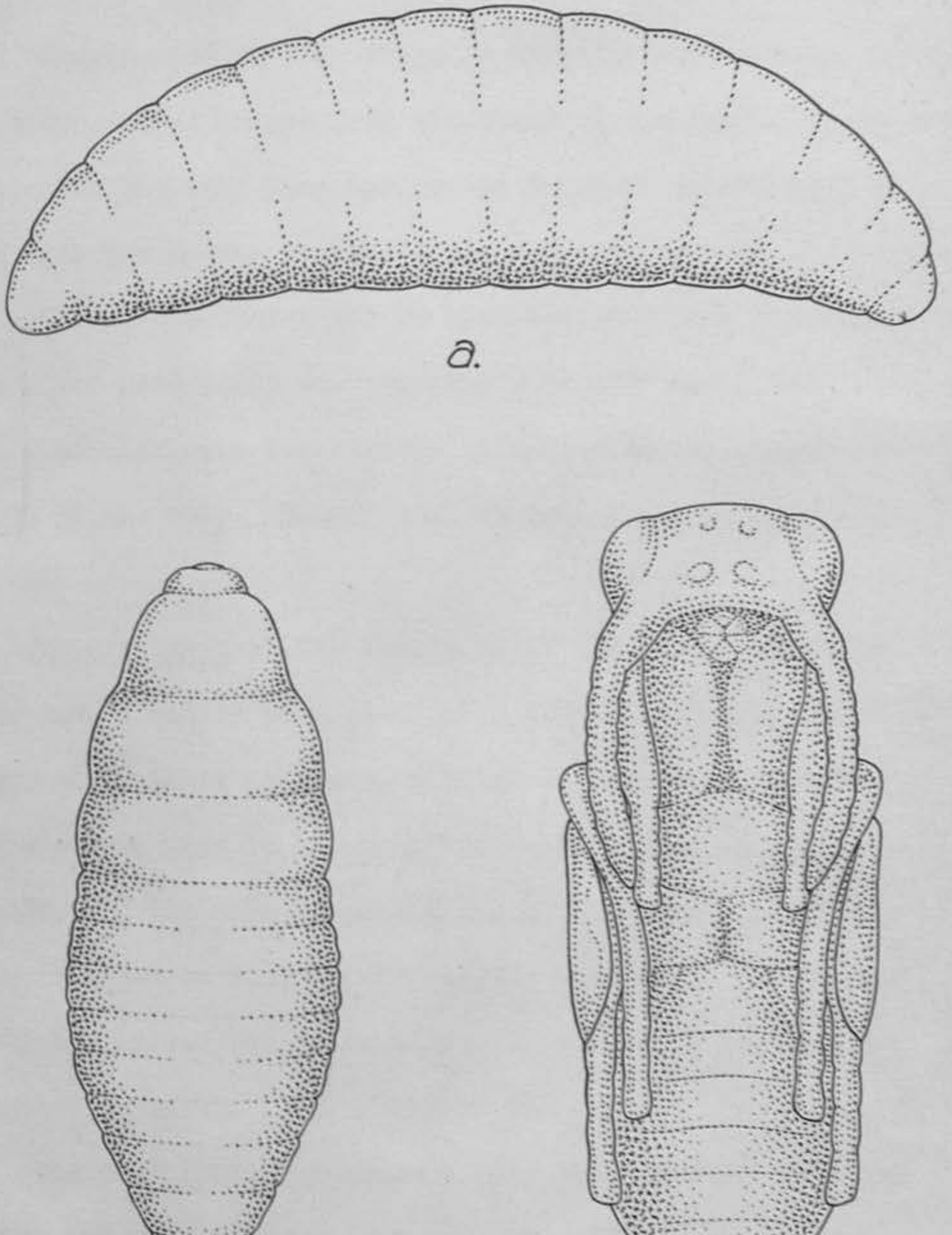


FIGURE 7. Chrysocharis gemma, (a) mature larva; (b) prepupa; (c) pupa.

(all x 67)

Respiration in this stage is effected cutaneously, that is by diffusion of oxygen from the blood of the host. There are no spiracles but very fine horizontal tracheal trunks partially filled with air may be traced in segments 2 - 7 or 8.

The second instar may be distinguished from the first by the wider head (.168 mm. compared with .105 mm.), the larger mandibles, and the absence of spines on the posterior segments of the body. Respiration in this stage is also apneustic.

Mature larva : The mature larva (Fig. 7a), like the primary one, consists of a head and thirteen body segments. It is somewhat fusiform in shape, whitish in colour, except for the dark faecal mass in the gut, which is visible through the body wall, and the skin is smooth and shiny. The larvae vary in size from 1.4 to 2.25 mm. in length, and .45 to .97 mm. in breadth, the larger larvae usually giving rise to females and the smaller to males.

The head is differentiated into three lobes, two upper or epicranial, and a lower median or labial lobe. Situated on the two former are a pair of antennae which measure 18 μ across at the base by 5 μ in height. The cephalic skeleton (Fig. 8) is rather characteristic, and in plan agrees very closely with

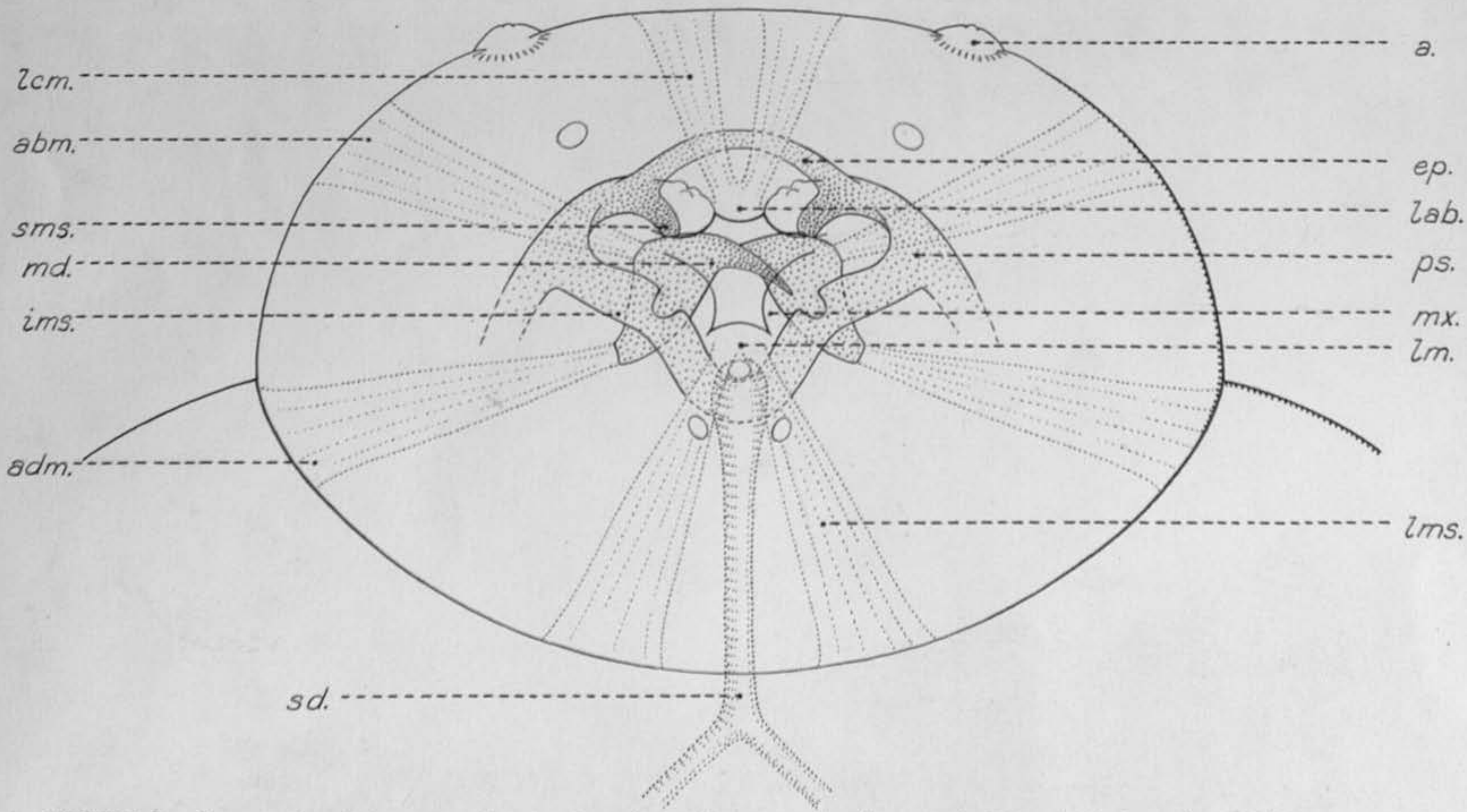


FIGURE 8. Chrysocharis gemma, head of mature larva, showing cephalic skeleton (x 600); a. antenna; ep. epistoma; lab. labrum; ps. pleurostoma; mx. maxilla; lm. labium; lms. labial muscles; lcm. labro-clypeal muscles; abm. abductor muscle of mandible; sms. superior mandibular strut; md. mandible; ims. inferior mandibular strut; adm. adductor muscle of mandible; sd. salivary duct.

that of the other internal Eulophid parasites of P. ilicis - C. syma and Pleurotropis amyntas. It is composed of the following parts :- a pair of inverted L-shaped mandibles, well chitinized at the tips; two superior mandibular struts, each of which afford articulation to one side of a mandible; the epistoma, a curved bar joining these two struts in the upper clypeal region, the pleurostoma consisting of two arms connecting the superior and inferior mandibular struts; the inferior mandibular struts, each of which provide an articulating socket for the condyles on the other side of the mandibles (these inferior struts are joined together in the labial region of the mouth so that the compound structure appears like a U-shaped rod); and a vestigial hypostoma arising from the juncture of the inferior mandibular strut and the pleurostoma. The large, well developed tentorium of the Pteromalids (Fig. 17, page 86), which is such a prominent feature of the head of the Pteromalid larvae, is absent from the mouthparts of the Eulophid parasites of the Holly Leaf-miner. In addition to the foregoing chitinized rods, a number of softer structures are also associated with the cephalic skeleton. These are - the clypeus and labrum above the mouth, a pair of maxillae one on each side of it, the median labium below it, and the common salivary duct formed by the union of two smaller ducts, which opens into it in the labial region. A number of papillae or sensoria are situated on the head in the following regions : above the epistoma, and rather widely separated from each other, one rather large pair; below the compound bar of the inferior mandibular struts in the sub-labial region and rather close together, a somewhat smaller pair, and two groups of three much smaller ones in the labial region. The main musculature of the cephalic skeleton (Fig. 8) is made up of one set of muscles for the clypeus and the labrum, another for the labium, and two groups for the mandibles. The latter consists of two abductors, or opening muscles, attached to the upper part of the mandibles in the region of the right-angled bend, and two adductors attached to the base of the mandibles and serving to close them.

The tracheal system (Fig. 9) in this stage is peripneustic. It consists of two longitudinal trunks joined by transverse commissures in segments one and eleven. From the anterior one, tracheoles are given off into the head region, and from the posterior, similar branches supply the last three segments. Spiracles are present on the anterior margins of segments 2 and 4 to 10, in all eight pairs. These are joined by short spiracular tracheae to the longitudinal trunks. From the junction of the spiracular tracheae and longitudinal trunks further tracheoles are emitted, which ramify in the various tissues of the body. The atrium of the spiracle is somewhat quadrangular in shape, but the corners are rounded. It varies in size, but its average measurements in the abdominal region are as follows : maximum breadth 11 μ, depth 7 μ, diameter of opening 4 μ. Those of the thorax are somewhat larger than those of the abdomen. All of these are characterized by a basal internal circle of short vertical rods (Fig. 9c). The spiracular trachea which joins the atrium on to the main tracheal trunk is composed of about 12 - 17 rings, a short length of simple tubing with no sign of valvular apparatus, and a further piece of trachea with only very faintly defined constrictions. In the absence of a definite valvular apparatus in the spiracular trachea, like that, for example, of _Sphegigaster_, it is quite possible that the basal circle of chitinized rods within the atrium acts as a closing device.

Prepupa : (Fig. 7b, page 40) At the end of the resting stage mentioned in the account of the biology of this parasite, the mature larva becomes demarcated into three distinct regions, the _head_, composed of the old larval head with mandibles and cephalic skeleton still clearly discernible, plus the first body segment, the thorax composed of segments 2 and 3, and the abdomen, made up of the 10 remaining segments. Although the prepupal stadium might be said to occupy the time from cessation of feeding until the actual formation of the pupa, it is not until these regions are demarcated that a definite prepupa can be identified. In this stage the faeces are voided so that the colour of the body becomes generally white.

Pupa : (Fig. 7c, page 40) When newly formed the pupa is pale yellowish-white in colour. Very soon it changes to a grey-black and some days later to a jet shiny black. The various parts are well differentiated, wing and leg rudiments, eyes, mouth appendages, as well as the thoracic and abdominal segmentation being clearly marked. No cocoon is formed and the pupa lies free inside the mine. It varies in size from 2.60 mm. in length by 1.04 mm. in breadth to 1.75 mm. by .65 mm. The imago emerges from the leaf by a small neat round hole, which latter coupled with the small mine, the absence of a puparium, and the conspicuous black cast pupal skin left behind, enables one to identify very readily, mines which have been occupied by this parasite.

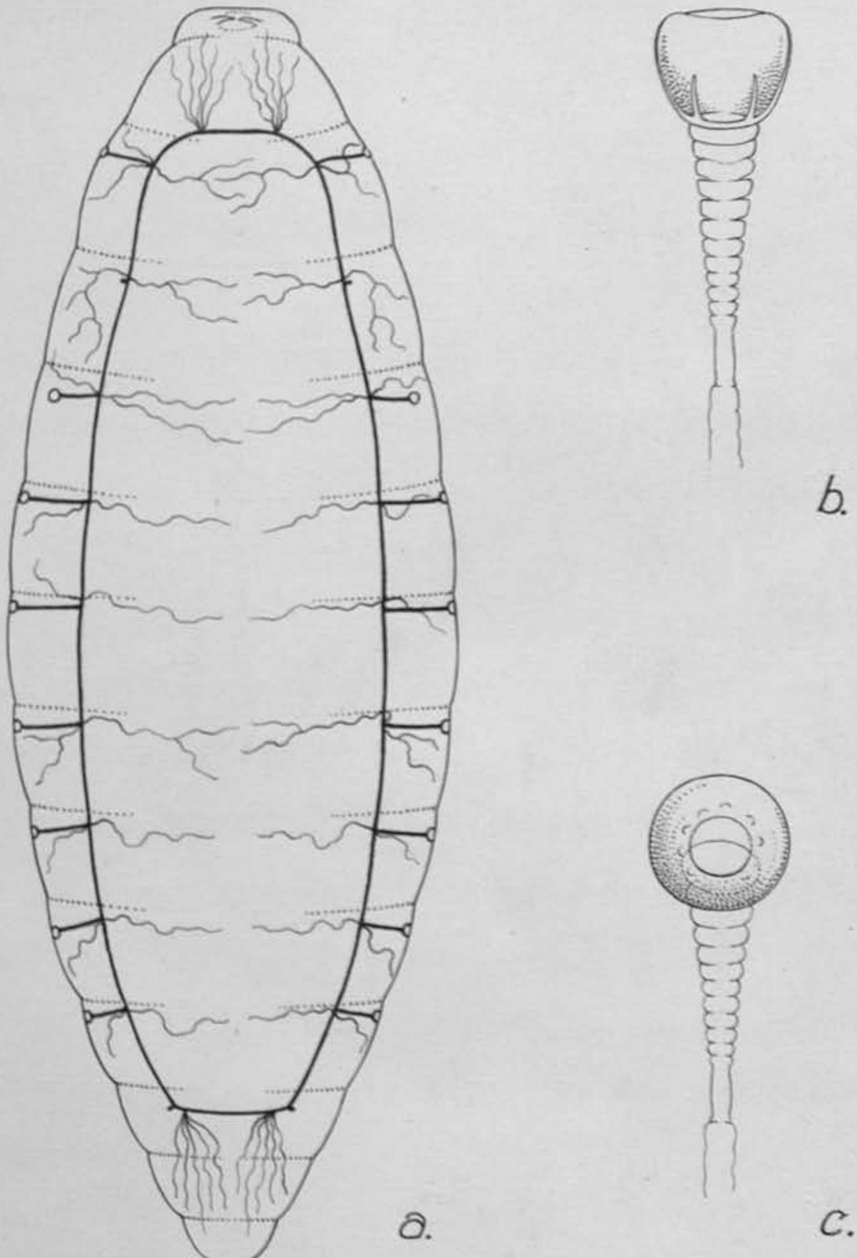


FIGURE 9. Chrysocharis gemma, (a) mature larva (somewhat flattened) showing tracheal system (x 67); (b) thoracic spiracle in side view; (c) Ditto from above.

((b) and (c) x 1600)

2. Chrysocharis syma, Walk.

C. syma, which is a parasite of the pupa, is the third most important parasite of the Holly Leaf-miner. It was found to be fairly well distributed throughout the holly areas kept under observation in the south-east of England. It was also reared from material collected in Inverness in the north of Scotland. The average parasitism for the year 1938, calculated on the total number of mines irrespective of the state of the host (i.e. whether in the larval or pupal stage), was about 5 per cent and the maximum 24 per cent (Kew Gardens). If the parasitism be calculated for the puparia only, these figures rise to 15 per cent and 28 per cent respectively.

It should be noted that the number of larvae which, after toll has been exacted by C. gemma and predatory birds, are left to pupate, has an important bearing on the percentage parasitism by pupal parasites. This point will be discussed in a subsequent section.

i. Systematic position and description of adult.

Like C. gemma, C. syma belongs to the Family EULOPHIDAE, so that the remarks on the genus Chrysocharis and the general systematics of that species will apply equally well here.

This parasite was formerly included in the genus Entedon and was called Entedon syma, Walk.

Description of Adult

Average length : Female 1.95 mm., male 1.65 mm.

General colour : Female metallic green with dark bronze areas, especially scutellum and part of abdomen; male dark bronzy green.

Head : Bronzy green (bronze more marked in male), reticulated, somewhat shiny, eyes large, brown, slightly pubescent, number of bristles present on head, especially on the occiput; three dark amber coloured ocelli on vertex.

Antennae : Inserted low down on face, black, flagellum hairy, the hairs in the male longer than in the female; the arrangement of adpressed spines, sensory papillae, and the last joint prolonged into a proboscis, is similar to that in C. gemma, already described.

Thorax : Metallic green in female, dark bronzy green in male, coarsely reticulated, shiny, a number of strong backwardly projecting bristles on dorsum, notauli well marked, parapsidal furrows wide, propodeon with central sculpturing and one pair of spiracles.

Wings : Both fore and hind wings strongly haired except for small clear area at base, front wing of female not infuscated as in C. gemma, marginal nervure much longer than the sub-costal, post-marginal slightly longer than radius, tegulae black.

Legs : Coxae black, with green tinge, trochanter of middle legs markedly pale, femora black except for small part of distal end which is pale, tibiae pale straw-coloured, tarsi mostly light brown.

Abdomen : Green, except for segments 2, 3, and 4 bronze green, and sub-oval in shape in the female; first segment mostly green, remainder bronze coloured and somewhat broadly pear-shaped in the male, hairy, shiny; petiole black, short, somewhat wrinkled.

The sexual dimorphism may be tabulated as follows :

Characteristics.	Male.	Female.
Average length.	1.65 mm.	1.95 mm.
Antennae.	Very plumose, hairs on flagellum about .055mm. long.	Much fewer and shorter hairs, about .032 mm. in length.
Colour.	Bronze coloured except for part of first segment of abdomen.	Green, except for segments 2, 3, and 4 of abdomen.
Abdomen.	Broadly pear-shaped.	Oval, ovipositor visible ventrally.

ii. Distribution and Host Records.

As already stated, the genus Chrysocharis has an exceedingly wide distribution, but C. syma itself is only recorded from England, Scotland, and France. The only previous host record is that of the present writer (1935), who reared it from Phytomyza atricornis, Mg., a leaf-miner on Senecio Jacobaea. I understand that an associate of mine, Mr. F. Wilson, has also bred it from the same host on Lepidium draba and from a leaf-miner on Echium sp., both in the South of France. De Gaulle (1908) also records it from Phytomyza geniculata, but does not give the host plant, although this leaf-miner is known to attack both Senecio Jacobaea and Sonchus sp.

iii. General Biology of C. syma.

The general biology of this species, when allowance has been made for the fact that it is a parasite of the pupa, is very similar to that of C. gamma. Eggs are laid internally in the puparia during April, and these hatch in from three to four days, according to the temperature. The development of the larva is on the same lines as its cogener. The prepupal stage lasts for one and a half days and the pupal for nineteen days. Adults emerge from the middle of June onwards, emergence generally being complete by the middle of July. Females are present in excess of males (144 females and 71 males obtained from samples in 1938), so the sex ratio is equal to .5. The preliminary courtship described in the account of the preceding species, C. gemma, is carried out in the same way by this species. One point worthy of notice in connection with both C. gemma and C. syma is the way in which individuals of these species jump and hop about like fleas or plant lice, when they are approached or interfered with in any way.

iv. Detailed Description of Developmental Stages.

The Egg : The egg is of a glassy white colour and is almost identical in shape and appearance with that of C. gemma. It measures .28 mm. in length by .08 mm. in maximum breadth.

First Stage Larva : This instar is also very like that of C. gemma, in fact the two are so similar that it is extremely difficult to distinguish one from the other. Their relationship to the host, C. syma being a pupal parasite and C. gemma a parasite of the larva, provides the best clue to identification. Externally the larvae present the same general appearance, both being characterized by the posterior body spines described for C. gemma, and the only morphological difference that could be discerned, was the trifling one, that the pair of long thin spines on the sub-labial region are much more distinct in the first stage larva of syma than they are in that of gemma. Incidentally the first instar of Pleurotropis amyntas, the third endoparasite of _P_. _ilicis_, is also characterized by posterior body spines and this is the only species with which _C_. _syma_ is likely to be confused, but there are quite striking differences, especially in the head region, which can be used for differentiating between them. These will be dealt with in the section assigned to _Pleurotropis_.

Mature larva : The fully grown larva (Fig. 10a) is rather fat, rotund, somewhat fusiform in shape, and measures about 2.14 mm. in length by .97 mm. in maximum breadth. It is shiny, smooth, and greyish white in colour with a central mass of black faeces and a large number of fat globules showing through the semi-transparent skin.

This instar can be distinguished from the corresponding stage in the other pupal parasites with the exception of _Pleurotropis_, by its inconspicuous antennae, its greater rotundity, by the way in which the black bristles of the host usually adhere to it, and by the untidy condition of the puparium, which it inhabits. If it is examined more closely and under greater magnification it will be seen that the cephalic skeleton (like that of _C_. _gemma_ and _Pleurotropis amyntas_) is devoid of a tentorium, which is such a strong feature of the larvae of the Pteromalids _Sphegigaster_ and

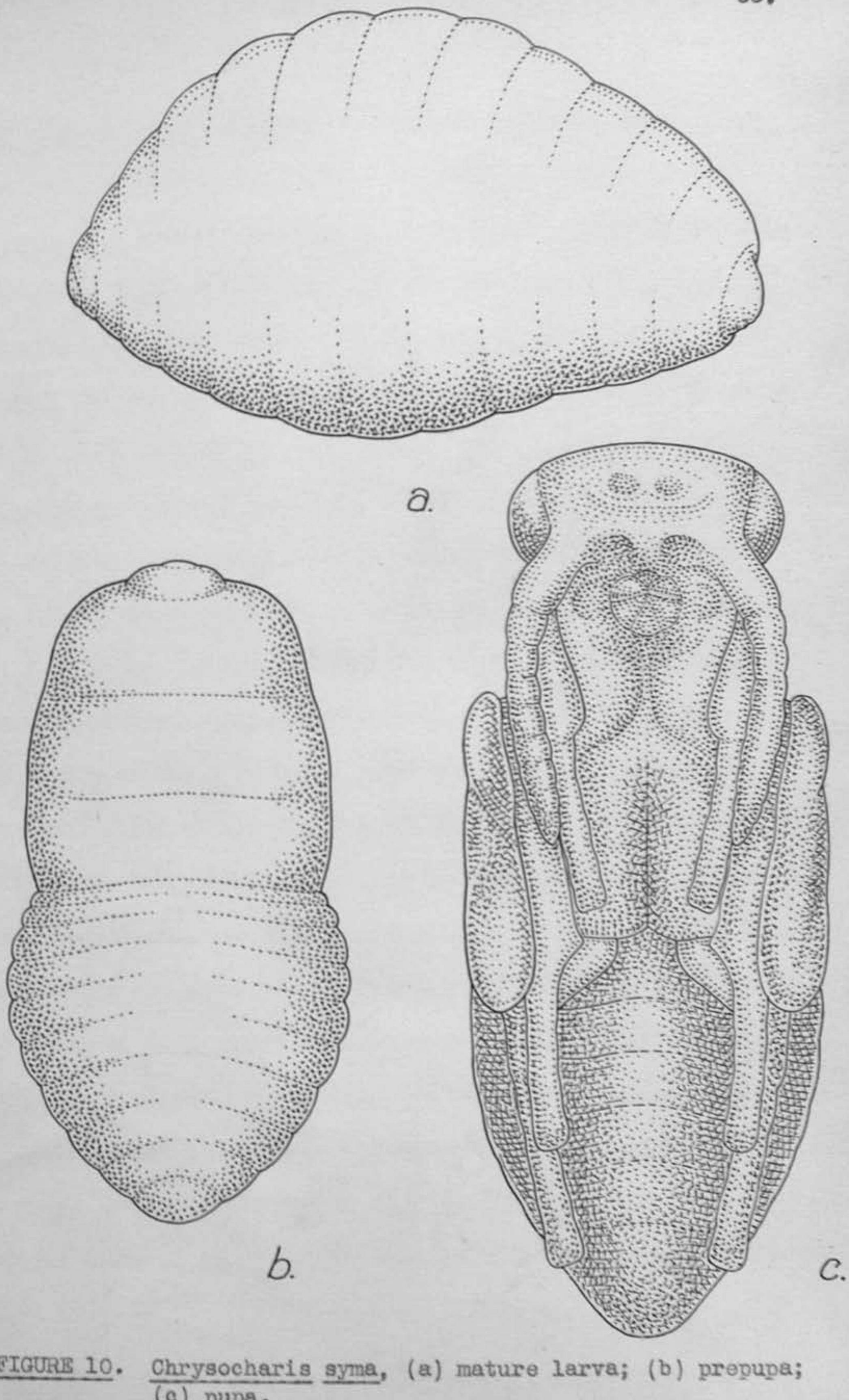


FIGURE 10. Chrysocharis syma, (a) mature larva; (b) prepupa; (c) pupa.

(all x 67)

Cyrtogaster. The spiracles in the two groups are also quite distinct. In the endoparasitic Eulophids, of which group *C. syma* is a member, the atrium is small and somewhat quadrate (Fig. 11b, page 58), whereas in the Pteromalids it is large and oval (Fig. 18b, page 88). The rings below the atrium in *C. syma* and the other members of its group are small and there are at least 10 - 17 of them, whereas in *Sphegigaster* and *Cyrtogaster* they are large and few in number, not more than 3 - 6. The conspicuous valvular apparatus in the spiracular trachea of the Pteromalids is absent from *C. syma*, *C. gemma*, and *P. amyntas*. Although it is relatively easy with these characteristics to separate the mature larva of *C. syma* from the larvae of the Pteromalid parasites of the puparium, it is much more difficult to distinguish it from that of its relative *P. amyntas*, but there are certain differences which, though small, are useful for this purpose. For example, the two large papillae in the pleurostomal region are circular in outline in the larva of *C. syma*, whereas in that of *Pleurotropis* they are in the form of vertical ellipsoids. The hypostoma is also somewhat longer and more conspicuous in *Pleurotropis* than in *C. syma*. Again the larvae of *C. syma* are all primary in habit whereas those of *Pleurotropis* are, for the most part, secondary parasites and remains of the primary host can usually be found beside them. The majority of the larvae of the latter species also overwinter in the larval stage within the host puparium and no other parasite of the Holly Leaf-miner has this habit. These overwintering larvae, being hyperparasitic, are usually much smaller in size than the larvae of C. syma (2.14 mm. in length as compared with 1.5 mm.).

The tracheal system of C. syma (Fig. 11a) is composed of two longitudinal trunks which are fairly wide apart in the abdomen and converge somewhat in the thoracic region. These trunks extend from segment one to ten and are joined together in each of these two segments by a transverse commissure. The ramification of tracheae and tracheoles throughout the body is similar to that of C. gamma. In this species, however, there are seven pairs of spiracles, one pair less than in the latter. These are situated on the anterior margin of segments 2 and 5 - 10. The spiracles (Fig. 11b) are small and similar in most respects to those of the other Eulophids. Those on the thoracic region are somewhat larger than those on the abdomen, the measurements being as follows :

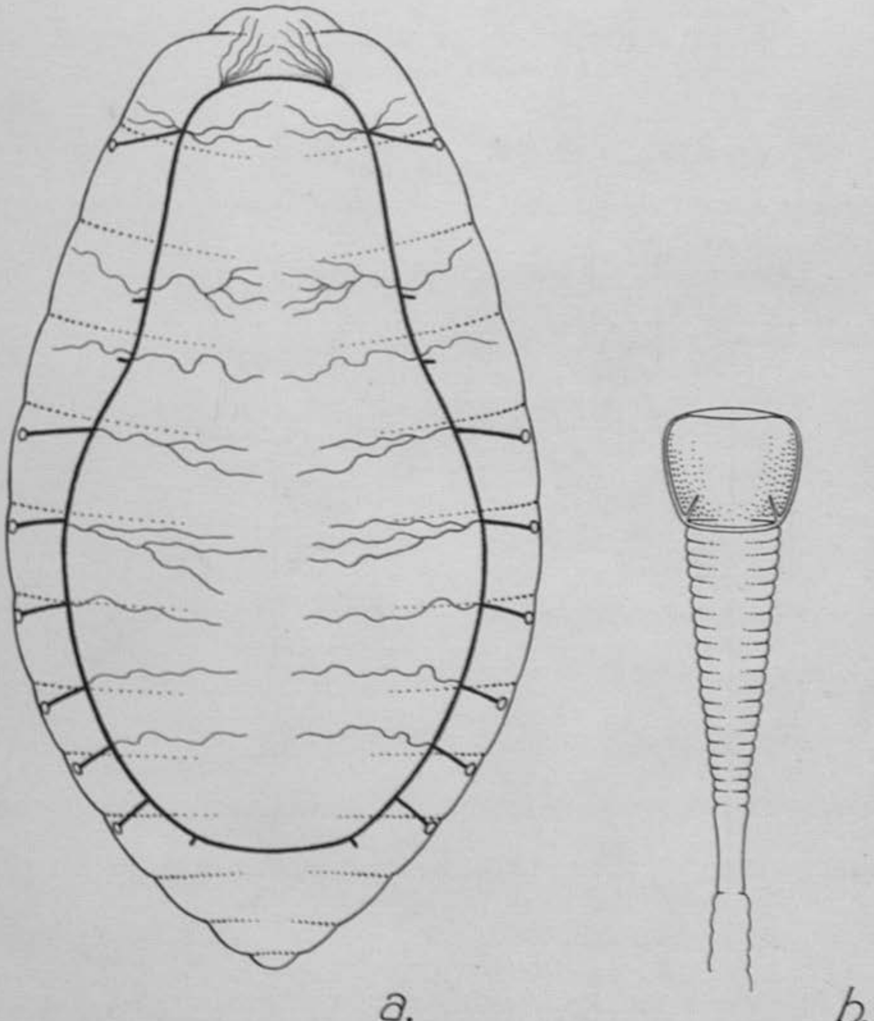


FIGURE 11. *Chrysocharis syma*, (a) mature larva (somewhat flattened) showing tracheal system (x 67); (b) thoracic spiracle in side view (x 1600).

	Thoracic.	Abdominal.
Breadth of atrium	13 - 14 µ	10 µ
Depth of atrium	9 µ	7.2 µ
Diameter of aperture	5 - 6 µ	4 - 5 µ

Prepupa : (Fig. 10b) This stage in C. syma is very distinct. Like the mature larva it is characterized by great rotundity, but the most distinctive feature is the thorax, which with the head region (larval head and first body segment) occupies the anterior half of the body. These thoracic segments, which are very broad, smooth, shiny, and greatly distended, form a strong contrast to those of the prepupa of the Pteromalids, like, for instance, Sphegigaster (Fig. 16b, page 84), where the segments of this region are narrow and more contracted, with deeply rounded sides. The more bulbous abdomen of C. syma, constituting the posterior half of the body and made up of the remaining ten segments, is also characteristic of this species. In colour the prepupa is yellowish and when newly formed it (female) measures 2.2 mm. in length by .84 mm. in breadth, but before entering the pupal stage it contracts so that its final measurements are 1.7 mm. by .8 mm.

Pupa : (Fig. 10c) At first the pupa is greyish-black in colour, but one day after pupation, it becomes quite black and shiny. It can be distinguished from the pupae of the other pupal parasites of P. ilicis by the bow-like shape of the body from the wing angle to the posterior segment of the abdomen. In the case of the Pteromalid pupae, the outer edge of the abdomen instead of being continuous with the wing margin, as in C. syma, curves inwards underneath it. There is also a difference in the way in which the antennae are attached to the head. In C. syma, C. gemma and , to a lesser extent, in Pleurotropis amyntas, the basal part of the antenna is more or less undifferentiated and is attached to the head just below the eyes, whereas in Sphegigaster and Cyrtogaster this part is well segmented and its point of attachment is near the mid-ventral line.

3. Pleurotropis amyntas, Walk.

This species was found in the majority of areas where collections of mined leaves were made in South-east England, but its average parasitism was low, usually never exceeding 1.5 per cent, calculated on the total number of mines, or 5 - 8 per cent on the number of pupae. The maximum figure recorded was 10 per cent at Cadnam, Hants, in 1938. P. amyntas is somewhat remarkable on account of its method of hibernating, the winter being passed in the mature larval stage within the host puparium, a habit shared by none of the other parasites of P. ilicis, and one that can be explained only on the ground of its hyperparasitic tendencies. As a result of a large number of dissections, and also of a certain amount of rearing work, it was definitely established that this species could act in the dual rôle of a primary parasite on the pupae of the holly fly itself, and of a secondary on the other pupal parasites of this host, such as Sphegigaster flavicornis and Chrysocharis syma, etc. When acting as a primary, development went forward in the normal way and adults emerged, along with those of the other primary parasites, in July. Apparently these adults then proceeded to parasitize the pupae of other parasites which were present in the puparia at that time, the resulting hyperparasitic larvae being found in August and throughout the winter.

i. Systematic Position and Description of Adult.

P. amyntas belongs to the Family EULOPHIDAE, Tribe

Entedonini, and sub-tribe Entedonina. The latter can be distinguished from the other sub-tribes of the Entedonini by the four-jointed tarsi, petiolate abdomen, and the complete parapsidal furrows.

The genus Pleurotropis was erected by Förster in 1856. In Ashmead's (1904) key it separates off from the remaining fifteen genera of the Entedonina by the following characters : scutellum without lateral or median longitudinal grooved lines; antennae ten-jointed with one ring joint; metathorax with lateral carinae, latter usually forked at apex; abdomen of female ovate, the first segment occupying about one third of the abdominal area; of the male, short oval, second segment occupying nearly half area of abdomen, the following segments after the third very short.

Schmiedeknecht (1909) catalogued fourteen species of Pleurotropis but since then at least 29 more, either new or transferred from other genera, have been added to the list, thus making the total number of known species up to 43.

This parasite was formerly included in the genus Entedon and was known as Entedon amyntas, Walk.

Description of Adult.

Average length : Female 1.95 mm., male 1.63 mm.

General colour : Female dark-, male light-steely blue.

Head : Head of female chiefly black in colour except for orbital margin which is broadly blue; of male brilliant metallic blue; shiny, reticulated, somewhat bristly, eyes large, pale brown in female, dark brown in male, three prominent dorsal ocelli.

Thorax : Dark blue in female, blue-black in male, shiny, strongly reticulated, somewhat bristly, parapsidal furrows deep, notauli faint, propodeon very characteristic, light metallic green in female, light blue with purple tinge in male, smooth, shiny, strong fielding present, consisting of two central crescent-shaped carinae, which are close together at the anterior end, and diverge posteriorly to join with a pair of lateral carinae, thus forming two D-shaped areas. Outside the lateral carinae, one on each side, is a pair of spiracles, while at the posterior corner of the propodeon there is a large projecting tooth.

Wings : Both pairs unclouded, uniform covering of fine hairs on surface of wings except for small clear area at the base, marginal vein much longer than the sub-costa, post-marginal slightly longer than radius.

Legs : Mainly dark with slight bluish tinge except for tarsi of anterior legs which are light brown, tarsi of middle and hind legs light glassy colour except for the last tarsal joint which is brown.

Abdomen : Male only : petiole broad, moderate length, black, strongly reticulated, shiny, abdomen sub-oval, first segment very large almost half the size of the abdomen, steely blue in colour, the remaining five segments black with the posterior margins of some of the segments blue, abdomen shiny, first segment smooth and glabrous, remainder finely reticulated, hairy.

Antennae : Of male steely blue, of female dark blue with a strong greenish tinge, inserted well down on face, very hairy in both sexes but hairs in male much longer than in female.

The female is easily distinguished from the male by the pointed abdomen with ovipositor, the shorter antennal hairs, darker general colour, and slightly larger size.

ii. Distribution and Host Records.

The genus Pleurotropis is a cosmopolitan one, with a wide distribution in Europe, America, Africa, Asia, and

Australasia. P. amyntas itself is known only from Britain, and no previous host record can be found in the literature, so that the present record from P. ilicis may be regarded as new. A history of hyperparasitism in this genus is well known. From a review of the literature it is evident that certain species are primary in habit, while others appear to be secondary, although the former are in the majority. It is quite possible, however, that many of the species, like the present one, are quite capable of acting either in a primary or a secondary capacity. As a rule Pleurotropis finds its hosts among Lepidoptera, Diptera (mostly AGROMYZIDAE), Coleoptera, and Hymenoptera. When reported as secondary, the hosts are said to be either Chalcids or Braconids.

iii. General Biology of P. amyntas.

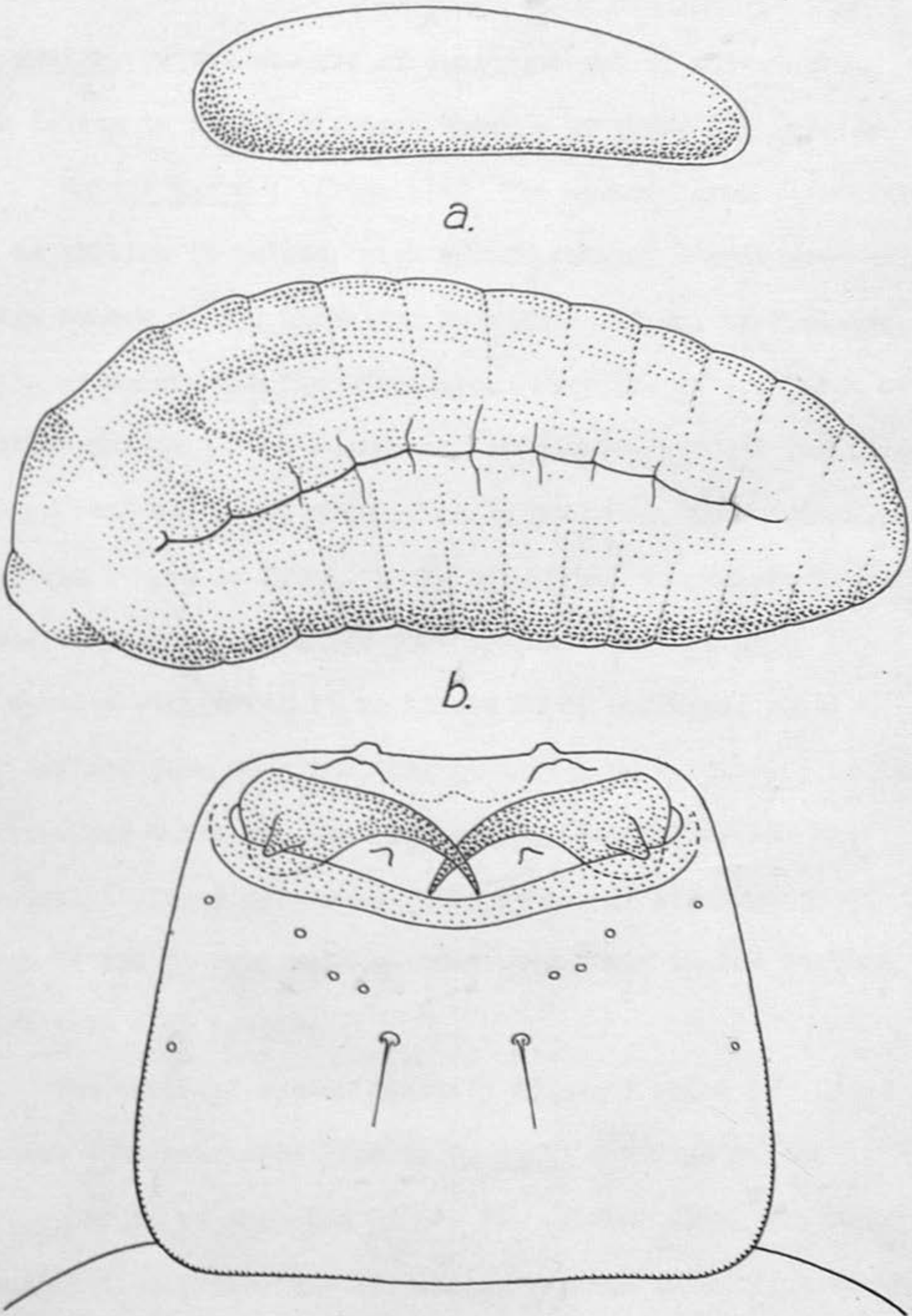
Adults emerge from overwintering larvae about the beginning of April (or towards the end of March in an early season like 1938). Mating was not observed to take place in the laboratory, but the preliminary courtship is similar to that of C. gemma and C. syma. Soon after emergence several females were placed in rearing jars with mined holly leaves containing puparia of P. ilicis. After four hours, puparia from one cage were opened, and one found to contain a second stage larva of Sphegigaster flavicornis, but no trace of eggs. This larva of Sphegigaster was then dissected and two eggs of Pleurotropis found floating freely inside (Fig. 12b). Later the same female laid directly in a puparium which had not previously been parasitized. For the most part adults which emerged from the overwintering larvae appear to give rise to a brood of larvae which are primary in habit. These latter emerge from their hosts during July and apparently proceed to parasitize further puparia of P. ilicis, which now contain only pupae of parasites such as Sphegigaster, C. syma, and Cyrtogaster (all flies having emerged or been destroyed by some agency or other before this date). The secondary larvae thus produced have been found in the puparia from August onwards and they are smaller in size than the primary ones. These hibernating larvae enter the prepupal stage about the middle of March. After two days in this stage they become pupae, and remain as such for at least fifteen days longer (at 70°F.).

The sex ratio is .66, or 60 females to 40 males.

iv. Detailed Description of Developmental Stages.

The Egg : The egg (Fig. 12a) is narrow, long and sub-reniform in shape and slightly longer than that of either *C. syma* or *C. gemma* (.33 mm. cf. .28 mm.). It is smooth, white in colour, and measures .33 mm. in length by .08 mm. in breadth.

First Stage Larva : The primary larva of *P. amyntas*, which when newly hatched measures .36 to .38 mm. in length by .09 in breadth, is very similar in many ways to that of either *C. gemma* or *C. syma*. It has the same fusiform shape, grey-white colour, and the last few abdominal segments are also characterized by backwardly projecting spines, but it can be distinguished from the first stage larva of the latter species by the more or less quadrate head and long, narrow, pointed mandibles (Fig. 12c), which are quite distinct from the smaller inverted, L-shaped ones of *C. gemma* and *C. syma*. The sub-labial spines are also much stronger and more distinct in this species than in either of the two latter. In addition to these there are a number of small papillae, about five pairs in all, situated in various positions on the skin of the face. This instar separates off from the corresponding one in the Pteromalids *Sphegigaster* and



a.

b.

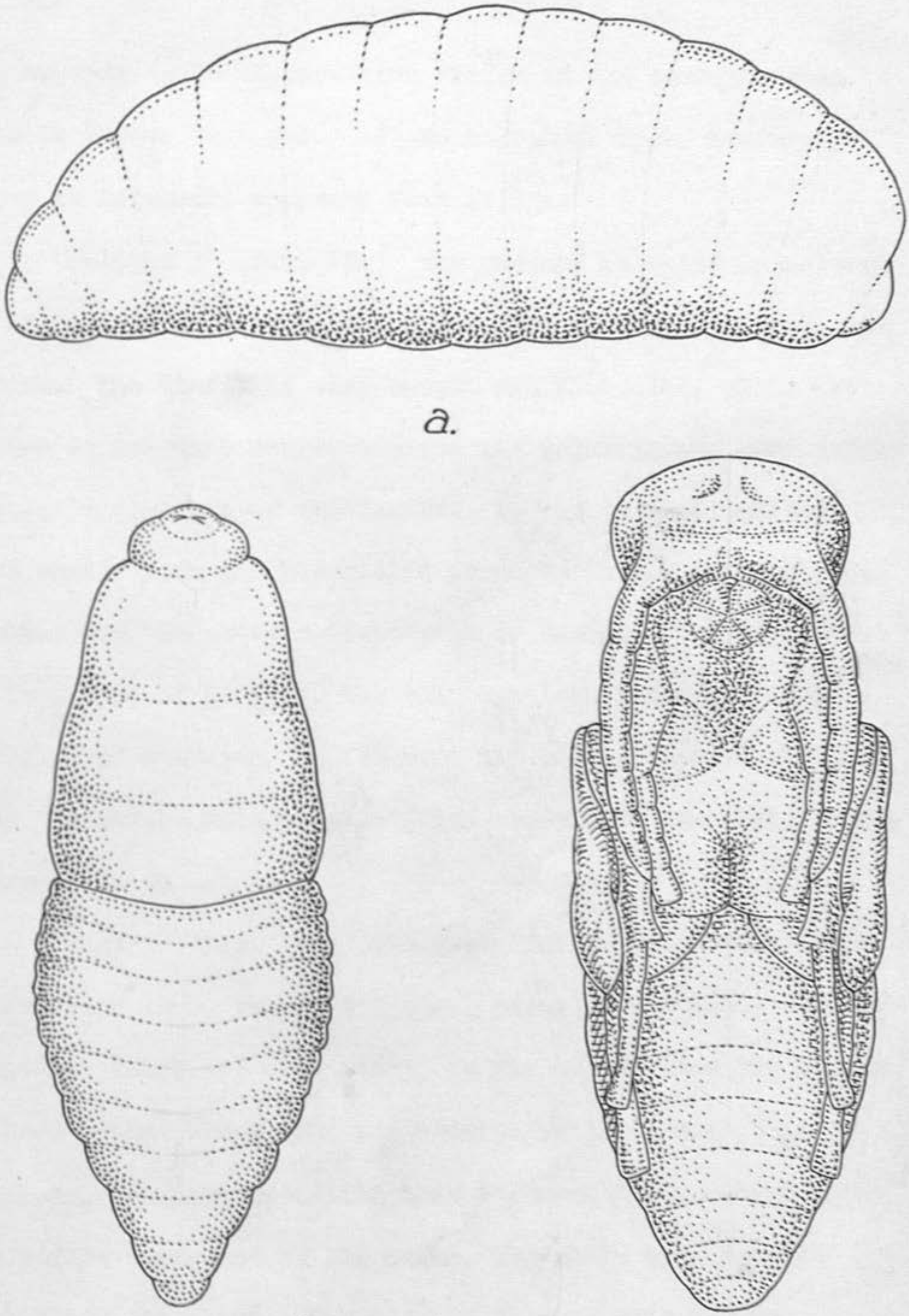
c.

FIGURE 12. Pleurotropis amyntas, (a) egg (x 225); (b) two eggs laid in first stage larva of Sphegigaster flavicornis (x 100); (c) head of first stage larva showing cephalic skeleton (x 900).

Cyrtogaster, by the absence of spiracles and of a tentorium, which latter is such a distinct feature of these two species.

Mature Larva : (Fig. 13a) The mature larva (overwintering) is whitish in colour, with a dark central faecal mass and a large number of fat globules, averaging .10 mm. in diameter, showing up underneath the epidermis. Like the mature larva of the other Eulophids, it is smooth, somewhat shiny and fusiform in shape, and measures, when normally extended, from 1.4 mm. to 2.1 mm. in length by from .51 mm. to .87 mm. in maximum breadth, the smaller larvae being the more common. Like C. syma, the only species with which it is likely to be confused, this stage differs from the remaining parasites of P. ilicis, by its inconspicuous antennae, the absence of a tentorium, and the small, multi-ringed spiracles. The points of difference between it and C. syma have already been given in the section dealing with that species.

The tracheal system consists of eight pairs of spiracles (one pair more than in C. syma) situated on the anterior margin of segments 2, 4 - 10. Number four, however, is usually incomplete, the spiracular trachea being very narrow and probably non-functional. There are ten to twelve rings on the spiracular trachea and a valvular apparatus in this



<u>FIGURE 13</u>. <u>Pleurotropis</u> <u>amyntas</u>, (a) mature larva; (b) Prepupa; (c) pupa.

(all x 67).

part appears to be absent. The atrium of the thoracic spiracles is larger than those of the abdominal ones, measuring 17.3 µ in diameter, compared with 12.9 µ.

Prepupa : (Fig. 13b) The prepupa is white in colour and is divided into the usual three regions, head, thorax, and abdomen. The thorax is very smooth and distended, while the abdomen is somewhat contracted and its segments are very narrow compared with those of the thorax. It can be distinguished quite easily from the Pteromalid prepupae by the inconspicuous antennae and the extreme distension of the anterior segments, and from that of <u>C. syma</u>, the only species with which it is likely to be confused, by its more tapering shape and smaller size. Length of male prepupa (from overwintering larva) 1 mm., maximum breadth .41 mm.

<u>Pupa</u> : (Fig. 13c) The newly formed pupa is mainly whitish in colour, except for small areas on the head, and the appendages which are dark grey. In one or two days the thorax and head become black, but the abdomen still remains whitish in colour, and continues like this for some days. About five days before emergence of the imago, the whole pupa becomes quite black and shiny. The pupa of <u>Pleurotropis</u> can be recognised by the way in which the antennae arise from the head -

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in the region of the eyes and not from the mid-ventral line as in the Pteromalids, its comparatively narrow abdomen as contrasted with the broad bow-shaped one of C. syma, and its small size, measuring 1.12 mm. to 1.53 mm. in length by .43 mm. to .56 mm. in maximum breadth.

4. Sphegigaster flavicornis, Walk.

As already stated, S. flavicornis is the second most important parasite of P. ilicis. It is also the most common and most generally distributed pupal parasite of this insect. The average parasitism for the year 1938, based on the number of mines present on the sample twigs, was about 8 per cent, and the maximum 27 per cent (Kew Gardens). If the percentage be calculated on the number of pupae present in the mines, these figures rise to 21 and 30 per cent respectively. S. flavicornis is primary in habit. Because it is the chief Pteromalid parasite of the Holly Leaf-miner, it has been made representative of this group, and is therefore treated in greater detail than Cyrtogaster vulgaris, the other member of this Family.

i. Systematic Position and Description of Adult.

S. flavicornis belongs to the Family PTEROMALIDAE, tribe Pteromalini, and sub-tribe Sphegigasterini.

In the Pteromalid genera there is only one apical spur on the hind tibiae, and this character separates the sub-family from the two-spurred Eulophids, the only other Chalcid group with which this paper deals. The Sphegigasterini can be recognised by the long and slender marginal vein of the forewing.

The genus *Sphegigaster* itself was erected by Spinola in 1811. From Ashmead's key it appears to be fairly easily separable from the remaining genera of this sub-tribe (with the exception of the closely allied *Trigonogastra*) by the petiole, which is longer than the hind coxae, and the second and third abdominal segments, which are very large, while the presence of a delicate cross furrow before the apex of the scutellum differentiates it from *Trigonogastra*. In *Cyrtogaster* (and the males of *Trigonogastra*), where the first and second abdominal segments are also very large, the petiole is not longer than the hindmost coxae.

Schmiedeknecht, in the "GENERA INSECTORUM" catalogues 59 species of *Sphegigaster* and a new species, *orobanchiae*, has recently been discovered in Russia, so that the total number known, up to date, is sixty.

The synonyms of S. flavicornis are as follows : Diplolepis pallicornis, Spin., Sphegigaster pallicornis, Spin., Merismus flavicornis, Walk., and Chrysolampus coronatus, Först.

Description of Adult. (Fig. 14)

Length : Average length of female 2.4 mm., of male 2. mm.

General Colour : Head and thorax of female black with very faint greenish tinge, of male green; abdomen polished bronze.

Head : Of female black with very faint greenish tinge, of male green; shiny, strongly reticulated; sparsely pubescent; eyes dark chestnut-red; three prominent ocelli on top of head.

Antennae : Inserted about middle of face or slightly below transverse mid-line; black and club-shaped in female, straw-coloured and filiform in male; both covered with whitish hairs which project away from the head; antennae divisible into scape - one very small and one long joint, pedicel - single jointed, then two small ring-like segments or anelli, and lastly the flagellum consisting of seven joints, the last being lightly sub-divided into three segments by two constrictions;

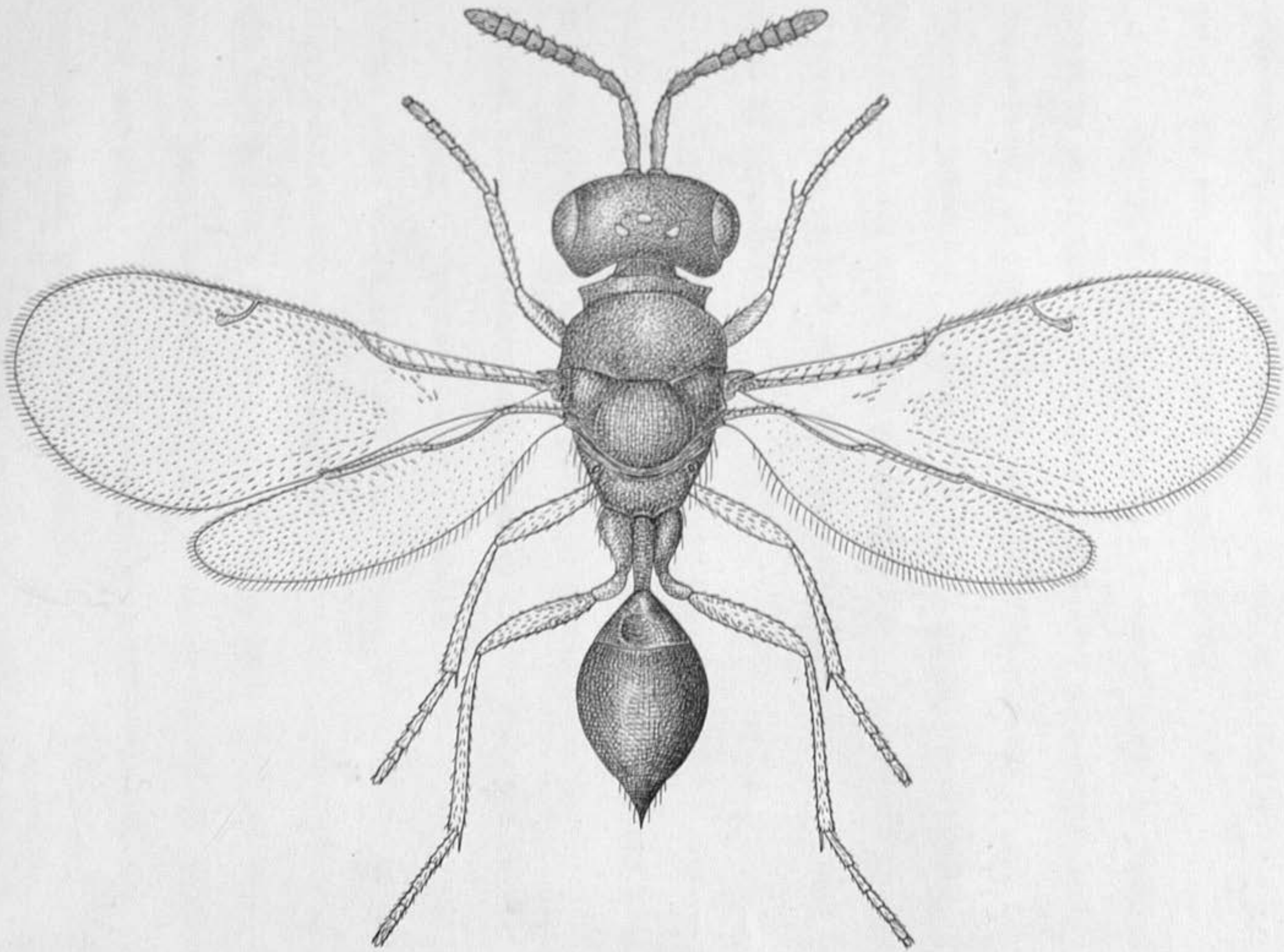


FIGURE 14. *Sphegigaster flavicornis*, adult female. (x 37)

flagellum characterized by a regular arrangement of strong adpressed spines which are longer in the male than in the female and are probably of a sensory nature.

Thorax : Black with slight greenish tinge in female, green in male; (prothorax of male with five anterior dorsal projections, of female two); strongly reticulated; shiny; sparsely pubescent; notauli very faint; propodeon strongly reticulated and black with greenish tinge; one pair of spiracles situated one on each side of antero-lateral angle of dorsal plate of propodeon.

Wings : Both pairs of wings unclouded except for uniform covering of hairs which are not present in clear area at base. Marginal nerve of forewing shorter than costa (costal area), post-marginal slightly longer than the radius.

Legs : General colour in female dark reddish-brown, except coxae which are black with a green tinge. Legs in male light reddish-brown, much lighter in female, coxae greenish, all tarsal joints of first pair of legs, last joint of middle and hind tarsi darkened (in a few specimens femora and tibiae also darkened). Tibiae of forelegs with one strong curved terminal spine, very long in male.

Abdomen : Strongly petiolate, petiole longer than hind coxae strongly but more finely reticulated than thorax, rest of abdomen in female fusiform, in male sub-oval and truncated; highly polished bronze, surface smooth, in female only three segments visible dorsally, the second being very large, slight depression at posterior end of segment one and anterior end of segment three, segment three pointed with number of backwardly projecting hairs on its surface; only two large segments and two very narrow ones visible dorsally in male, unless the remainder are extruded beyond the truncated end when two more can be seen.

The sexual dimorphism can be tabulated thus :

Characteristics.	Male.	Female.
Average length.	2 mm.	2.4 mm.
General colour.	Head and thorax green.	Head and thorax black with greenish tinge.
Antennae.	Filiform, straw-coloured.	Club-shaped, black.
Thorax.	Reticulation small.	Reticulation large.
Legs.	Light reddish brown.	Dark reddish brown.
Abdomen.	Small, sub-oval, truncated.	Large, fusiform.

ii. Distribution and Host Records.

This species was found to be fairly well distributed in the holly areas examined in the south-east of England, and although no previous host record could be found in the literature, it has previously been taken on several occasions. Its geographical range, according to Schmiedeknecht, is North and Central Europe.

From the few host records available, it appears that members of the genus Sphegigaster for the most part parasitize leaf-mining and stem-boring Diptera, also gall-making species of the Family CECIDOMYIIDAE, and a certain number attack Aphids.

iii. General Biology of S. flavicornis.

This parasite becomes active on the holly tree about the beginning of April, and oviposition by field collected females was quite common in the laboratory from the 14th to the 26th of this month. The act of oviposition, which involves a good deal of boring through the cuticle of the leaf and the tough skin of the puparium, occupies a relatively long time, at least half an hour, and the egg is deposited externally on the pupa of the host. Incubation lasts for a period of 4 - 7 days, after which a typical first stage larva - described in detail in the next section - makes its appearance, and proceeds to feed on its host from the outside. During the course of its larval life the skin is moulted four times, so that altogether there are five larval stadia. The larva is actively engaged in feeding for about eleven to thirteen days and then enters a resting period lasting a further four or five days before it changes to a definite prepupa. It remains in the prepupal and pupal stages for two and from five to six days respectively, before completing its metamorphosis and emerging as an imago about the middle of June. The peak of emergence is reached in the latter half of this month and a number of individuals do not reach the adult stage until the earlier part of July, while a few have been as late as the middle of August.

Males are slightly more numerous than females, but the sex ratio is almost equal to one (182 males to 161 females).

The mating, or at least the preliminary courtship of S. flavicornis is quite different to that of C. gemma and the other Eulophids. When the male senses the presence of the female he vibrates his antennae violently and sways his body from side to side for a few seconds before setting off in pursuit. On catching up with her he mounts quickly, taking up a position well forward, with the first and second pair of legs clasped round her thorax and the third pair placed over her abdomen. He then, with a quick up and down movement, caresses her antennae, which are held pointing downwards, with his own. This lasts for a few seconds, and if the female is not sufficiently stimulated to desire copulation, he jumps off and moves away. He repeats this performance several times until she becomes receptive, when she bends up her abdomen slightly - he moves back, and copulation, which lasts for about ten seconds, is ultimately effected.

iv. Detailed Description of Developmental Stages.

The Egg : (Fig. 15a) The egg is glassy white or hyaline in colour, and of a distinctive shape, - somewhat sub-reniform with a long tapering point at one end, and a narrow nipple at the other. It measures .34 mm. in length by .13 mm. in maximum breadth.

Primary Larva : This stage (Fig. 15b) consists of a

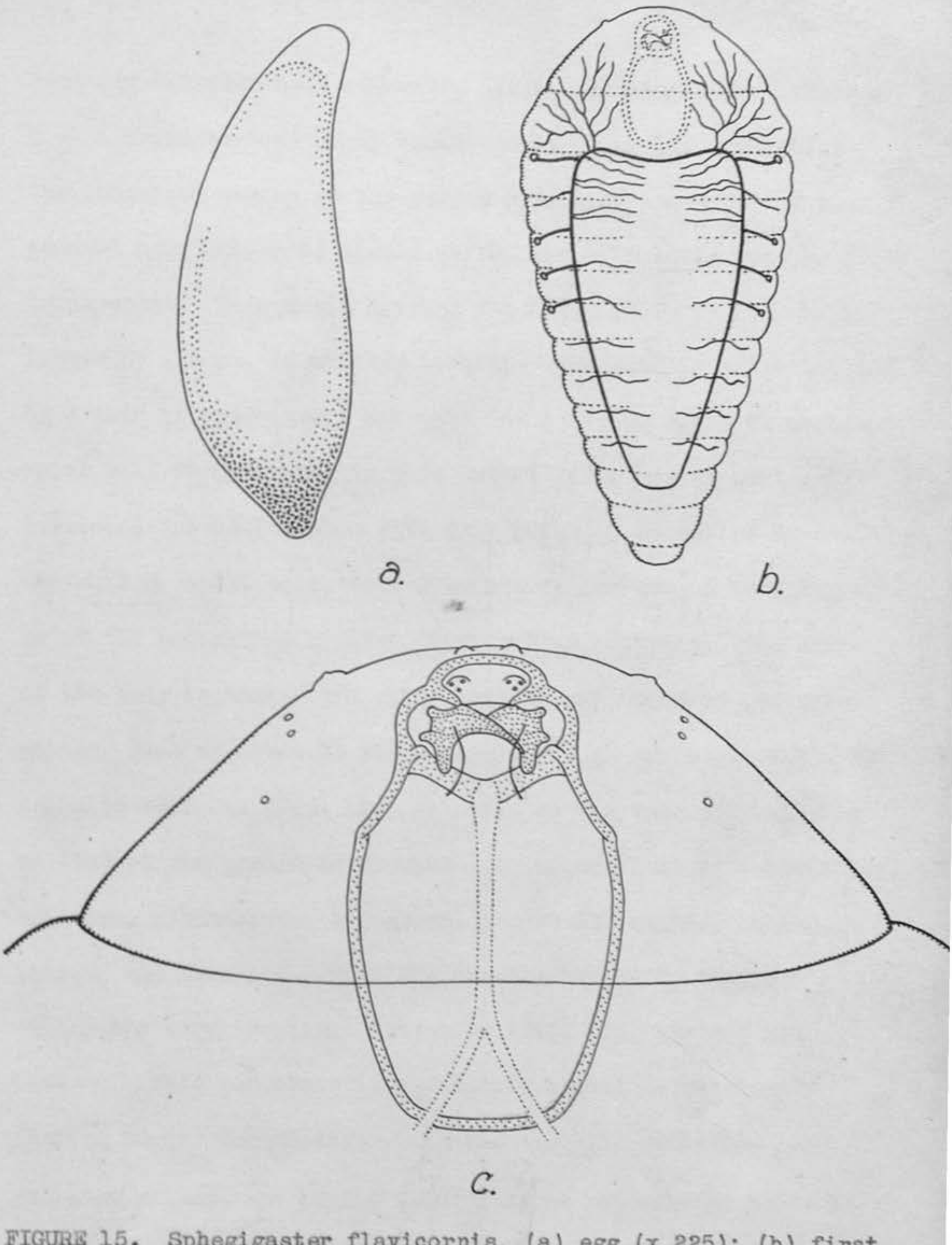


FIGURE 15. Sphegigaster flavicornis, (a) egg (x 225); (b) first stage larva showing tracheal system (x 225); (c) head of first stage larva showing cephalic skeleton (x 900).

head and thirteen body segments. It is somewhat carrot-shaped, with a hemispherical head, broad thorax, tapering throughout the abdominal region to the narrow posterior segment, and the general body colour is glassy white, the skin being more or less transparent. When newly hatched the larva measures .35 mm. in length by .13 mm. in maximum breadth. The head is characterized by a pair of conspicuous antennae and a strong cephalic skeleton, which will be described in more detail later on. A well developed tracheal system with four pairs of spiracles in segments 2, and 4 to 6, is a distinctive feature of this larva, as of the succeeding species, Cyrtogaster vulgaris. The skin of the body is smooth and shiny without any trace of posterior spines, such as occur in the Eulophids C. gemma, etc. The cephalic skeleton (Fig. 15c) is built on the same general plan as that of the preceding species - being complete with mandibles, epistoma, pleurostoma, hypostoma, mandibular struts, labium, labrum, and maxillae - with the notable exception that a strong and very prominent tentorium (Fig. 15c, ttm) is now present. This structure is presumably useful in externally feeding larvae for strengthening the cephalic skeleton. In prepared slides, and in the figure, it is necessarily shown on the same plane as the rest of the mouthparts, but actually, in the living larva, the long lower part from the bend (shown in the figure) projects into the head at right angles to the main skeleton. In addition to the system of rods and soft structures around the mouth, there are a number of papillae on the surface of the skin, notably a group of three on each side of the head below the antennae, a pair just above the epistoma, and a third lot of three smaller ones on each side of the labrum.

The primary larva of S. flavicornis, and also of Cyrtogaster vulgaris, the other Pteromalid parasite of P. ilicis, can be distinguished very readily from the corresponding instar in the Eulophids, by the conspicuous antennae, the strong tentorium and the tracheal system complete with four pairs of functional spiracles. The difference between this larva and that of Cyrtogaster is extremely slight and will be found in the description of the latter species.

Mature Larva : This stage is whitish in colour with a large brown internal faecal mass and fat globules showing through the semi-transparent skin. It is fat and flabby, and fusiform in shape, the cuticle being smooth and devoid of spines. When normally extended it measures from 2.1 - 2.3 mm. in length by .92 to .97 mm. in maximum breadth. The head is somewhat hemispherical in shape and is characterized by a pair

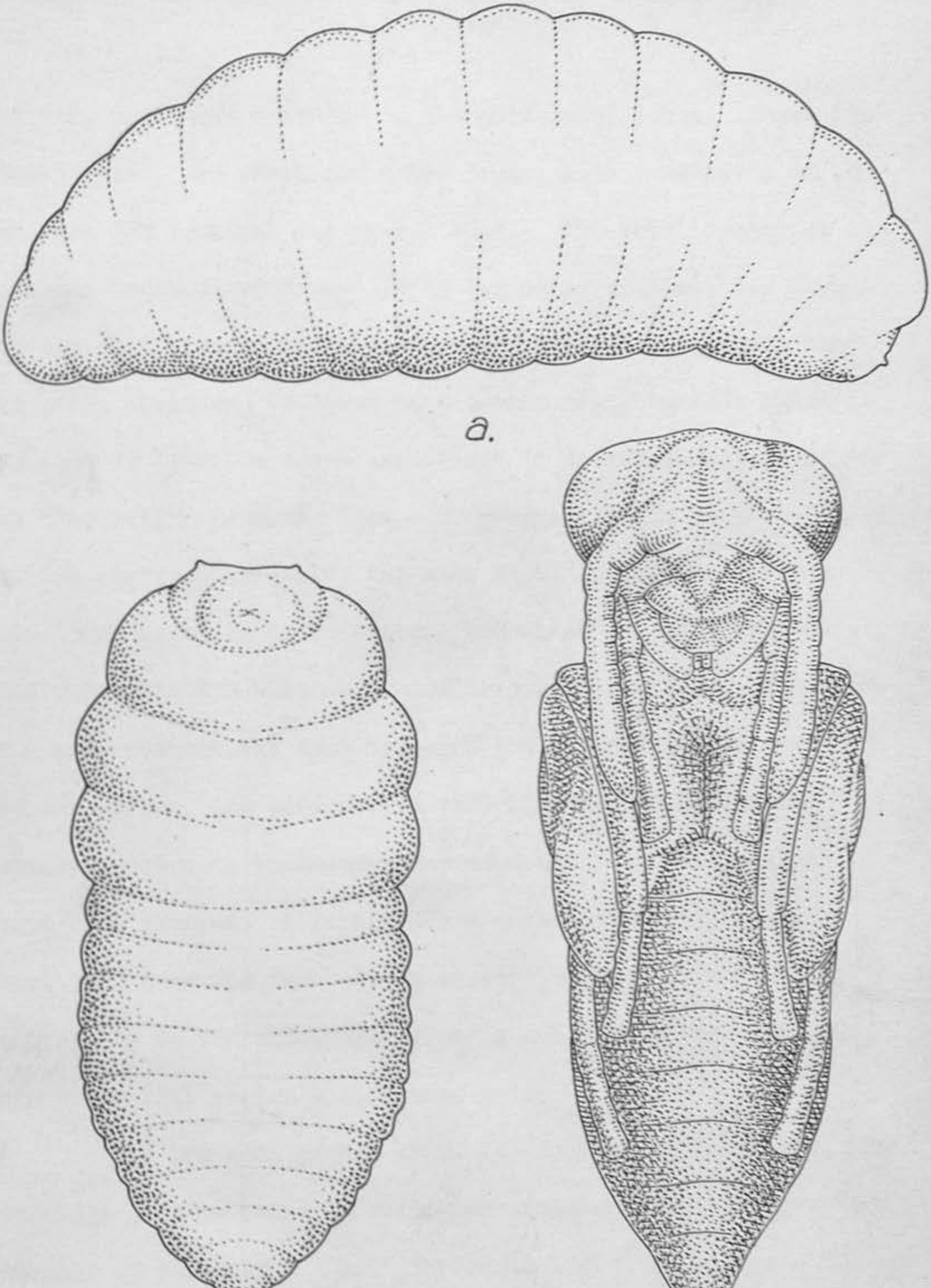


FIGURE 16. Sphegigaster flavicornis, (a) mature larva; (b) prepupa; (c) pupa.

(all x 67)

of very prominent antennae on the epicranial lobes. These are two-jointed, the basal one being large, with a diameter of .03 mm. and the terminal one rather small. The total length of the antenna is about .025 mm. As in the other species, the layout of the chitinized rods and associated structures forming the cephalic skeleton, is based on a common plan, so that there is no need to describe these structures in detail except in so far as they differ from the type - C. gemma. In the cephalic skeleton of Sphegigaster (Fig. 17) the most significant features are the large rectangular tentorium, described for the first stage, and the mandibles which are more triangular in shape, stronger and more workmanlike than those of the Eulophids. In contrast to the latter, the epistoma is very lightly chitinized and almost appears to be incomplete, especially in mounts which have been cleared. A fairly large number of papillae are scattered over the face of the mature larva of this species, especially in the sub-labial area (about twelve) and also in the epicranial region - one large pair.

The tracheal system (Fig. 18) is very well defined. It consists of nine pairs of spiracles situated near the anterior margins of segments 2 - 10. These are linked up with two longitudinal trunks which are joined by transverse commissures

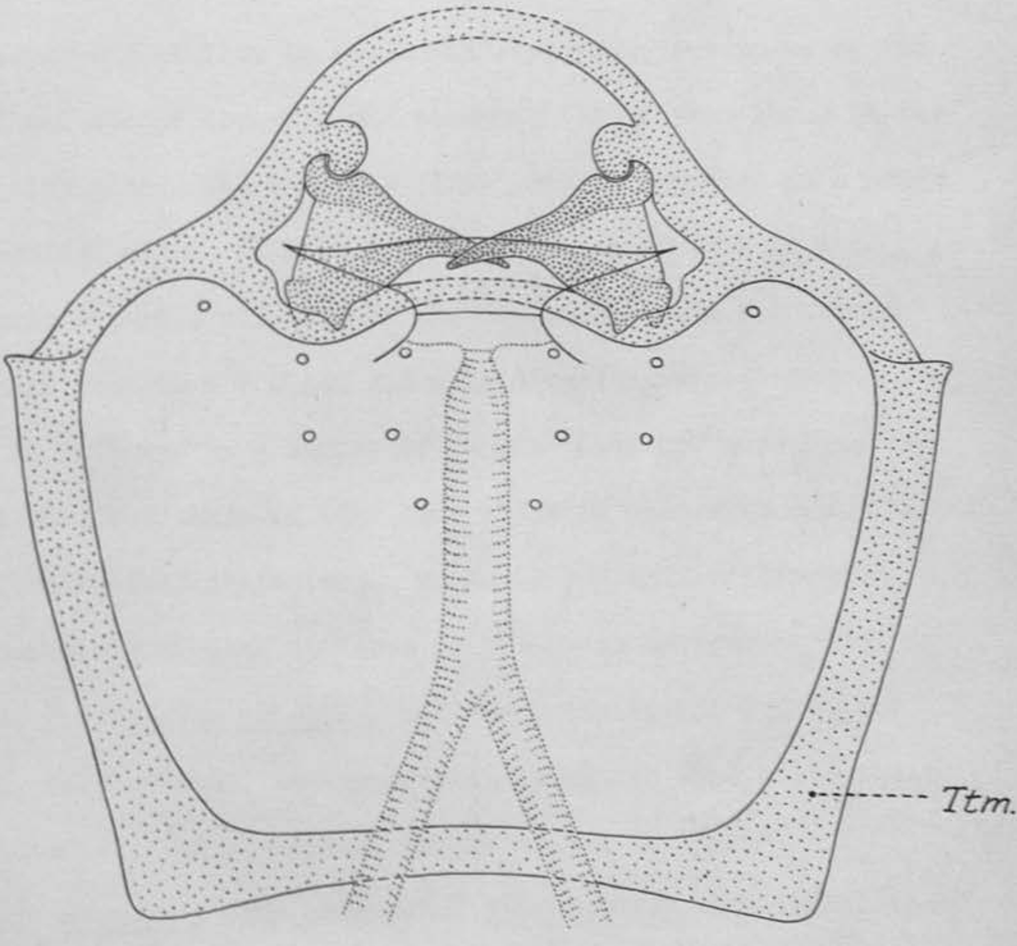


FIGURE 17. Sphegigaster flavicornis, cephalic skeleton of mature larva (x 520). ttm. tentorium.

in segments 2 and 11. From the main spiracular-longitudinal trunk junctions, ramifying tracheae and tracheoles carry a supply of air to the different organs of the body. All the spiracles are similar in shape and structure, but those on the first and second segments are somewhat larger than those on the remaining ones. The spiracle (Fig. 18b) is composed of a large ellipsoidal atrium with an average diameter of 23 µ in the thoracic segments and 19 µ in the abdominal, with a somewhat circular apperture 9 µ and 6.5 µ in diameter respectively. This is followed by a series of broad rings not more than six in number, and these in turn by a valvular tube with transverse and longitudinal striations. These large, well constructed spiracles are similar to those of the other externally feeding larva, Cyrtogaster vulgaris, and are quite distinct from the small, multi-ringed, and apparently valveless type which are so characteristic of the mature larvae of the Eulophids.

Prepupa : The prepupa of Sphegigaster (Fig. 16b), when newly formed, is whitish in colour with a yellow tinge. This stage is characterized by the old larval head with its conspicuous antennae, which along with the first body segment will form the head of the pupa and eventually of the adult, the two thoracic segments, which are large and stand out sharply from

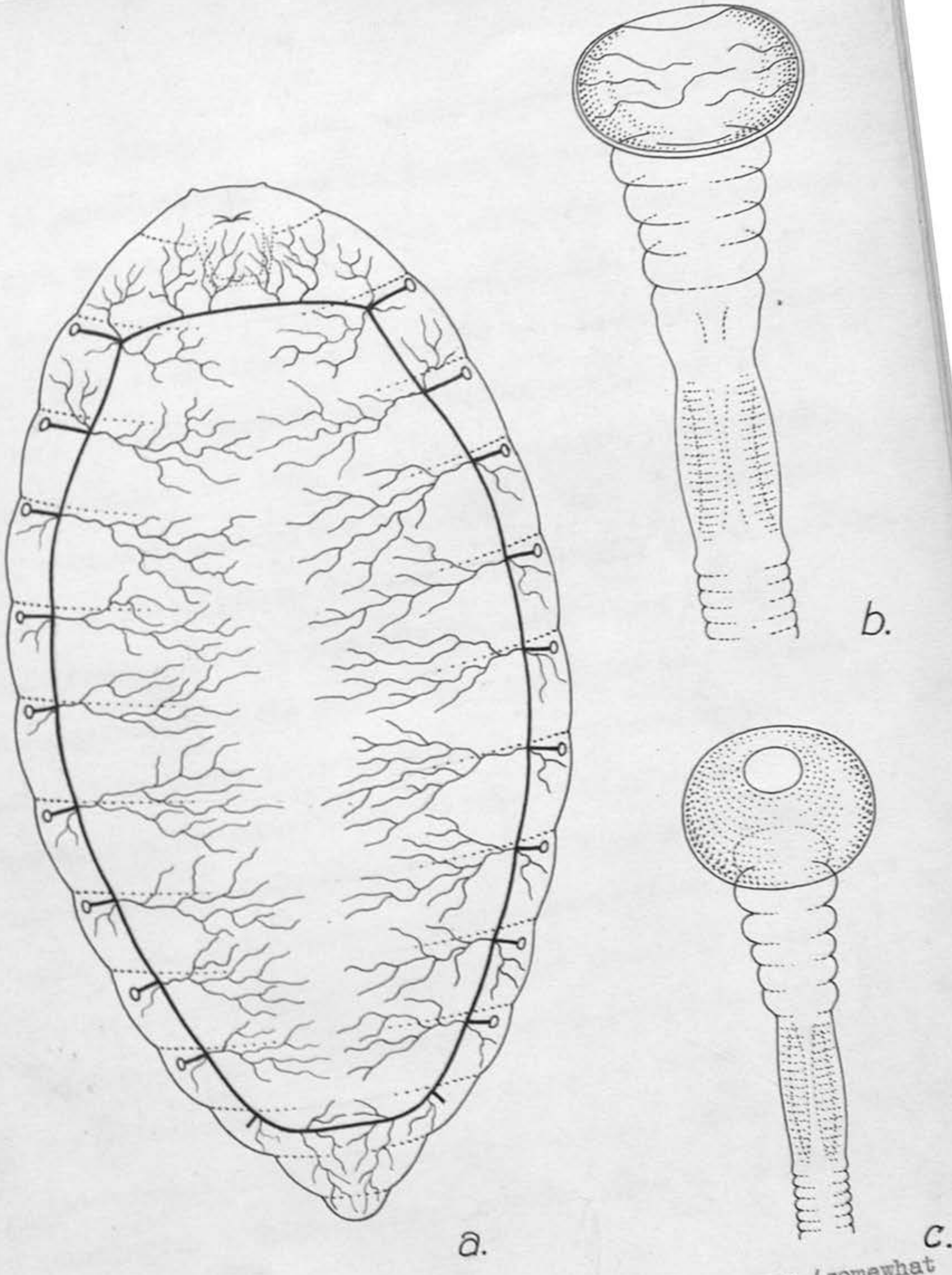


FIGURE 18. Sphegigaster flavicornis, mature larva (somewhat flattened) showing tracheal system (x 67); (b) thoracic spiracle in side view; (c) abdominal spiracle from above. ((b) and (c) x 1600)

each other by means of the well rounded pleurae, and the abdomen which is constricted off from the thorax and consists of the remaining ten segments of the mature larva. The prepupa measures 1.95 mm. in length by .73 mm. in maximum breadth.

Pupa : At first the pupa (Fig. 16c) is white in colour, but in a few days the main part, with the exception of the antennae, wings, and legs, which are of a light, glassy-brown hue, changes to black with a dull bluish tinge. The contrasting colour of the appendages and body gives a useful clue to the identification of this pupa. In the early stages it can be distinguished from the pupa of *Cyrtogaster*, the only one with which it is likely to be confused, by the absence of the black markings on the venter of the abdomen, such as occur in the latter species, while after it has become darker in colour the angle formed by the antennae enables one to distinguish it from the other member of this group. Fuller details of these differences will be given in the section devoted to *Cyrtogaster*. The general colour, as described above, and the way in which the antennae arise from near the mid-ventral line of the head enables one to distinguish it from the pupae of the Eulophids.

5. Cyrtogaster vulgaris, Walk.

C. vulgaris is the second Pteromalid and the fourth most important parasite of P. ilicis. Like S. flavicornis it attacks the host in the pupal stage. The average parasitism of this species in 1938 in places where it occurred, reckoned according to the total number of mines and thus including larvae and puparia, was .7 per cent, with a maximum of 6.7 per cent at Hedgerley, Bucks. If calculated on the number of puparia present in the mines, these figures rise to 3 and 13 per cent respectively. It was obtained from several, but not all the places examined, but this was probably due to the low parasitism and the samples not being very large.

i. Systematic Position and Description of Adult.

This species, like the preceding one, belongs to the sub-tribe Sphegigasterini, and the systematic notes on the latter will apply equally well here. It can be distinguished from S. flavicornis by the petiole, which in this case is shorter than the hind coxae, and by the colour of the legs which in Cyrtogaster are mainly black, while in Sphegigaster they are medium brown. The male of Cyrtogaster is also very easily identified by the globular distal end of the palpi.

According to Schmiedeknecht, C. vulgaris is synonymous with Dicormus aquisgranensis, Först., and possibly also with Chrysolampus tristis, Nees.

This species is so closely allied to S. flavicornis that the differences between them, as previously described, together with the systematic notes on Sphegigaster, will be sufficient for identification and a detailed account of the adult will therefore be unnecessary.

ii. Distribution and Host Records.

C. vulgaris has been taken both in Europe and in America, but only three host records can be found in the literature, one from France on Stilpnotia salicis, the White Satin Moth which attacks poplar and willow, a second from Germany on the dipterous fly, Oscinella frit, and a third, also from Germany, on the Braconid Coelinius niger. To these may now be added a fourth from England, on P. ilicis. Schmiedeknecht gives a list of fifteen species for this genus, most of which have been taken and named by Walker in Britain and a few by Ashmead in America.

In the Farnham House catalogue only six host records are listed. These are (1) C. glasgowi from Brachydeutera argentata (Ephydriid), (2) C. liqueatus from Phytomyza delphiniae (Agromyzid), (3) C. occidentalis from Cerodonta dorsalis (Agromyzid), all three from the U.S.A., and four, five and six, those mentioned previously for France and Germany. In view of the fact that five of these records (including my own) state Cyrtogaster to be a primary parasite on dipterous puparia, it seems doubtful if C. vulgaris actually did act as a hyperparasite in the case of Coelinius niger, although we must not altogether exclude this possibility.

iii. General Biology of C. vulgaris.

The life-history of this species is in most respects similar to that of S. flavicornis, so that an account here would mean unnecessary duplication. Two points of interest may, however, be mentioned, one that several females of C. vulgaris lived right through the winter in the laboratory and a new generation was reared from them in the following spring, and, two, that a remarkable characteristic of this species is its ability to feign death. This is so strong and real that,

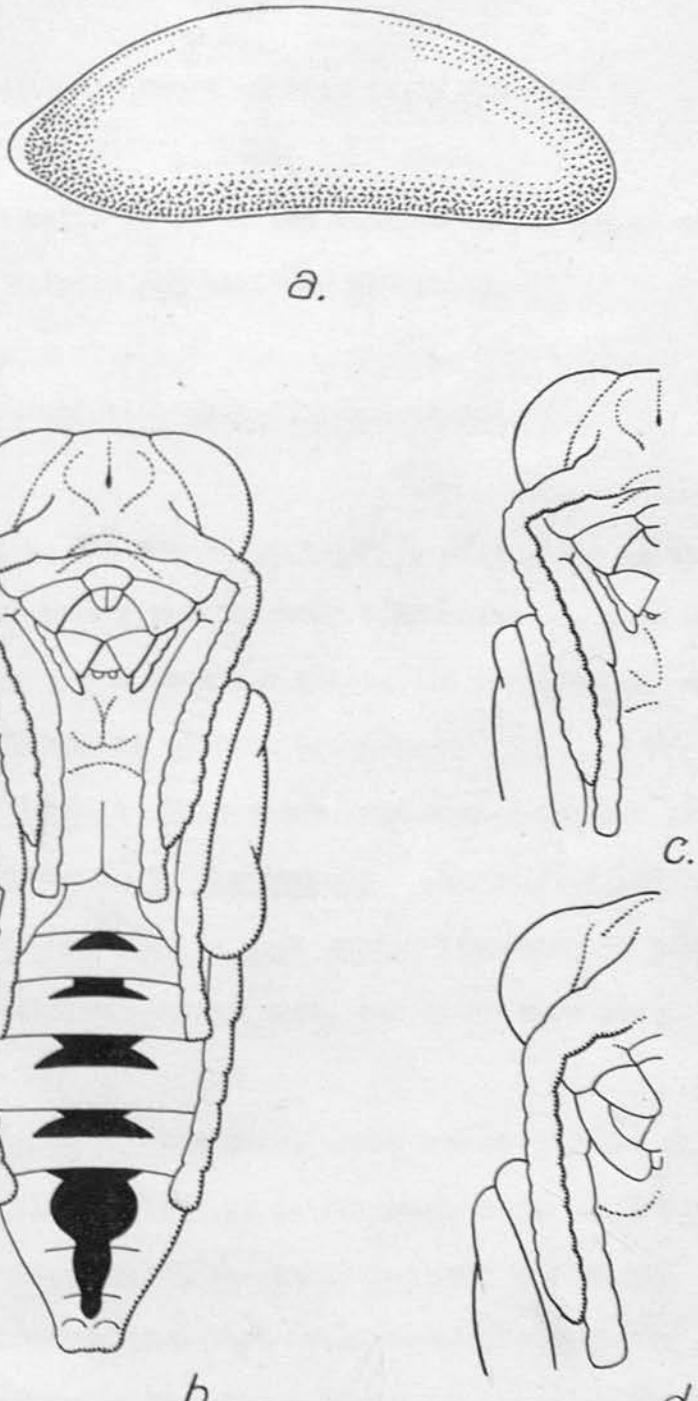


FIGURE 19. Cyrtogaster vulgaris, (a) egg (x 225); (b) early pupa with characteristic black markings on venter of abdomen; (c) view of antenna for comparison with that of (d) Sphegigaster flavicornis.

((b), (c) and (d) x 67).

unless the observer is aware of this habit, he will be completely fooled.

The sex ratio is .5 or two females to one male, and the species is primary and solitary in habit.

iv. Detailed Description of Developmental Stages.

The Egg : The egg of Cyrtogaster (Fig. 19a) is dull greyish-white in colour and somewhat kidney-shaped, with one end rather more pointed than the other. It measures .38 mm, in length by .105 mm. in maximum breadth.

Primary Larva : This stage is almost a replica of the corresponding instar in S. flavicornis. The only difference that was observed was that in Cyrtogaster two pairs of papillae were present in the sub-labial area, and these were abdent from Sphegigaster.

Mature Larva : This stage again resembles that of Sphegigaster so closely that it is extremely difficult, if not impossible, to separate the two. The only method of distinguishing between them that could be adopted was the unusual one of allowing the larvae to pupate, when, both in the early and late pupae, useful characteristics were found which admitted of relatively easy identification.

Prepupa and Pupa : The prepupa is similar to that of *Sphegigaster*, but quite appreciable differences can be made out in the pupa. When newly formed the pupa of *Cyrtogaster* is mainly white in colour, save for certain striking black markings on the venter of the abdomen (Fig. 19b). These dark areas are sufficient to separate the early pupa of *Cyrtogaster* from that of *Sphegigaster*, which is entirely white in colour. Another very useful characteristic is the internal angle of the antenna (see Fig. 19c); this in *Cyrtogaster* is almost a right angle, while in *Sphegigaster* it is obtuse, something like 135°, a point which can be appreciated better by reference to Figure 19 *c* and *d*. After a few days the remainder of the pupa begins to darken and ultimately becomes black in colour, except for the wings and appendages, which are of a very dark smoky-brown hue. The pupa of *Cyrtogaster* appears to be somewhat more shiny than that of *Sphegigaster*, which has more of a matt appearance. It may be interest to relate that it was often possible to establish with a fair degree of accuracy the identity of the parasite which had emerged from any particular host puparium. If the latter had contained one of the Eulophids, the contents of the puparium would be extremely untidy, with many black remains scattered about inside, while if a Pteromalid had occupied it, the interior would be clean, the only thing left being the parasite exuviae in a neat bundle, in the case of Sphegigaster towards the end of the puparium, and in that of Cyrtogaster at the side.

6. Opius ilicis, sp.nov.

This pupal parasite was reared from only three areas, Farnham Royal, Bucks, Sunninghill, Berks, and the New Forest, Hampshire. It is quite possible that it occurs elsewhere, but being comparatively rare, large numbers of puparia would have to be collected in order to get further examples. On an average not more than 2 - 3 per cent of the mines were attacked by this species. Specimens of the imago were submitted to the British Museum experts for identification. Mr. Nixon of the latter institution thought that the species was new, as it did not correspond with any in the collection, nor did it answer to any known description. Acting in collaboration we have therefore decided to give it the provisional specific name of ilicis, and are deferring a general description of it until

Mr. Nixon has had time to arrange the Museum collection of this large genus, after which it will be easier to place the new species in its appropriate position in the group to which it belongs. As this particular parasite is a relatively unimportant one on P. ilicis, less attention has been paid to it, and the general account of its biology and metamorphosis is therefore somewhat shorter than those of the preceding species.

i. Systematic Position and Description of Adult.

Family BRACONIDAE; division Polymorphes; tribe Opiidae. This parasite of the holly fly can be distinguished from the Chalcids very readily by means of the complex wing venation and the long antennae, which are not 'kneed', as in the latter group. The Polymorphes are characterized by the rigid articulation between the second and third abdominal segments, the mandibles which are closed in repose, the entire epistoma, and the large quadrangular cubital cell. Opius itself can be separated off from the other six genera of the Opiidae by the clearly bordered occiput, the smooth shiny body, the completely closed radial cell, the second abcissa of the radial nervure which is not shorter than the first cubital nervure, and the absence of impressions on the second abdominal segments.

As there is only one Braconid parasite of the Holly Leaf-miner and it is very easily identified by means of the foregoing characteristics and for the reason mentioned at the beginning of this section, a detailed description of the adult at the present moment will be unnecessary.

ii. Distribution and Host Records.

The distribution of the genus Opius is worldwide. As a genus it is chiefly parasitic on Diptera, and in the Farnham House catalogue, there are 118 records of various species of opius, 115 of which are on dipterous hosts, the remaining 3 being members of the Order Lepidoptera.

iii. General Biology of O. ilicis.

Although a few adults were obtained in the spring, none of the females would lay in the mines in captivity, although they were kept under exactly the same conditions as the Chalcids, which oviposited freely. As a consequence it was impossible to obtain the earlier developmental stages of this insect.

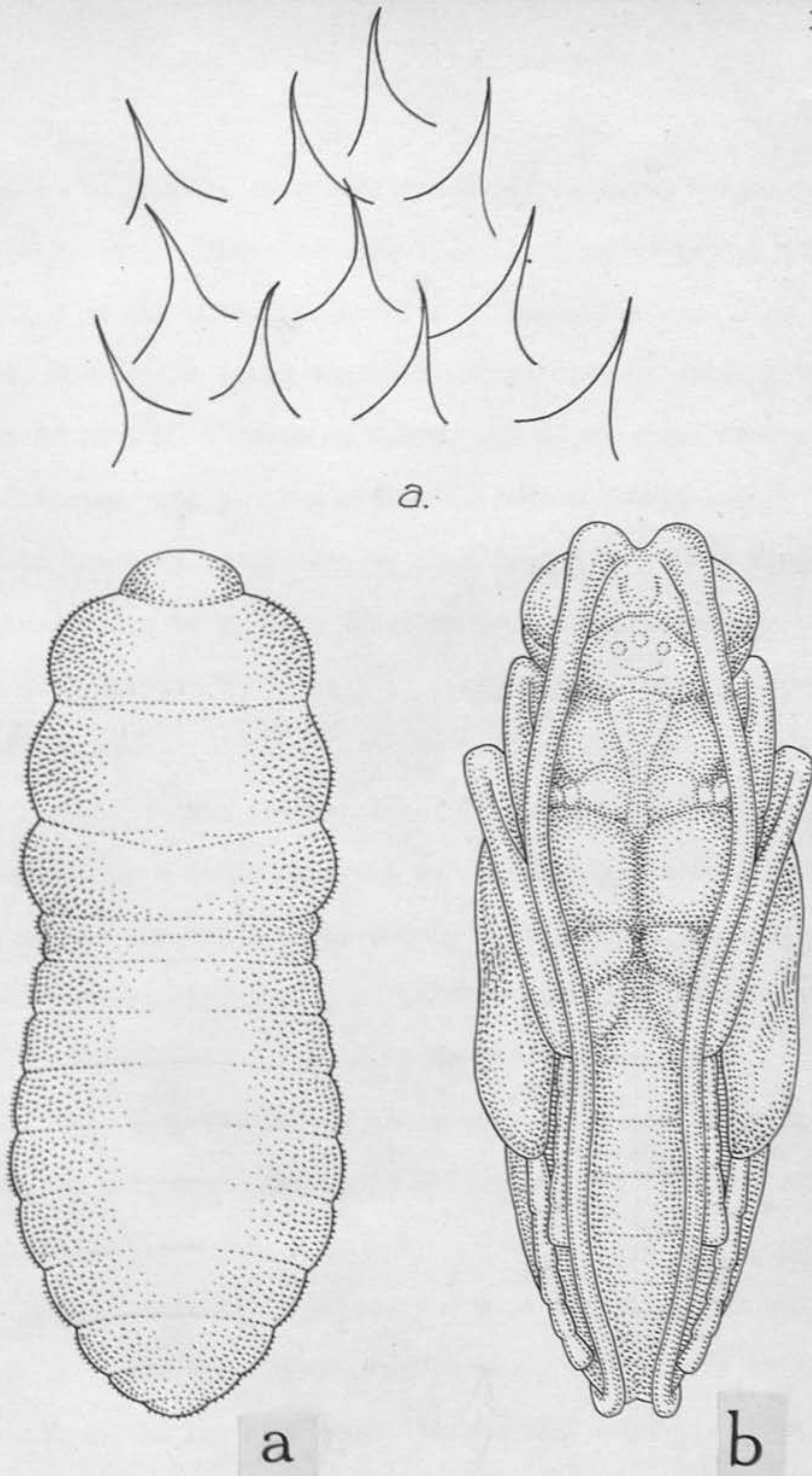
Strangely enough, mating took place quite readily in the laboratory. No preliminary courtship was observed, as in the CHALCIDOIDEA. When aware of the presence of the female, the male moves its wings rapidly up and down as if preparing to fly. Pursuit follows, the male mounts and copulation, which lasts for only a second or two, is effected.

Mature larvae of this species are present in the host puparia as early as the end of the first week in April, so that it is almost certain that this parasite overwinters in the adult stage. The prepupal stage lasts for two days and the pupal one for just over three weeks at room temperature (65°F.). Imagos emerge early, towards the end of May and the beginning of June.

This species is a primary, solitary and internal parasite of the puparium of P. ilicis. Males and females are present in about equal numbers, so that the sex ratio is equal to 1.

iv. Developmental Stages.

Mature Larva : A mount of the cast skin was prepared and on examination under high magnification, the latter was



<u>FIGURE 20</u>. <u>Opius</u> <u>ilicis</u>, sp.nov., (a) skin armature of mature larva (x 1600); (b) prepupa; (c) pupa).

((b) and (c) x 67)

observed to be closely covered with sharply pointed triangular spines (Fig. 20a). These measure about 10 µ in height by 7.2 µ in diameter at the base. Nine pairs of spiracles were also observed, the atrium being somewhat ellipsoidal in shape with a diameter of 10.5 µ, a depth of 7.2 µ, and an external aperture with a diameter of 3 µ. The atrium is followed by a long spiracular trachea, consisting of some twenty to thirty rings. Below these there is a small valvular apparatus, somewhat similar in construction to that of Sphegigaster, but of course very much smaller.

Prepupa : The prepupa (Fig. 20b), like the larva, is characterized by a dense covering of spines. It is whitish-grey in colour and consists of the old larval head, with its inconspicuous cephalic skeleton, perched on top of the first body segment. This is followed by two thoracic and ten abdominal segments, the former being very large and constricted off from the abdomen. The length of the prepupa is 2 mm. and breadth .75 mm.

Pupa : When newly formed the pupa (Fig. 20c) is white in colour with the eyes light brown. It is very characteristic in appearance, the long antennae which extend down over the ventral surface of the body and curve back over the posterior end on to the dorsum of the abdomen, being sufficient to separate it off from the pupae of all the other parasites of *P. ilicis*. This instar remains white in colour for some considerable time, but about 15 - 17 days after pupating the head and thorax become quite black, the abdomen still remaining white, and a day or two later the abdomen also darkens and the wings and antennae become dark grey, and the legs straw-coloured.

The pupa measures 1.8 mm. in length by .71 mm. in maximum breadth.

7. Rare Parasites of *P. ilicis*.

A single specimen of each of the following pupal parasites was obtained from a large collection of puparia made at Bagshot in 1936 :

i. *Closterocerus trifasciatus*, Walk.

(synonyms: *Eulophus trifasciatus*, Nees, *Entedon trifasciatus*, Walk.)

ii. *Tetracampe* sp. near *nemocera*.

8. Parasites from Eastern America.

The following five parasites were reared by F.W. Poos in Virginia, some 3,000 miles from the present outbreak of P. ilicis in British Columbia. Specimens were kindly sent over to me by Mr. Gahan, who determined them, but on examination it was found that all of them were quite distinct from the English parasites. It is possible that these can be utilized in British Columbia along with the English species. This point is discussed in a later section.

CHALCIDOIDEA :

EULOPHIDAE :	1. Pleurotropis lithocolletidis, Ashm.
	2. Closterocerus tricinctus, Ashm.
PTEROMALIDAE :	3. Sphegigaster sp.
MISCOGASTERIDAE :	4. ? Herbertia sp.

BRACONIDAE :

Opiinae :	5. Opius striativentris, Gahan

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III. PREDATOR ATTACK ON P. ILICIS.

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Toward the end of March a number of characteristic V-shaped markings may be observed on some of the mines of P. ilicis on the holly leaves (Fig. 21). These have been made by the beak of a bird in extracting the puparium, or occasionally the larva of the insect from the mine. The percentage of the holly fly population destroyed in this way is comparatively high. In 1937 at Bagshot, Surrey, 55 per cent of the mines were attacked by birds, and at Langley, Bucks, 61 per cent, whereas the general average of attack over several areas was about 25 per cent or more. The evidence I have obtained points to the common Blue Tit - Parus caeruleus, Linn.

sub-spec. obscurus, Praz., as the bird responsible for this useful work. Newstead (1908) confirms my suspicions, when he states that - "many pupae and seven larvae of the holly fly (Phytomyza aquifolii) were found in the stomach contents of a blue tit dissected at Chistleton, Chester on 6th April 1905." The blue titmouse with its characteristic colouring is easily distinguished from other birds - the crown of the head is blue, forehead whitish, the cheeks greyish-white with a dark blue line passing through the eyes to the chin; neck, wings and tail are blue; back yellowish-green, under surface of the body yellow; the bill black and legs leaden blue. It is common throughout the British Isles, and on the Continent its distribution extends eastwards to the Ural Mountains and the Caucasus in Russia as high as latitude 61°N, and in Norway 64°. South of the Mediterranean its place is taken by allied species (Lloyd's Nat. History).

Although the Blue Tit has been considered by gardeners and others to be destructive, actual observations by experienced observers show that it is exceedingly useful to man. An examination of the stomach contents of nestlings by Collinge (1927) showed that its food was made up as follows :

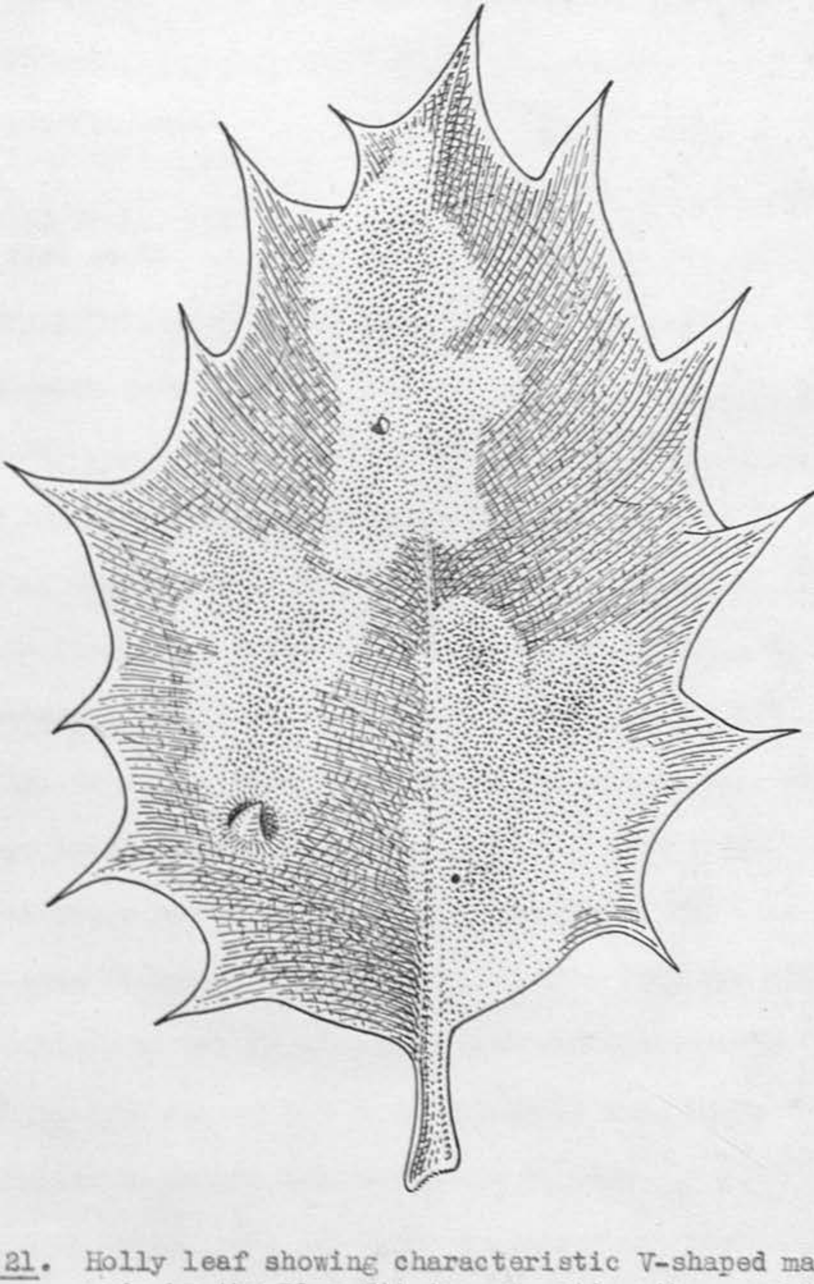

FIGURE 21. Holly leaf showing characteristic V-shaped marking made by the Blue Tit in extracting the puparium of P. ilicis from a mine; also showing mode of emergence of fly -- triangular flap, and of parasite -- small round hole.

(x 2)

Injurious insects	-	78.0 per cent.
Spiders	-	1.0 " "
Miscellaneous vegetable matter	-	2.5 " "
Wild fruits and weed seeds	-	8.5 " "
Fruit pulp	-	6.0 " "
Blossom buds	-	2.0 " "
Wheat	-	2.0 " "

The false impression of supposed harm done by the bird is due to its habit of picking at fruit-tree buds. Actually it is the insects inside the buds which the tits are seeking, and these insects, if not kept in check by them would, in all probability, cause irreparable injury to the trees. The only real damage which Collinge observed to result from this bird's activities was holes picked in ripe pears, but this amount of loss is small when compared with the generous aid which it renders to man in his fight with noxious insects.

The percentage of attack on the holly fly, which can be obtained in detail from the table on page , was influenced by at least two other factors - one the percentage of attack by <u>C. gemma</u>, the larval parasite, and two by the position of the holly tree, whether near cultivated and inhabited land or isolated in the forest, areas near the former getting a heavier pro-rata attack than the latter. This may be explained on the ground that the tits are attracted by the better supplies of food, which are generally available when a variety of agricultural and fruit crops are grown. The influence which C. gemma exercises on the percentage of bird attack is due to the fact that the mines of the victims of C. gemma are usually small and inconspicuous and are not thought to contain a worthwhile meal, and are therefore left alone. If C. gemma is common, the percentage of bird attack is lower than it is when the parasite is scarce. The relation between bird and parasite attack will be discussed further under the section dealing with biological control.

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IV. ABORTED OR DISEASED LARVAE.

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A certain number of mines never develop beyond a millimetre or two in diameter and if these are opened up, a small corky area surrounding a few black specks, which is all that remains of the tiny larvae, will be found. Sometimes the mines are much larger than this when the larva dies, and occasionally a few of the latter reach maturity or even the early pupal stage before succumbing to this mysterious disease. On examination these larger larvae are seen to be shrivelled up and very dark in colour, with the calcium carbonate deposits showing up very prominently as yellow globules. There is also a certain amount of dark brown 'mush' inside the skin in the earlier part of the summer. The actual cause of the death of these individuals is uncertain but it is thought to be a bacterial infection of some sort. Owing to the difficulties of isolating lethal bacteria of this nature and the absence of a competent specialist to undertake this type of work, it was found impossible to get the responsible organisms identified.

The percentage of larvae which succumbed to this cause during the years 1937-38 varied from 3 - 30 per cent (in one area it reached 55 per cent) and averaged 21 per cent. Exact figures for each area may be obtained from the table on page .

A small number of pupae, about 1 - 2 per cent on the average, are destroyed by dry conditions in the leaf and death is probably accelerated, in a few instances, by the attack of fungi.

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V. THE NATURAL CONTROL OF P. ILICIS.

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The term - natural control - is generally held to include the action of all physical and biological agencies on the insect in its natural environment. In this thesis, however, as indicated in the programme of work drawn up before the commencement of the investigation, the problem is viewed from the economic standpoint, and for this reason only the biological agencies, which have a much greater practical value, are considered. A study of all physical factors acting on the holly fly, its host, and parasites, such as, for example, climate, soil, etc., would be quite outside the compass of the present work, and in any case, since most of these influences are not amenable to manipulation, they are of secondary importance from the utilitarian point of view.

i. GENERAL SURVEY OF PARASITISM, ETC. IN 1937-38.

Before entering into a discussion on the effect of the natural enemies of P. ilicis and its host in England, during the period under review, I should like to insert the following quotation from a paper by H.S. Smith (1935), because it will lead to a better understanding of some of the conclusions drawn from Table I. - "Population densities of organisms are continually changing, but their values tend to oscillate about a mean, which is relatively stable, though itself subject to change - - species become economic problems because their average density is above the economic zero, or the amplitude of their oscillations is such as to cause the insect numbers periodically to exceed that point above which damage occurs. The really significant characteristic of population density is the value of the equilibrium position. If this is high, the amplitude of the oscillation, although not particularly great, can easily bring about economic damage, whereas if it is low, the same amplitude will have no effect."

From the following table, which is based on work carried out in the counties of Buckinghamshire, Berkshire, Hampshire, and Surrey, during the years 1937-38, several important deductions related to the control of P. ilicis have been drawn. Perhaps the most important of these is the following; - an upward oscillation of very high amplitude having occurred in the holly fly population in 1938, it seems very likely that similar oscillations will recur in the future, so that, even if the value of the equilibrium position is below the level of economic damage, occasional outbreaks causing severe injury to the foliage must be expected.

Area. (1)	Year. (2)	Leaves mined. % (3)	Total No. mines per 100 leaves. (4)	Attacked by *C.gemma*. % (5)	Attacked by Blue Tit. % (6)	Aborted and diseased. % (7)	Pupal parasites. % (8)	Dried pupae, etc. % (9)	Flies emerged. % (10)	Total mortality. % (11)
Bagshot	1937	30.4	31.1	35.4	9.7	26.8	25.6	-	2.5	97.5
Surrey.	1938	21.5	23.2	59.7	1.5	29.8	6.0	1.5	1.5	98.5
Langley	1937	47.5	55.0	6.9	59.5	3.5	23.2	.9	8.0	92.0
Bucks.	1938	68.0	96.7	32.1	14.1	12.5	19.8	6.5	15.0	85.0
Sunning-	1937	57.4	71.5	56.2	4.6	23.9	5.7	1.4	8.2	91.8
hill,2,	1938	62.8	90.5	58.5	3.9	30.5	3.1	.9	3.1	96.9
Berks.										
Hedgerley	1937	37.0	40.0	26.9	22.4	19.4	14.9	1.7	14.7	85.3
Wood,	1938	46.8	57.4	45.9	15.5	23.8	8.4	1.8	4.6	95.4
Bucks.										
Sunning-	1937	43.0	43.8	40.0	6.9	11.1	24.7	1.4	15.7	84.3
hill,1,	1938	53.3	65.5	29.0	2.1	55.4	9,2	2.7	1.6	98.4
Berks.										
Burnham	1937	28.0	28.2	38.7	27.4	9.7	4.8	1.7	17.7	82.3
Beeches,	1938	60.4	86.4	71.2	3.3	17.7	3.9	.6	3.3	96.7
Bucks.										
Windlesham,	1937	11.5	11.5	42.8	10.7	21.4	7.2	1.6	17.9	81.3
Surrey.	1938	29.3	32.3	59.9	0.	18.7	11.2	3.7	6.5	93.5
Cadnam,1,	1937	21.0	22.1	21.8	29.0	23.6	5.6	2.0	18.0	78.0
Hants.	1938	41.0	47.0	57.5	3.5	22.5	4.6	2.3	9.0	91.0
Cadnam,3.	1937	20.0	21.3	24.3	16.2	29.7	2.8	1.0	26.0	72.0
	1938	28.0	33.7	54.5	8.5	26.6	0.	1.1	9.2	91.8
Cadnam,2.	1937	16.2	16.2	38.4	5.7	17.5	0.	1.4	37.0	63.0
	1938	34.8	38.5	56.0	4.3	29.0	2.2	1.0	7.5	92.5
Hedgerley	1937	3.1	3.1	0.	0.	14.3	28.6	0.	57.0	43.0
Common,	1938	28.8	30.6	28.0	2.5	17.8	16.1	12.7	22.9	77.1
Bucks.										

The figures in the preceding table have been arranged according to magnitude of mortality in the holly fly population in 1937. Column (3) - Leaves Mined - gives the percentage of leaves mined by the insect irrespective of the number of mines on each leaf. The figures in this column, therefore, represent the damage from an economic point of view, because it does not matter very much to the grower whether the leaf contains, one, two, or more mines, since one normal mine per leaf is enough to spoil the general appearance of the foliage. In column (4) all the mines are accounted for, doubles, trebles, etc., and these figures being the significant ones from the biological standpoint, are used as a basis for calculating percentages of parasitism, predatism, etc. A study of the table revealed several points of great interest. These are as follows :

1. The average attack of the holly fly in 1937 throughout the areas examined was 31 mines per 100 leaves, the range varying from 3 to 70 per cent. In 1938 these figures rose to 54, and 23 to 97 per cent, the average increase in the population in this year being 23 per cent. This large oscillation in an upward direction (Graph - Fig. 22) will be discussed later.

2. The total percentage mortality in the fly population in all areas was extremely high. In 1937 this averaged 79 per cent, and in 1938, 92 per cent, an increase of 13 per cent. Such high mortality brought about by the action of natural enemies is, I venture to think, not very common. A satisfactory explanation of this rate is forthcoming when it is realised that the host is confined within narrow limits, and having no means of escape from its foe, falls an easy prey to parasite and predator alike. This disadvantage is shared by other leaf-miners, and also by gallicolous insects.

3. Although the mortality in *P. ilicis* was generally high in 1937, yet in only one instance was there a reduction in numbers of the fly in the following season. This happened at Bagshot, Surrey, where the population in 1937 was 31 per 100 leaves, the total mortality 97.5 per cent, and the population in 1938, 23 per cent, a drop of 8 per cent. In all other areas examined, even although mortality figures as high as 85 to 92 per cent were occasionally obtained, there was no decline, but an actual increase in the population. It would therefore appear that in order to bring about an appreciable reduction in the numbers of the fly, an

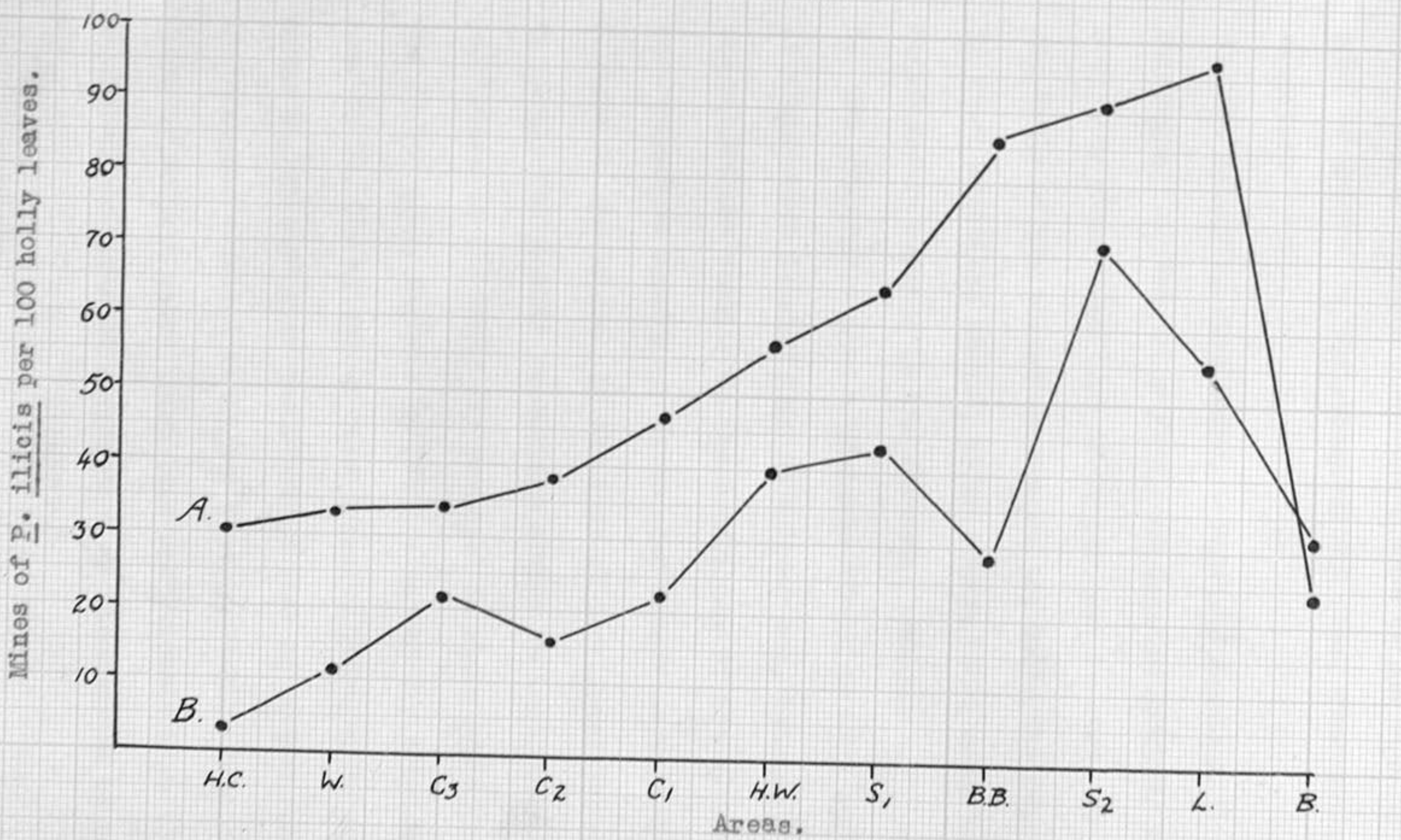

FIGURE 22. Graph showing general rise in the population of the Holly Leaf-miner in 1938. (B) Population level in 1937; (A) Ditto in 1938. At B area there is a reduction in the 1938 population due to the very high parasitism in the previous year.

extremely heavy toll - something like 95 per cent or more - must be exacted by the parasites and other destructive agencies.

4. The following five areas, - Bagshot, Sunninghill 1, Sunninghill 2, Hedgerley Wood, and Burnham Beeches, had mortality figures in 1938 of 95 per cent or over, so that on the basis of the preceding example the holly fly population in these districts should, (other things being equal), be considerably reduced in the following season.

5. The hypothesis that a parasite should be more efficient at a high host density than at a lower one, because one of the conditions tending to the production of its optimum environment is operating, is to some extent supported by the figures in the table. In the case of the larval parasite, C. gemma, the average percentage attack in 1937, when the population of the holly fly averaged 31 mines per 100 leaves, was 30 per cent, whereas in 1938, when the fly population rose to 54, the attack by this parasite averaged 50 per cent, an increase over the previous year of 20 per cent. This increase has resulted in higher total mortality figures, which in certain cases (No.4) are sufficiently high to enable one to forecast a reduction in the numbers of the fly

in 1939.

6. The converse of the aforementioned hypothesis should also be true, and data in support of this contention is found in column (8). Because of the great reduction in the numbers of larvae effected by _C. gemma_, fewer puparia were available for the pupal parasites. As a result of this, perhaps, there was a big drop in the numbers of the latter in 1938 as compared with 1937, the average attack in 1937 being 13 per cent and in 1938 only 7.6 per cent, a drop of 5.4 per cent.

7. The predatory bird, _Parus caeruleus_, was also affected by the abundance of _C. gemma_, which latter being the first species on the scene, could take full advantage of the increased numbers of the host. When a host is attacked by this parasite it usually fails to develop any further, so that the mine in which it lives remains small, and such mines are ignored by the tits, because they do not contain a large enough meal. In 1937, the average attack by this bird was 17.5 per cent, and in 1938 only 5.4 per cent, a drop of 12.1 per cent.

8. An interesting point may be brought in here. Although the natural enemies are present in all these areas, their individual importance in each one is not the same. If a

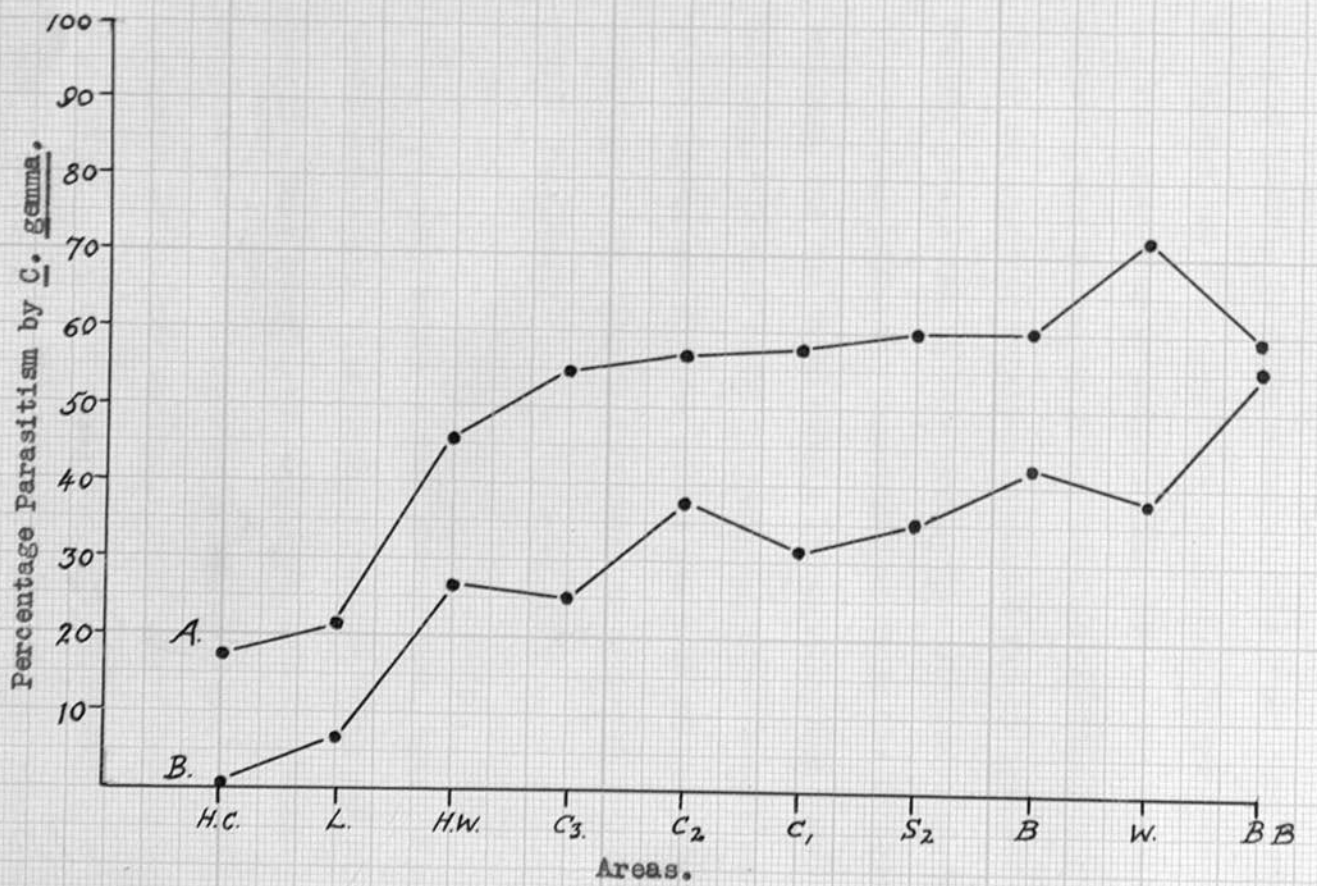

FIGURE 23. Graph showing general rise in the population of the larval parasite *Chrysocharis gemma* in 1938, as a result of increased host density. B. Population level in 1937; A. Ditto in 1938.

parasite has a low density in any particular district, the deficiency in the total mortality resulting from its ineffectiveness, may be made up by some other agency; e.g. in Langley (1937), C. gemma attacked only 6 per cent of the hosts, but the Blue Tit, because the fly larvae were thus allowed to develop to eatable size, was extraordinarily efficient and destroyed 59 per cent of the larvae and pupae. These two agencies together accounted for 65 per cent of the fly population in this area. In Sunninghill, 2, area, on the other hand, the importance of these two factors was reversed, yet the final result in mortality was very much the same. In this area, C. gemma accounted for 56 per cent of the larvae and the Tit only 5 per cent of the pupae, the total mortality being 61 per cent, as compared with 65 per cent in Langley.

The main value of this survey work, apart from the points made above, lies in the inference which may be drawn from it - that despite the very high mortality which takes place in the holly fly population in England as a result of the action of natural enemies, large upward oscillations from the equilibrium density can, and do, occur. It is clearly evident that annual surveys of this nature should be made over a long period of years - a minimum perhaps of five - before the value of the equilibrium density can be accurately determined, and it is the writer's intention to carry out a separate piece of research on these lines when the present work is concluded. If, for the sake of illustration, we take the equilibrium density from the five lowest figures for 1937 (Column (3)) as being in the neighbourhood of 20 per cent (it is possible and, indeed, very probable that it is higher than this, because the insect is not altogether uncommon in England, but it may be lower), this figure is very satisfactory when compared with the annual Canadian average of 80 per cent, but even if only 20 out of every 100 leaves were mined the pest might still be regarded as a nuisance, so that when this low density is taken in conjunction with the big oscillations which take place in England (even up to 68 per cent - Langley, column (3)), the prospects of biological control proving successful year after year in British Columbia, are not particularly bright. However, as Thompson (1930) has pointed out - - "if parasites and predators attack the insect in its native home, the parasitologist is quite justified in introducing them, since if they become acclimatized, they are certain to produce some diminution in the rate of increase and destructive powers of the pest." This is certainly true in the case of the Holly Leaf-miner in British Columbia, where, so far as we know, no native parasites have been found attacking the pest. One thing which should result from the introduction of these parasites is a lowering of the equilibrium density of the fly popylation, and this should be reduced still further by the elimination of the hyperparasite Pleurotropis amyntas from the Canadian parasite complex. Whether this will be brought down low enough for a measure of economic control to be obtained, no one can foretell, because the final result of the action of these parasites in their new environment, with its different climatic, biological and cultural constituents, is from the very nature of things, unpredictable.

This project does not end here, however, for apart from the usual 'straight' biological control, which consists in the introduction of parasites from the natural home of the pest to the adopted country of the latter, there are three further methods which can be used in conjunction with the preceding one. These are :

1. The Importation of Parasites from Eastern America.

On page 103 will be found a list of five parasites bred from P. ilicis in a district of Virginia on the eastern seaboard. These latter are quite distinct from the English ones. Because of the immense distance - some 3,000 miles, equal to the distance between Southampton and New York, and also because of the absence of intervening hosts - these parasites have not found their way across the American Continent to British Columbia. The suggestion is, therefore, now being put forward that the authorities in Canada should take steps to obtain supplies from this area. If this were done the parasite complex of the Leaf-miner in British Columbia would be enlarged and made more effective, and although it is possible that a certain degree of competition might arise between the different species, the effect of this would be largely discounted by the more beneficial end result which would follow when the new parasites occupy niches left vacant by those introduced from England. This procedure would also be quite in line with the accepted practice of applied entomologists, whose aim, at the present time, is the collection and introduction of all primary parasites of a pest throughout the whole of its range.

2. The alteration of the host/parasite ratio in favour of

the latter, by means of certain chemical dusts which are to be applied at a certain period of the year. This method is discussed in detail in a separate section.

3. The use of 'immune' varieties of holly, which is also described under a separate heading.

ii. INTER-RELATION OF BIOLOGICAL AND CHEMICAL METHODS OF CONTROL.

As is well known, leaf-mining insects, on account of the protection which the cuticle of the leaf affords them, are notoriously difficult subjects to control by means of chemicals. The holly fly is no exception to this rule, and the use of chemical compounds in this case is further complicated by the leaf-shedding reaction of the tree, which follows the apllication of some of the stronger sprays. However, in spite of these difficulties, there still remains the possibility that a small amount of chemical control may be advantageously employed to supplement the biological method. The only stage of the insect against which such control could be successfully directed is the adult, and a suitable chemical for this purpose would be a nicotine-lime dust as used by Downes in Victoria, British Columbia. Although the latter got some results by applying this mixture with a rotary duster at weekly intervals from the time when the flies made their appearance, it is very unlikely that this method will ever control the fly. The suggestion now being put forward by the writer is that the two methods - biological and chemical - should be combined in such a way that the parasites are favoured at the expense of the host. This could be done by applying the nicotine dust at a time when flies are abundant on the foliage, and parasites comparatively scarce. Such a time occurs, in England, during the first week of June, when the adult flies are busy ovipositing, and the majority of the parasites are still in the later developmental stages protected by the cuticle of the leaf, or, in the case of the pupal parasites, by the puparium of the host as well. Dusting operations at this time should result in a good kill of flies, whilst the majority of the parasites would probably be little affected. The first result of this procedure would be a great increase in the numbers of the latter relative to those of the host, and although according to conclusion 6, page 119, the parasites under these conditions would be less efficient, it seems reasonable to assume that a greater number of the hosts would be killed off by the parasites plus the dust, than by the parasites alone. Indeed, the work of Gröswald, which is reviewed in a later paragraph, supports this contention.

A certain number of experiments have already been carried out with various insects on these lines, and a brief account of some of them, quoted from Clausen (1936) may be inserted here. - In 1905, Froggatt observed that Cryptochaetum, a dipterous internal parasite emerged normally from cottony cushion scales which had been killed by fumigation. Again in 1917, Green found that a quantity of Lecanium scales confined for 18 hours in a jar containing strong cyanide, yielded large numbers of living Chalcids later, while Morrill in 1931, stated that larvae and adults of the predator beetle, Hippodamia convergens, the larvae of SYRPHIDAE, and the adults of the Braconid Aphidius were unaffected by nicotine dust, which had been applied to melon vines attacked by Aphids. In Germany, Gröswald working on the Nun Moth came to the conclusion that the parasitism in areas dusted with pyrethrum was higher than in untreated areas, because during dusting operations the hosts were killed but the parasites being protected within the latter, escaped injury. In this type of work the value of organic over inorganic compounds is stressed. When an inorganic chemical, such as arsenic, is used, a certain amount of the compound usually remains on the foliage and causes the death of the later emerging parasites, whereas organic substances, such as nicotine, pyrethrum, etc., soon vaporize, and become quite innocuous in a comparatively short time.

It is interesting to note that, as Clausen points out, the actual relative value of insecticides under field conditions may not lie entirely in their toxic properties, but to some extent on their effect on the parasite population. This, he says, would be particularly true in dealing with insects having a normally high parasite population, such as the cabbage butterfly, etc. The Holly Leaf-miner, with its high average parasitism, would come under this heading, so that the prospects of some useful work being done with the combined methods, in the way we have indicated, are quite encouraging.

A final suggestion in this connection, is that a dust with a selective action on the flies might be used. If this "discriminating" chemical were discovered, dusting could be carried out over a longer period with the result that greater numbers of flies would be killed off and a still higher parasite/host ratio obtained. It is not altogether impossible that a dust of this type exists, indeed it seems very likely, jüdging from Morrill's experience, that a nicotine compound may have this quality. At any rate, it should be well worth while for the authorities in British Columbia, after the parasites have become well established and their effect noted, to make further experiments in this direction.

iii. IMMUNE VARIETIES OF HOLLY.

The use of immune or resistant varieties of economic plants as a method of combating the onslaught of insect pests is well known. Strictly speaking, it is one that does not fall within the province of the entomologist, but rather of the plant breeder who has been specially trained in the technique of producing new strains, which will combine the desirable qualities of a good yield, and a maximum degree of resistance to at least one particular insect pest. So far as holly and the Holly Leaf-miner are concerned, it would not appear, having regard to the comparatively low value of the plant, that the services of such a specialist would be worth while. Nevertheless, judging by the list of varieties and sub-varieties which come under the heading _Ilex aquifolium_ in the catalogues of leading nurserymen, the production of new ornamental types of the common holly must be commercially remunerative. An inspection of several dozen of these varieties, for the purpose of selecting any particular strain which appeared to have some degree of resistance to the attack of _P. ilicis_, was carried out in 1938, in the fine well-grown collection in Kew Gardens. The summer of this year was considered to be especially good for this purpose, because of the high level to which the population of this insect had attained in the South of England. After a thorough examination, however, only one variety, _Ilex aquifolium_ var. _Hendersonii_, was found to be more or less free from attack. It is true that an odd leaf was mined, but not more than half-a-dozen such were found on the whole tree. This degree of immunity is the more remarkable when the severe attack - as much as 50 per cent of the leaves - on other varieties in the close vicinity, is taken into account. A sub-variety of <u>Hendersonii-Lawsonia</u> - was also practically free from mines, whilst <u>Hodginsii</u>, <u>Wilsonii</u>, and <u>doningtonensis</u>, had only slight attacks.

The main features, apart from the red berries, which give holly its unique character, and a great part of its value as a decorative plant, are the dark glossy hue of its foliage, and the relatively small spiny leaves. Many of the varieties differ widely from this type, some being more like laurels with flat spineless leaves, and these, to the uninitiated bear very little resemblance to the orthodox holly, with which everybody is familiar. The two 'resistant' varieties previously mentioned, do not altogether fall into this class, but they have fairly large, dry, tough, and leathery leaves, and although they are recognizable as holly trees, they fall short of the popular conception of this plant. In these circumstances growers in British Columbia, who cater for the decorative trade, might not like to experiment with them, but they should certainly prove of great value for planting as ornamental trees in public parks and private estates.

In conclusion it may be mentioned that up to the time of writing, over 200,000 mined holly leaves containing parasites have been collected and shipped to Canada, for liberation in the affected areas of British Columbia.

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VI. SUMMARY.

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1. In Canada, European holly (Ilex aquifolium) can only be grown successfully in the mild, humid climate of western British Columbia. For this reason the cultivation of the plant in this Province is commercially remunerative, and the sales of cut holly for decorative purposes amount to several hundred thousand dollars annually. The tree is also in good demand for ornamental planting in public parks and private estates.

2. The most serious pest of holly in this part of the world is the Agromyzid fly, Phytomyza ilicis, or the Holly Leaf-miner, which was accidentally introduced from Europe

without its attendant natural enemies. As the name "leaf-miner" suggests, the larvae of this insect mine or burrow in the sub-epidermal tissues of the leaf, and in course of time produce large unsightly blotches which greatly lower the value of the cut foliage. As a rule 75 - 80 per cent of the leaves are attacked in this manner.

3. Since chemical forms of restraint offered little hope of success because of the inaccessibility of the larvae, and the leaf-shedding reaction of the tree to some of the stronger sprays, it was decided that the natural method of control should be given a trial. Accordingly, the writer undertook a general survey of the fly and its parasites in England, for the purpose of obtaining a comprehensive knowledge of the latter, and in order to find out what part they play in the control of the pest in this country.

4. Part I of the Thesis deals with the holly fly itself, and includes a general account of its systematics, synonymy, morphology, distribution, host relationship, and biology. On reading through the literature it was discovered that the synonymy of the flies whose larvae mine the leaves of holly was in a state of some confusion. This tangle was

straightened out and the number of species reduced to two - (1) Phytomyza ilicis, Curt., and (2) P. ilicicola, Löew, the former being a European species, while the latter appears to be indigenous to North America.

5. During the course of the investigation eight species of parasites, seven of which are Chalcids and one a Braconid, were obtained from holly fly material collected in the South of England. All of them were reared for the first time, so that eight new host records are thus established. The Braconid parasite on examination proved to be a new species.

6. The several parasites fall into three systematic groups, EULOPHIDAE, PTEROMALIDAE, and OPIINAE, and they are described under their respective Families, and not according to their individual importance as parasites of P. ilicis.

7. In the Chalcid larvae certain important characteristics were discovered which, curiously enough, enabled me to classify them in the same systematic groups as the adults. On this basis it might be inferred that a general system of classification for Chalcid larvae, coinciding with that already in existence for the imagos, could be drawn up. This is not the case, however, as the distinguishing characteristics of the different species have been found to be related to the

endo- or ecto-parasitic habit, but it seems possible that (even if some exceptions do occur) these characters can be used to come extent for determining the mode of life of any particular Chalcid larva. This is useful when dealing with advanced larvae, as it will often provide a valuable clue to subsequent identification.

8. Identification keys for the parasites, both in the adult and mature larval stages have been drawn up, and these precede the general description of the various species.

9. Chrysocharis gemma (EULOPHIDAE), which attacks the host larva, is the most important parasite of the Holly Leaf-miner. On an average it was responsible for the destruction of some 30 - 35 per cent of the fly larvae, whilst the maximum parasitism attained by the species was 71 per cent.

10. In the descriptive part of the thesis, C. gemma is regarded as the type of the Eulophid parasites of P. ilicis, and is therefore treated in greater detail than any of the others, with the exception of Sphegigaster flavicornis, the type of the Pteromalids. It has been the author's aim to present a fairly full account of the systematics, adult, larval and pupal morphology, distribution, host relationship,

and biology of each species. This has been done very fully in the case of both types - C. gemma and S. flavicornis, but in the others, whenever possible, points of difference from the type are stressed and thus unnecessary repetition is avoided.

11. It is interesting to note that the genus Chrysocharis, according to some fifty host records examined by the author, consists of species which are all parasites of leaf-miners, although the latter may belong to such diverse Orders of insects as Diptera, Lepidoptera, Hymenoptera, and Coleoptera.

12. Chrysocharis syma, like its cogener C. gemma, is also a primary parasite of P. ilicis. It comes third in order of importance in the parasite list. This species attacks the pupa and its average parasitism was in the neighbourhood of 5 per cent, with a maximum of 24 per cent.

13. Pleurotropis amyntas is a parasite which acts in both a primary and secondary capacity - the species victimized in its hyperparasitic rôle being Sphegigaster flavicornis and Chrysocharis syma, etc. P. amyntas had not been recommended for liberation in British Columbia.

14. Sphegigaster flavicornis, which is primary in habit,

attacks the pupa of its host. It comes second in order of importance as a parasite of P. ilicis, with an average parasitism of 8 per cent of the mines and a maximum of 27 per cent. This species, being a type like C. gemma, is treated in greater detail than the following one.

15. Cyrtogaster vulgaris is also a primary parasite of the pupa and like Sphegigaster belongs to the Family PTEROMALIDAE. Its average parasitism was low, not more than 1 per cent, with a maximum of 7 per cent. A remarkable characteristic of this species is its ability of feigning death when approached. Several females were kept in the laboratory throughout the winter, and a new generation reared from them in the following spring.

16. The main points of difference between the Pteromalids as typified by S. flavicornis, and the Eulophids by C. gemma, are as follows :

i. In the cephalic skeleton of the Pteromalids there is a large rectangular tentorium (Fig. 17, page 86), which is absent from the system of facial rods in the Eulophids.

ii. The spiracles of the former group (Fig. 18, page 88) are large and ellipsoidal in shape and the spiracular trachea consists of 3 - 6 large rings, followed by a complex valvular apparatus, whereas in the latter (Fig. 9, page 47), the spiracle is small and quadrangular, and the spiracular trachea is composed of some 12 - 17 or more small rings, followed by a simple tube without any trace of a closing mechanism.

17. Opius ilicis, sp.nov., This is the only Braconid parasite of the Holly Leaf-miner, and it is easy to separate it, both in the adult and larval stages, from the Chalcids. In the adult the long straight antennae and the typical Braconid venation of the forewing are characteristic. The presence of strong spines on the skin gives the larva and prepupa a shagreened appearance, which makes the identification of this species in these stages very simple. O. ilicis is not an important parasite of the Holly Leaf-miner, specimens having been obtained from only three areas.

18. The following rare parasites of P. ilicis were reared from host puparia during the course of the investigations :

i. Closterocerus trifasciatus.

ii. Tetracampe sp. (near nemocera).

19. A few parasites were reared from the Holly Leaf-miner

in a small area in Eastern Virginia, U.S.A., some 3,000 miles from the present outbreak in British Columbia. Specimens were kindly sent over by the American authorities for comparison with the English species, but they were found to be quite distinct from the latter.

20. On an average 20 per cent or more of the puparia (and a few of the advanced larvae) were eaten by a bird, which is believed to be the Blue Tit, Parus caeruleus. In one area where C. gemma was not very common, as many as 61 per cent of the mines were emptied of their contents by this useful bird. The habits and food of the latter are described, for the purpose of showing that, contrary to general belief, the Blue Tit is an extremely useful ally of man.

21. A number of larvae died in the younger stages, with the result that the mines which they inhabited never developed beyond a milimetre or two in diameter. The actual cause of the death of these larvae was not determined, but it is thought to be due to a bacterial infection of some sort. In addition to these, a small percentage of pupae succumbed to dry conditions in the leaf.

22. The final division of the thesis deals with the

problem of control, by means of biological agencies. In the first place, equilibrium density, and oscillations therefrom are discussed. This is followed by a table showing the percentage of attack of the fly, percentage parasitism, predatism, and total mortality, etc., for the years 1937-'38. From this statistical survey of the fly and its parasites in four of the southern counties of England, various conclusions are drawn.

23. The most important of these is the following - An upward oscillation of some magnitude having occurred in the holly fly population in 1938, it seems very likely that similar oscillations will recur in the future, so that, even if the value of the equilibrium position is below the level of economic damage, occasional outbreaks, causing severe injury to the foliage, must be expected.

24. Further results of the survey are summarized as follows :

i. The average population level of the holly fly in 1937 was 31 mines per 100 leaves. In 1938 it was 54, an increase of 23 per cent.

ii. The total percentage mortality in the fly population as a result of the action of the natural enemies was extremely high. In 1937 an average of 79 per cent and in 1938 92 per cent of the population was destroyed by these agencies.

iii. Despite this high mortality in 1937, there was no reduction in the numbers of the population in 1938, except in one area where the total mortality reached the very high figure of 97.5 per cent.

iv. Five areas had a total mortality, in 1938, of 95 per cent and over and in these districts a drop in the population is expected in 1939.

v. The hypothesis that a parasite should be more efficient with increasing host density, is to some extent supported by the figures obtained in the survey. In 1937, when the average number of mines per 100 leaves was 31, the population level of Chrysocharis gemma stood at an average of 30 per cent, while in 1938, when the average number of mines increased to 54, the population of C. gemma also rose - from 30 per cent to 50 per cent - an increase of 20 per cent.

vi. Because of the reduction in the quantity of puparia available for parasitization consequent on the increase in the population of the larval parasite, C. gemma, the number of mines attacked by the pupal parasites and the predatory Blue Tit in 1938 was less than in 1937, thus proving the converse of the preceding theory to be true.

vii. Although most of the natural enemies were present in all the areas examined, their individual importance in each area was not the same. In one area, the larval parasite _C. gemma_ was scarce and destroyed only 6 per cent of the host, but the Blue Tit, because of the greater number of larvae left to pupate, was extraordinarily efficient and accounted for 59 per cent of the puparia, a total mortality for the two agencies of 65 per cent. In another region, the importance of these two agencies was reversed, yet the combined mortality effected by them was much the same as in the preceding area, _C. gemma_ - 56 per cent; Blue Tit - 5 per cent; total mortality - 61 per cent as compared with 65 per cent.

25. Because of the upward oscillation which occurred in the holly fly population in 1938, the prospects of biological control in British Columbia are not considered to be very bright. However, the introduction of these parasites is

justified because they must produce some diminution in the rate of increase and destructive powers of the pest. Their action should also be intensified to some extent by the elimination of the hyperparasite Pleurotropis amyntas, while it is possible that they may become more efficient in their new environment, with its different climatic, biological and cultural constituents.

26. Three further methods, supplementary to the main one, which consists of the importation of parasites into the affected area, are suggested as worthy of consideration. They are as follows :

i. The importation of parasites from Eastern America in order to reinforce the parasite complex introduced from England. These American species have not yet reached and are unlikely ever to reach British Columbia by natural migration, because of the immense distance and the absence of intervening hosts.

ii. The alteration of the host/parasite ratio in favour of the latter by applying nicotine dust at a time when flies are abundant on the foliage and parasites are comparatively scarce. This should be carried out early in June before the main lot of parasites have emerged. In this way the numbers of the latter relative to the number of hosts, could be increased.

iii. The use of immune varieties of holly. Two varieties - Ilex aquifolium var. Hendersonii and I. aquifolium, Hendersonii, sub-var. Lawsonia, were found to be practically free from leaf-miner attack, and although the foliage is not so suitable for decorative purposes, these two strains are being recommended to the Canadian authorities for planting as specimen trees in public parks and private estates.

27. During the course of the work over 200,000 holly leaves containing parasites, were collected and shipped by the author to Canada.

28. An extensive bibliography is appended.

29. Twenty-three figures, dealing mostly with the developmental stages of the various parasites, complete the thesis.

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VII. ACKNOWLEDGEMENTS.

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