PULLUS IMPEXUS (MULS.) (COLEOPTERA, COCCINELLIDAE), A PREDATOR OF *ADELGES PICEAE* (RATZ.) (HEMIPTERA, ADELGIDAE), WITH NOTES ON ITS PARASITES.*

By Vittorio Delucchi.
European Laboratory of the
Commonwealth Institute of Biological Control,
Feldmeilen. (Zurich).

(Plates XI–XXVIII.)

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* European Investigations.

Introduction.

The study of the biotic factors causing mortality among the Balsam Woolly Aphid, *Adelges piceae* (Ratz.),* in Canada was first undertaken between 1932 and 1934 at Fredericton, New Brunswick, about 30 years after the introduction of the Aphid into Nova Scotia (Balch, 1952). None of the native Canadian predators indicated by Balch seems to be present in Europe.

In 1933, *Leucopis* (*Leucopomyia*) *obscura* Hal. (Diptera, CHAMAEMYIIDAE) was introduced into Canada and 2,000 adults were liberated in New Brunswick. According to Balch " within a period of 14 years the insect has spread more than 150 miles from the nearest point of liberation and this establishes a remarkable case of rapid dispersal and successful establishment ". From 1935 to 1937 the following three additional predators were introduced from England to Canada, *Exochomus quadripustulatus* (L.) (Coleoptera, COCCINELLIDAE), *Hemerobius nitidulus* F. and *H. stigma* Steph. (Neuroptera, HEMEROBIIDAE). None of these latter species survived the severe winter climate. In 1950, the Commonwealth Institute of Biological Control, at the request of the Canada Department of Agriculture, initiated a study of the natural control agents of *A. piceae* in Europe in areas climatically most similar to eastern Canada. The study areas were established in eastern Switzerland, in southern Germany and in the Vosges area of France. In 1951 and 1952 it was possible to rear and ship to Canada *Pullus impexus* (Muls.), *Aphidecta obliterata* (L.) (Coleoptera, COCCINELLIDAE), *Laricobius erichsoni* Rosenh. (Coleoptera, DERODONTIDAE) and *Cremifania nigrocellulata* Cz. (Diptera, CHAMAEMYIIDAE) in the adult stage.

The purpose of the present study was to accumulate information on the natural enemies of *A. piceae* with special reference to the biology and habits of *P. impexus* and its parasite complex.

One hundred years have passed since the original description of the species *impexus* (Mulsant, 1850) was made. This species was referred to as predacious upon *A. piceae* by Komarek and Pfeffer in 1937 (Hofmann, 1938). Other entomologists who found *P. impexus* in the forest (Weise, 1884; Baudi, 1889;

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* Annand (1928) arranged the species of the ADELGINAE under *Adelges* and *Pineus*, and the Genus *Dreyfusia* (Börner, 1952) was therefore included in the Genus *Adelges*. This arrangement is followed here.

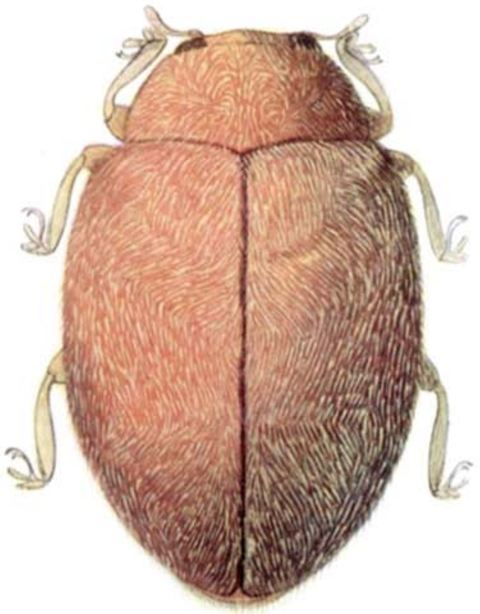


FIG. 1. *Pullus impexus* (Muls.), dorsal view.

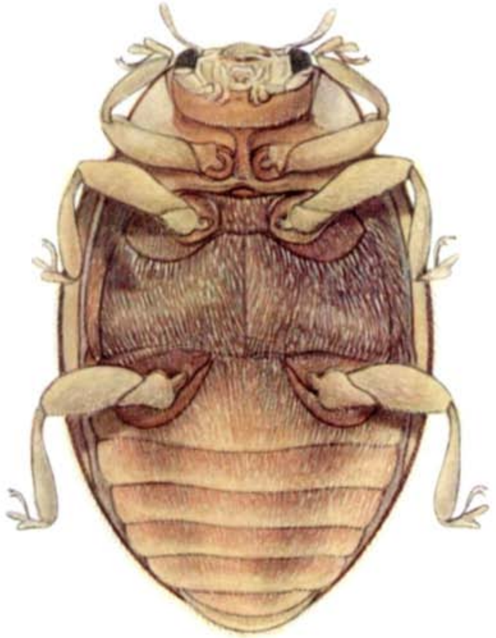
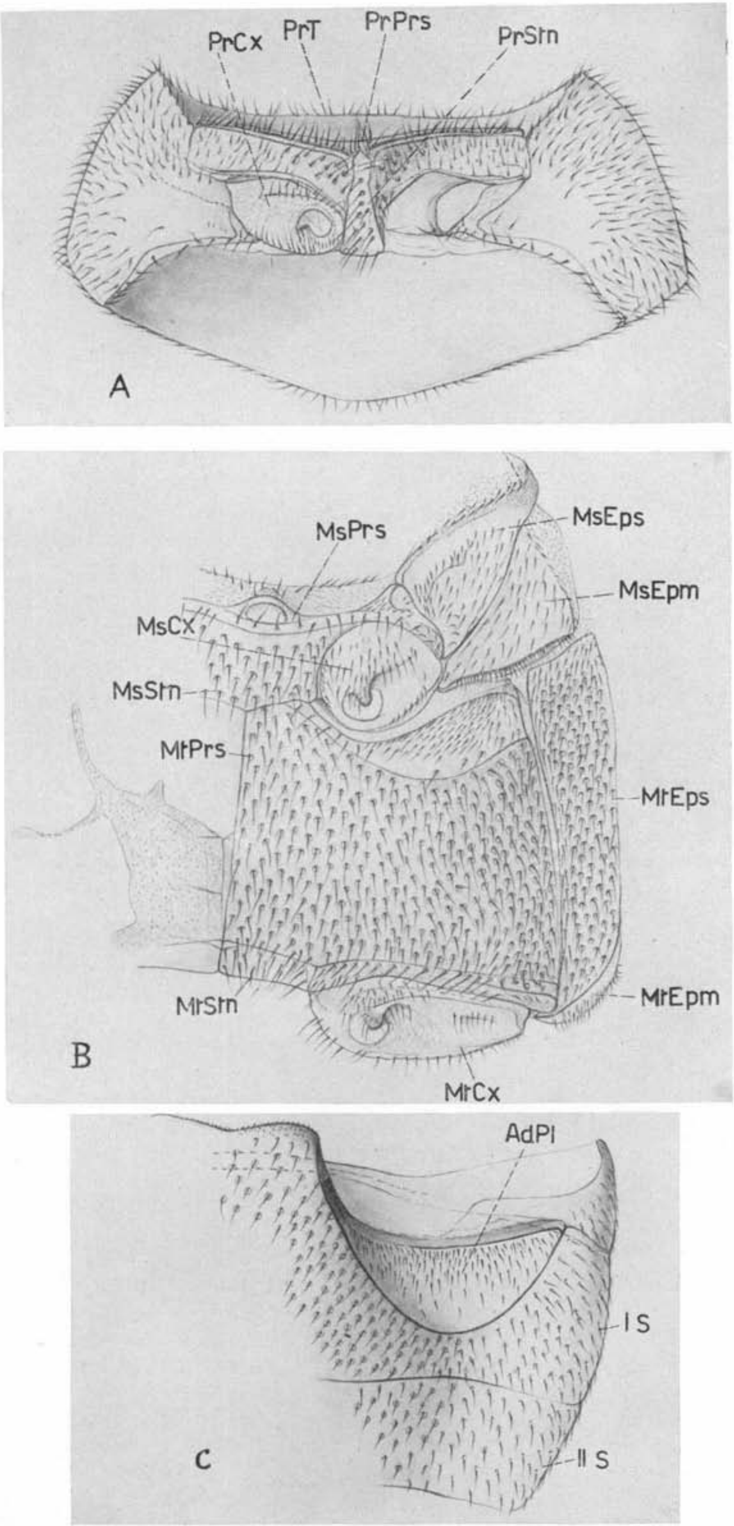


FIG. 2. *P. impexus* (Muls.), ventral view.



A, prothorax and B, pterothorax of *P. impexus*, ventral view: *PrCx*, *MsCx*, *MtCx*, pro-, meso-, metacoxa; *PrT*, protergite; *PrPrs*, *MsPrs*, *MtPrs*, pro-, meso-, meta-presternum; *PrStn*, *MsStn*, *MtStn*, pro-, meso-, metasternum; *MsEps*, *MtEps*, meso-, meta-episternum; *MsEpm*, *MtEpm*, meso-, meta-epimeron. C, abdominal plate of the first abdominal sternite of adult of *P. impexus: AdPl*, abdominal plate; I S, II S, first and second sternites.

Schatzmayr, 1943; etc.) have not recorded the host upon which the Coccinellid feeds.

Three years' observations on the problem of *A. piceae* indicate that in general the most important predators comprise at most ten species (fig. 1). Three of these belong to the Coleoptera:

Pullus impexus (Muls.) (COCCINELLIDAE)
Aphidecta obliterata (L.) (COCCINELLIDAE)
Laricobius erichsoni Rosenh. (DERODONTIDAE),

six to the Diptera:

Leucopis (Leucopomyia) obscura Hal. (CHAMAEMYIIDAE)
Leucopis griseola (Fall.) (CHAMAEMYIIDAE)
Cremifania nigrocellulata Cz. (CHAMAEMYIIDAE)
Cnemodon latitarsis Egg. (SYRPHIDAE)
Syrphus arcuatus (Fall.) (SYRPHIDAE)
Aphidoletes thompsoni Moehn (CECIDOMYIIDAE)

and one to the Neuroptera:

Chrysopa ventralis Curt. (CHRYSOPIDAE).

In the spring, during the oviposition period of the Aphid, all ten species are present. *Aphidoletes thompsoni* is the first to make its appearance; the adults were noticed in 1951 on 23rd March (at Seegraeben). In April the adults of *Pullus impexus* leave their wintering places and in addition the larvae hatch from the eggs deposited the preceding autumn. At the same time *Laricobius erichsoni* is depositing its eggs in the Aphid brood; also during this period the first generation larvae of *A. thompsoni*, the hibernated larvae and pupae of *Leucopomyia obscura* as well as the larvae of *Chrysopa ventralis* are present. In May, when the oviposition by *Adelges piceae* reaches its peak and the trees are densely covered with white wax, the adults of all the other above-mentioned predators appear and deposit their eggs in the Aphid population. In May, therefore, the larval stages of all ten predatory species are present on the infested bark. Then the *Aphidoletes* produces its second generation and the larvae of Coleoptera and other Diptera develop into pupae. In June, when the population of *Adelges piceae* is heavily decimated by the predators, the adults of the new generation of *P. impexus* and of *L. erichsonii* are found on the trees. Among the wax remains, a few larvae of *Syrphus arcuatus* of the second generation, larvae of *Leucopomyia* and *Aphidoletes* (present in varying numbers until autumn) are roving about, and *Aphidecta* and *Chrysopa* adults emerge.

At this time a dispersion of some of the predacious species is noticed, and a slowing down of the activity of the remaining species to coincide with the end of the first host generation. It is quite obvious that successive waves of predators disorganise the *Adelges* population on the infested trunks. This is evidenced by the disturbed condition of the wax and wool secreted by the Aphids. From June to August the activity of the predators is continued by *Leucopomyia obscura* and *Aphidoletes thompsoni*, although even this is almost imperceptible. Other species, if present, are of no numerical significance.

The autumn generation of the *Adelges* begins with oviposition in August. A thin white wax layer again collects on the trunks among the greyish wax remains of the spring generation or on the trees newly attacked by the Aphid. At this time some of the predators resume their activity. The *Cremifania* adults emerge (first generation), a few *Syrphus arcuatus* show themselves, and *Aphidoletes*, *Leucopomyia* and *Cremifania* (second generation) increase rapidly. The adults of *P. impexus* are frequently observed and begin oviposition. Some *Cnemodon* are noticed as well as the first small larvae of *Chrysopa ventralis*. The components of the predator community on the autumn Aphid generation has changed slightly. There are neither thousands of Coleopterous larvae nor hundreds of Syrphid larvae and no particular disorder of the wool, as in the spring generation, is noticed.

Between the very small larvae of the three Diptera (*Aphidoletes*, *Leucopomyia* and *Cremifania*) and the Aphid there appears an orderly struggle, which almost escapes our notice. The intensity of the autumn Aphid generation depends, for the most part, upon the number of survivors remaining after the destructive action of the predator community on the spring generation. The three Coleoptera and *Syrphus arcuatus* are generally numerous on the spring infestation of the Aphid, whereas *Cremifania*, *Leucopomyia* and *Aphidoletes* reach their greatest numbers in the autumn. However, it is the combined activity of all the predator species in May that is responsible for the reduction of *Adelges* to a low level.

Each predator possesses one or more parasites (fig. 1) and some predators are affected with disease organisms causing at times serious mortality in their populations.

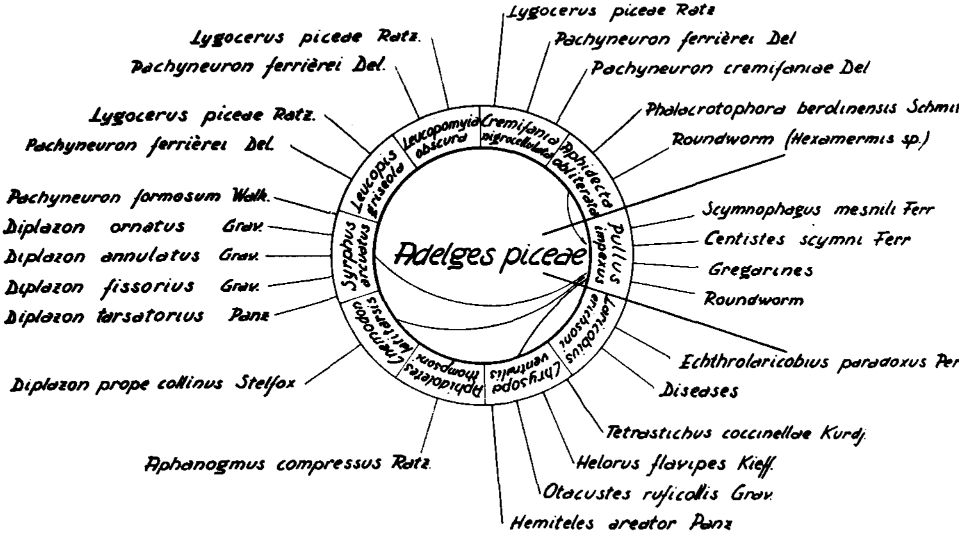


Fig. 1.—The predators of *Adelges piceae* and their parasite complex.

To the above predator community, forming the basis for biological control of the Aphid, we may add some occasional predators which, either isolated or with a life-cycle not coinciding with that of the host, have little or no importance in the destruction of the *Adelges*. Among those most often encountered were:

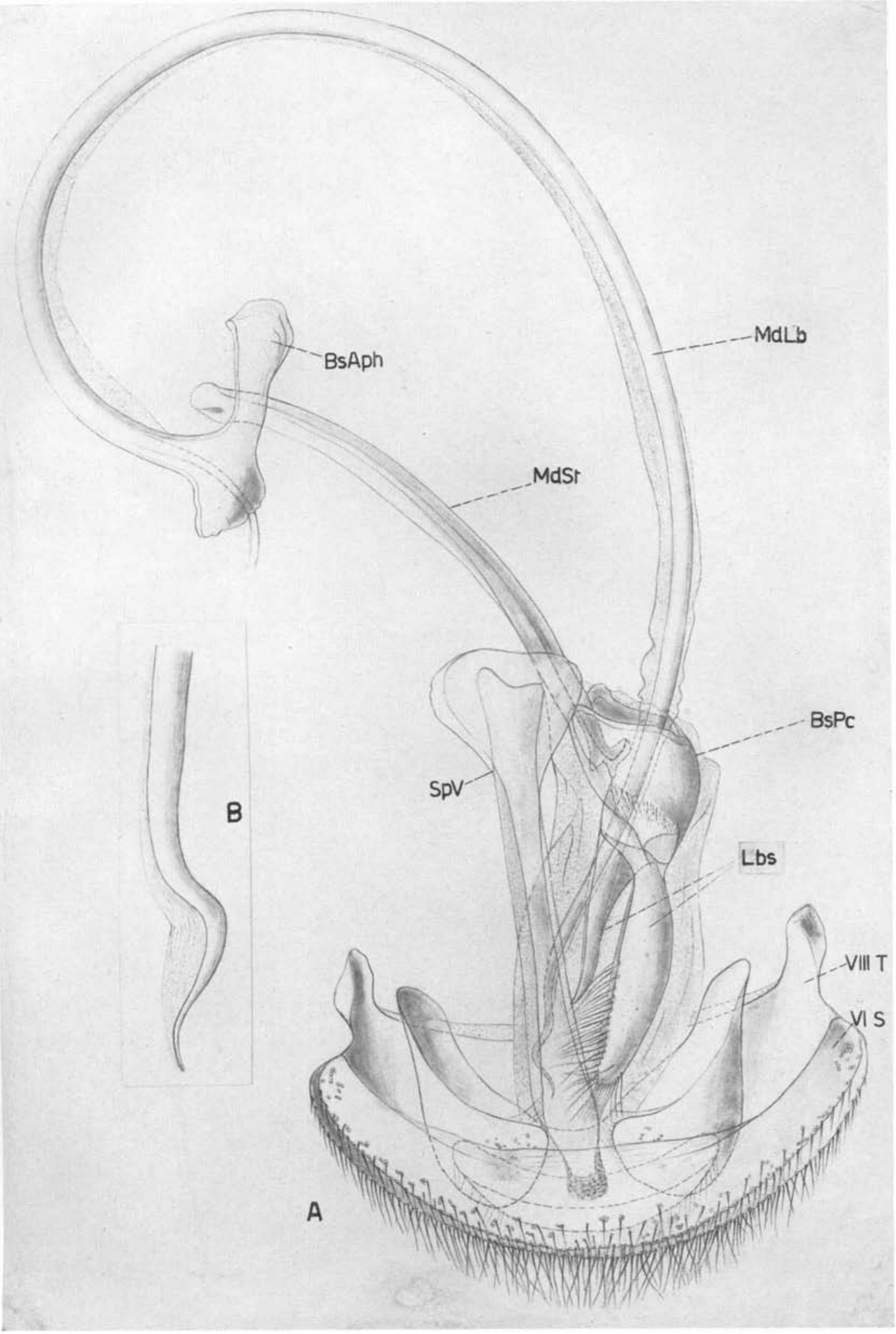
Anatis ocellata (L.)	(Coleoptera, Coccinellidae)
Neomysia oblongoguttata (L.)	,, ,,
Propylea 14-punctata (L.)	,, ,,
Exochomus 4-pustulatus (L.)	,, ,,
Coccinella 7-punctata L.	,, ,,
Epistrophe balteata (Deg.)	(Diptera, Syrphidae)
Raphidia sp.	(Neuroptera, Raphidiidae)
Triphleps sp.	(Hemiptera, Anthocoridae).

In addition to the insects some Mollusca such as *Limax maximus* L. and *L. tenellus* Nilss. were found by Dr. Wichmann at Munich. Mites are also recorded, among which *Lephthyphantes obscurus* Blackwall is stated by Dr. Wichmann to be most frequent.

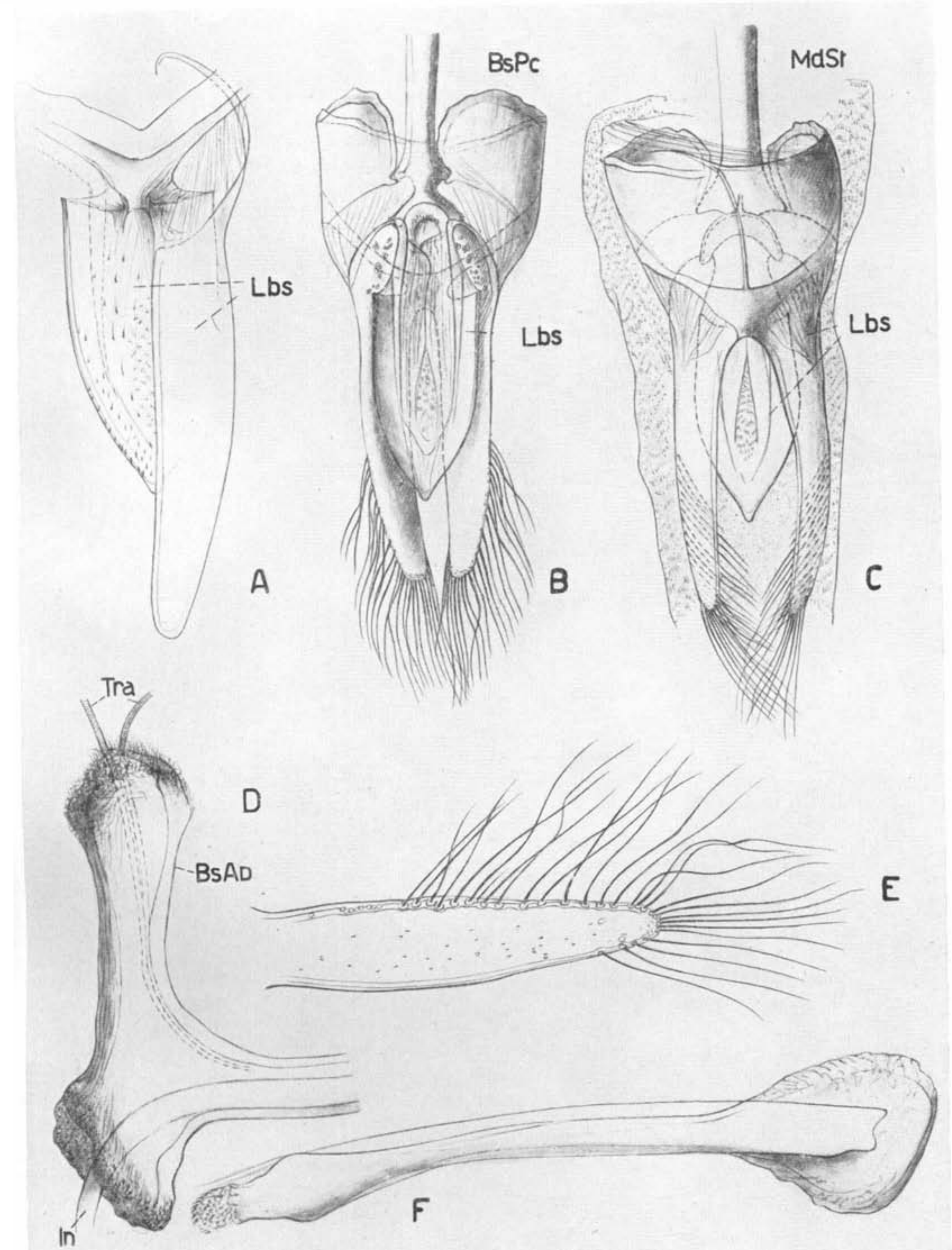
Method of Rearing and Techniques employed in the Study of *Pullus impexus*.

Rearing in the laboratory.

The predators reared on bark infested with *A. piceae* in petri dishes, open or covered with organdie, or containing moist cotton or earth, always suffered a



Male genitalia of *P. impexus:* A, ventral view of the genitalia; B, virga: *BsAph*, basal apophysis; *MdSt*, median strut; *MdLb*, median lobe; *BsPc*, basal piece; *Lbs*, basal and lateral lobes; *SpV*, spicula ventralis; VIII T, 8th tergite; VI S, 6th sternite.



Parts of the male genitalia of *P. impexus:* A, basal and lateral ventral lobes, schema; B, C, latero-internal, latero-external view of the tegmen; D, basal apophysis; E, a lateral lobe of the tegmen; F, spicula ventralis: *Lbs*, basal and lateral lobes; *BsPc*, basal piece; *MdSt*, median strut; *BsAph*, basal apophysis; *Tra*, trachea; *In*, intima of the ductus ejaculatorius.

rather heavy mortality. This was chiefly due to the growth of mould on the bark surface. Therefore an attempt was made to simulate the natural conditions. The data supplied by a small meteorological station established on the Pfannenstiel (Zurich) in an *Adelges* infestation were utilised.

In studying the problem of *Adelges* a method was adopted which had already been successfully employed by Prof. L. P. Mesnil in rearing parasites of *Carulaspis visci* (Schr.) on *Juniperus communis* L. Pieces of bark, freshly detached from the infested trees were introduced into tubes 4 cm. in diameter and 20 cm. in length. Through these tubes an air flow which could be regulated was directed. The tubes were exposed to room temperature, which remained more or less constant in the laboratory during rearing. Two important details were considered, the relative humidity control to prevent the bark from drying too rapidly, and the air flow control to prevent mould from forming. In the winter, the material was exposed to the natural conditions in the forest in the Pfannenstiel area. With this method there was no mortality in rearing *P. impexus*.

Fixation of the material.

For the fixation of the material, alcoholic Bouin (Langeron, 1949) was used exclusively with excellent results. After having slit the insects open laterally to allow the fixative to penetrate the body rapidly and uniformly they were left in alcoholic Bouin for 48 hours. Then the material was washed frequently in 80 per cent. alcohol until any trace of the picric acid had disappeared. It was then placed in small labelled tubes containing 80 per cent. alcohol and stored in large jars.

Microscopic preparations.

Generally, special oculist's bistouries were used for dissections under the binocular microscope. For histological studies the microtome was used, *e.g.*, in the study of the Gregarines. For paraffin inclusions the object was passed through the dehydration series in alcohol (two baths in absolute alcohol) and then to xylol. The material was left for 24 hours in a methylbenzoate bath containing 1 per cent. of celloidin; afterwards through three successive toluol baths within 24 hours, and finally into paraffin M.P. 52°–54°. The object was left in the paraffin for four to five days at a temperature of 58°C. For the study of sclerotised parts 10 per cent. potassium hydroxide was used.

Methods of staining.

The sclerotised parts, cleared with potassium hydroxide, were stained with basic fuchsin in absolute alcohol and mounted in Canada balsam. For the staining of organs of relatively large size (heart, pericardial cells, muscles, etc.) the Mann biacid technique was used (Langeron, 1949) replacing eosin with xilidin ponceau, and differentiating simply in 80 per cent. alcohol after washing in distilled water. For histological staining and for staining of very small entire organs (salivary glands) the modified method of Dominici (Langeron, 1949) was used. The organs and the microtome sections after having passed through the xylol and alcohol series, were washed in distilled water, then left 15 minutes in a solution composed of 1 per cent. erythrosin blue and 1 per cent. xilidin ponceau. After two washings in distilled water, they were stained with 0·1 per cent. toluidin blue solution until the object assumed a violaceous shade. This is one of the most critical moments in staining, because too deep toluidin staining may ruin the differentiation process. Both staining and differentiation must be performed beneath the binocular microscope. For this reason it is advisable to glue the microtome sections on the glass slides and to handle them in strongly concave watch glasses of 5 cm. diameter. From the toluidin the sections are passed to distilled water, then to differentiation in 80 per cent. alcohol, to a rapid dehydration, to xylol and mounting in Caedax. The Caedax, made in Germany, has taken the place of Canada balsam, because in the latter the staining loses its freshness with time.

Drawings, photographs and microphotographs.

The most satisfactory drawings were made on Sihl Superbus cardboard 540 gr. with Wolff's carbon drawing pencils (HH, H, HB and BBB) together with water colours for coloured plates. They were drawn with the use of the Leitz stereoscopic binocular with Leitz camera lucida or with Leitz microscope with double iris. For the coloured plates of the two Hymenopterous parasites of *P. impexus* a Leitz Ultropak with "Relief Kondensor" adapted to the microscope was employed. Nearly all the *P. impexus* photographs were taken in the laboratory with a Leitz camera using photographic plates. For microphotographs an Exakta-Varex camera adapted to the Leitz monocular microscope was used.

Systematic Position of *P. impexus.*

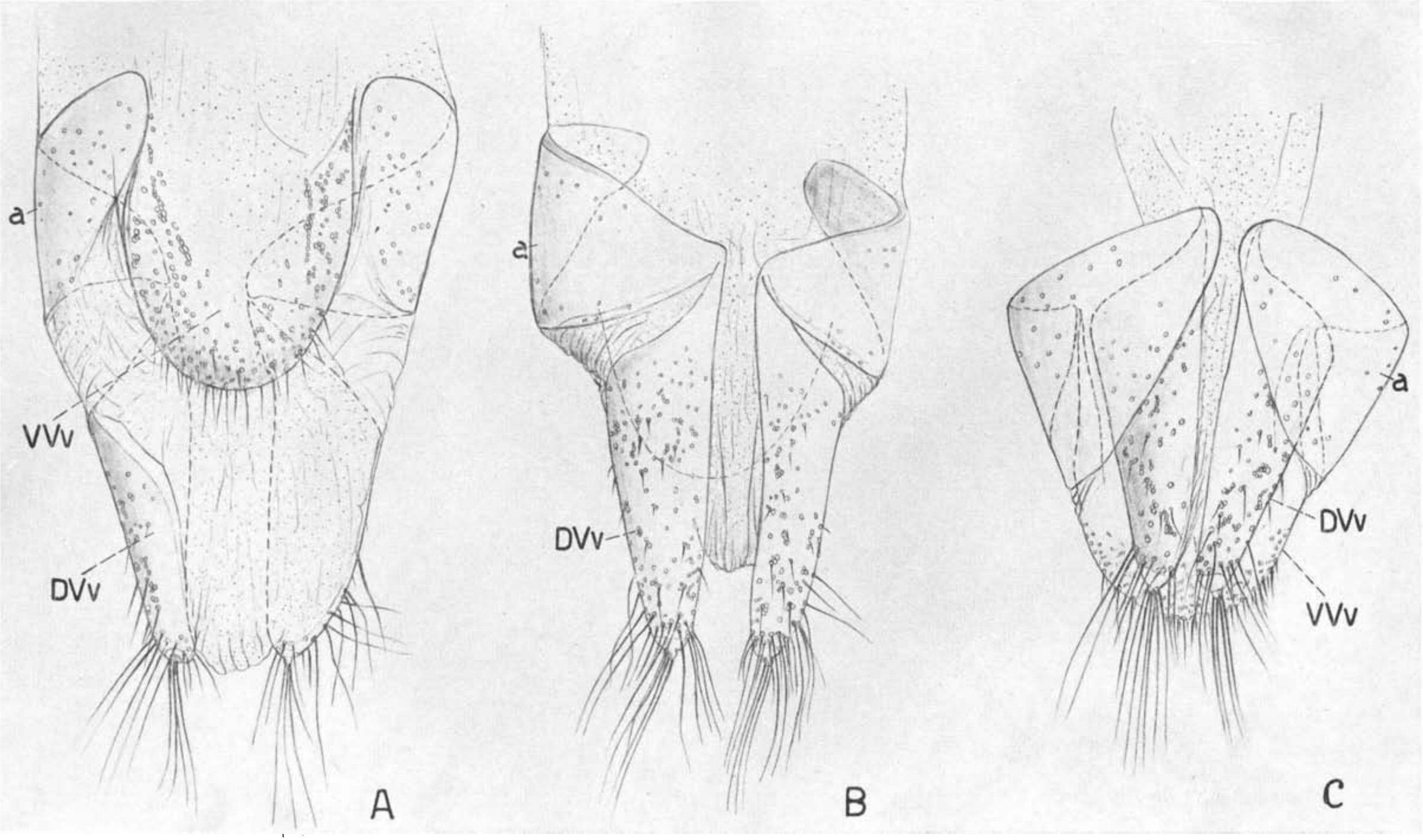
Adult.

P. impexus (COCCINELLIDAE, COCCINELLINAE) (Pl. XI, figs. 1 & 2) belongs to the well known tribe SCYMNINI, including insects which—with very few exceptions—are predators of COCCIDAE, APHIDIDAE, ALEURODIDAE, Thysanoptera and mites. The genus *Scymnus* Kugelann *s.l.* includes a great number of species generally of small size, sometimes difficult to determine and has been subdivided by Mulsant and Weise (Reitter, 1911) into subgenera, with a particular view to the marginal outline of the prosternal carinae and to the form of the abdominal plates (metacoxal lines) at the sides of the first abdominal sternite; the species *impexus* belongs to the subgenus *Pullus*. Later authors (Kuhnt, 1913; Schaufuss, 1916; Caprà, 1927; etc.) accorded generic status to *Pullus*. The generic characters separating *Pullus* from the other genera of the tribe SCYMNINI are reproduced in Plate XII, and do not require special explanations.

Schilder and Schilder (1928) pointed out the necessity of correlating the genus with the particular diet of the different species. The species attributed to the genus *Pullus* feed particularly on APHIDIDAE, but not every species of specific Aphid predators are included in the genus *Pullus*. From the systematic standpoint, constant characters for the separation of the genera *Pullus* Muls. and *Scymnus* Kugelann *s.str.* have not yet been found. The species *impexus* is a predator of *A. piceae* and in the present work it is placed in the genus *Pullus*.

P. impexus is distinguished from the congeneric species and especially from *Scymnus abietis* (Payk.) by the peculiar varying hair direction on the elytra. Anteriorly, near the median body line, this thin light brown, almost yellow, pilosity (Pl. XI, fig. 1) is directed, at first more or less longitudinally, slightly towards the external margin of the wing, then strongly outwards. On the central part of the elytra the pilosity is directed again towards the median line, then it turns outwards on the posterior part of the wing. Along the external posterior margin of the wing, almost at the level with the penultimate abdominal tergite, the lateral pilosity is directed towards the median line, meets with the externally directed one and follows the longitudinal direction as far as the end of the wing. The hairs on the elytra of *P. impexus* are relatively long. The body is oval in shape, one and a half times longer than broad, with a total length of 2–2·3 mm. The colour is uniformly light brown, sometimes dark brown on the meso- and metasternites and partially on the first abdominal sternite.

To supplement possible systematic studies, the genitalia of both of male and female are described. *Male* (Pls. XIII, XIV): The genitalia open between the 8th



Female genitalia of *P. impexus:* A, ventral view; B, C, dorsal view: *DVv*, dorsal valve; *VVv*, ventral valve; *a*, superior part of the dorsal valve.

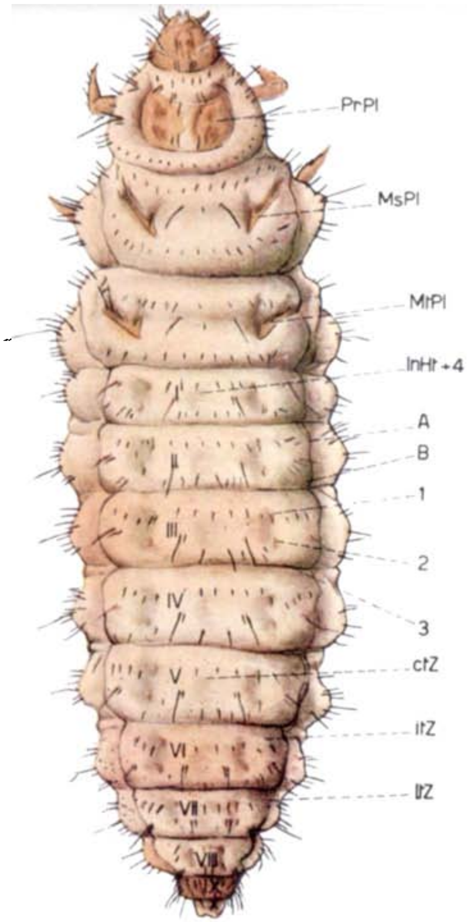


FIG. 1. *P. impexus*, 4th-instar larva, dorsal view: *PrPl*, *MsPl*, *MtPl*, pro-, meso-, metathoracic plates; *InHt* + 4, attachment of the cone-shaped portion of the heart-ostium + insertion of the median external dorsal muscles; 1, 2, 3, insertion of muscles, see text fig. 2; A, B, insertions of lateral muscles; *ctZ*, *itZ*, *ltZ*, central, intermediate, lateral zones of the body; I—X, 1st—10th abdominal segments.

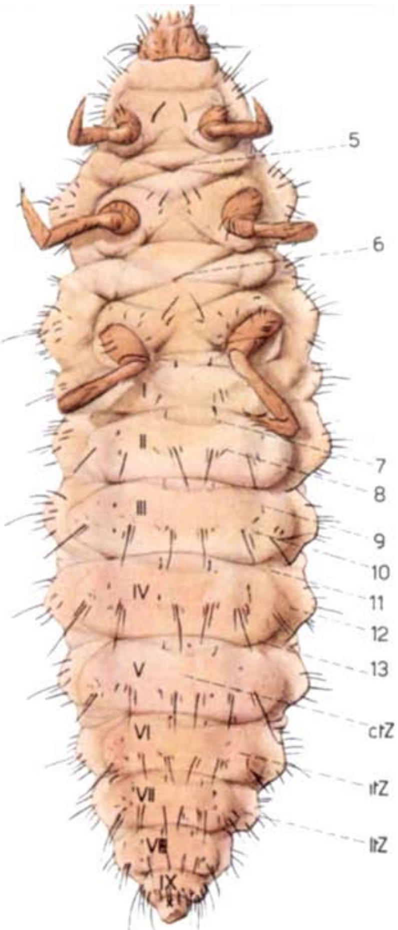


FIG. 2. *P. impexus*, 4th-instar larva, ventral view: 5, 6, muscle complex of the sternal thoracic region, attachment to the skin; 7, 8, 9, 10, 13, insertion of muscles, see text fig. 2; 11, 12, insertion of lateral muscles.

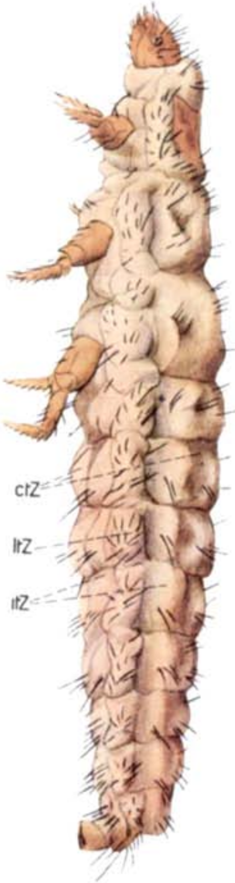


FIG 3. *P. impexus*, 4th-instar larva, lateral view: *ctZ*, *itZ*, *ltZ*, central, intermediate, lateral zones of the larval body.

tergite and the 6th sternite of the abdomen, below the digestive tract. The tergite as well as the sternite is provided with terminal bristles, the latter also with groups of supposed sensilla distributed near the bristles along its posterior margin. The 7th and 8th sternite form a single sclerite situated between the 8th tergite and the 6th sternite. The spicula ventralis constitutes the 9th sternite of a segment of which the tergite has a special form (Pl. XIII); it is laterally elongated and situated below the 8th. The median lobe receives at its base the ductus ejaculatorius which is strongly arched and passes through the basal piece. The basal piece forms a sort of ring closed at its base by the median strut. The basal piece bears three appendages, the basal and lateral lobes; the lateral lobes are more external, elongated, with marginal bristles, whereas the basal one is more internal and has the form of a pointed spade. It has no bristles but seems to be well provided with nerve endings. These appendages are extruded during the act of copulation. The basal piece, basal and lateral lobes together form the tegmen (Wilson, 1927). *Female* (Pl. XV): the genitalia are very simple, composed of a rounded ventral valve with the terminal portion well chitinised, and by two dorsal valves. These valves are posteriorly elongated like the two lateral lobes of the male and anteriorly (a) widened and join the sides of the ventral valves ventrally. The two parts of the dorsal valves are joined by a membrane, except at the median dorsal point. This membrane allows the anterior part of the dorsal valves (a) to descend on the posterior one when the insect is resting (C). The ventral valve and the posterior part of the dorsal valves are provided with bristles and groups of sensilla. On the anterior part of the dorsal valves are isolated sensilla only.

Larva.

The morphological characters of the Scymnid larvae used in van Emden's keys (1949) allow us to arrive at the genus *Scymnus s.l.* but not at the genus *Pullus* Muls. (subgenus in van Emden's keys); in the work of van Emden the species *impexus* Muls. is not mentioned. For the determination of the larvae of *P. impexus* as many details as possible have been set out and some are illustrated in fig. 2 and Plates XVI–XIX. The characters described are common to the four larval instars; thus the mature larva only will be considered.

The fourth-instar larva (Pl. XVI, figs. 1, 2, 3) is 4–5 mm. in length; its maximum width does not exceed 1·5 mm. The larva is rather flat and the body fusiform. The head is very small and slightly sunken into the thorax. The thorax is a little more than a third of the total body length. In nature the mature larva is covered with wax, as are the other larval stages, and appears as a white mass in which it is possible to distinguish both the thoracic segments and the first abdominal ones. With the wax removed, the mature larva is dark orange with a much deeper pigmentation than that found in the first stage larva. The head (Pl. XVII), the thoracic tergal plates (Pl. XIX), the tergum of the penultimate segment and part of the anal segment (Pl. XIX), the legs and points of insertion of the muscles on the skin are brown.

Both dorsally (Pl. XVI, fig. 1) and ventrally (Pl. XVI, fig. 2) the body is divided into three longitudinal zones well defined by the muscular system. The muscular system causes numerous folds which are particularly accentuated on the side of the body and on the sternal thoracic region. The central longitudinal zone (ctZ) is defined between the segments of the thorax and of the abdomen by the large tergosternal muscle (3, Pl. XVI, fig. 1 & 3, text fig. 2; 13, Pl. XVI, fig. 2 & 13, text fig. 2) which limits the mesenteron laterally and the digestive system in general. The separation of the central zone from the intermediate one is marked on the abdominal segments by the points of insertion of two muscles on each tergite (1, 2, Pl. XVI, fig. 1 & 1, 2, text fig. 2) and sternite (9, 10, Pl. XVI, fig. 2 & 9, 10, text fig. 2). On the pro-, meso- and metathoracic tergites the central zone extends between the thoracic plates (Pl. XVI,

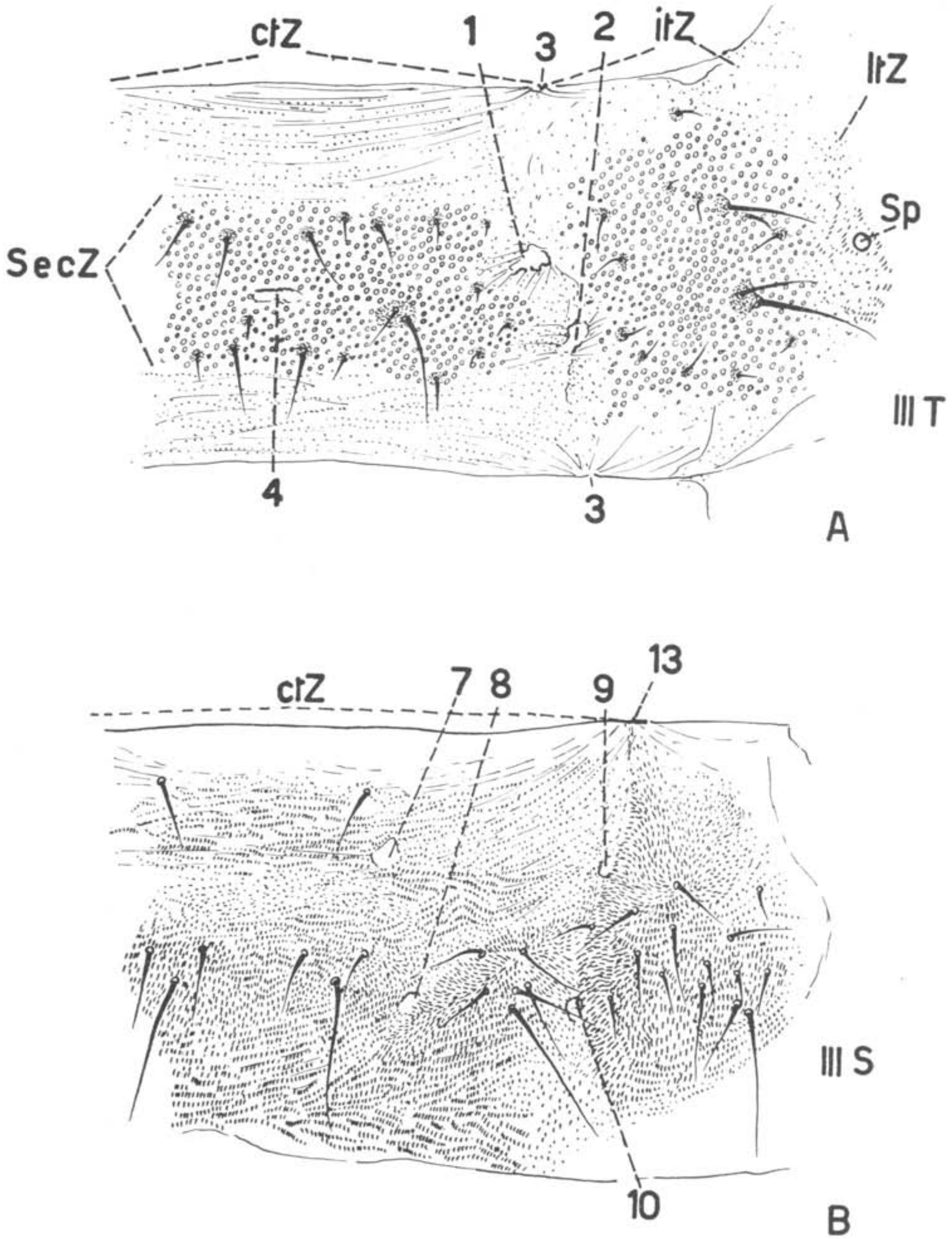
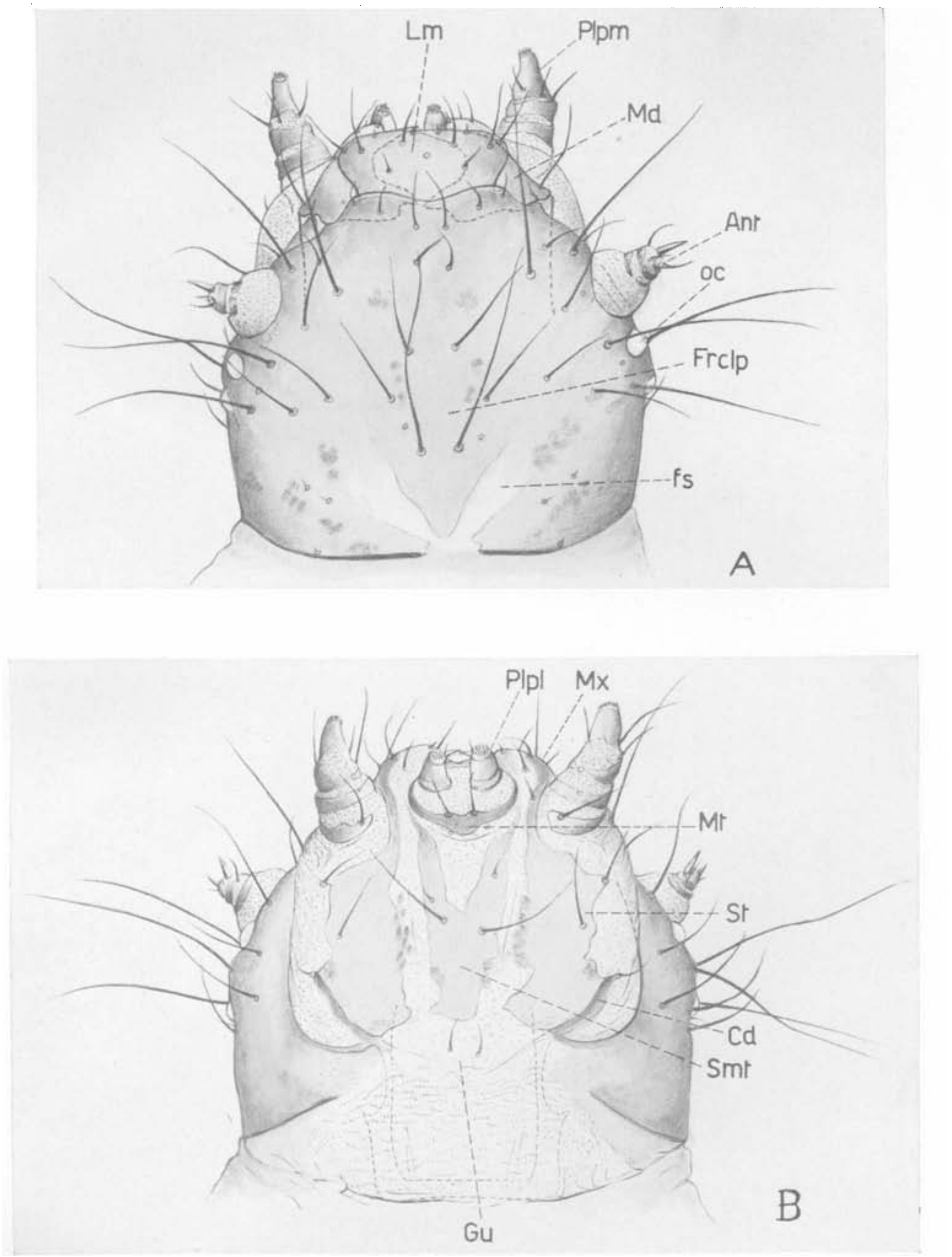
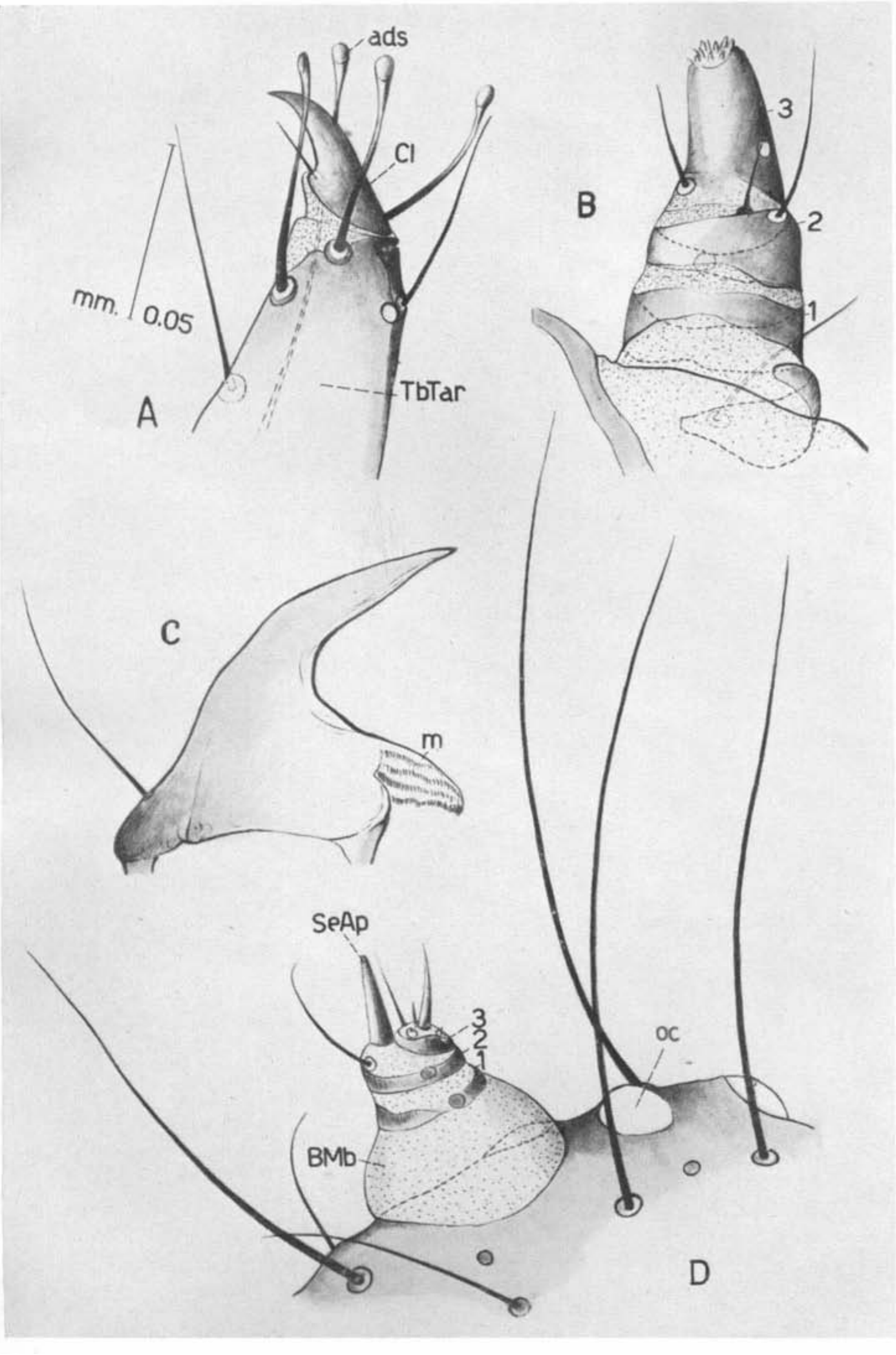


Fig. 2.—Muscle insertions and chaetotaxy on third abdominal tergite A, and sternite B, of fourth-instar larva of *P. impexus*. Insertion of muscles: 1, lateral external dorsal; 2, lateral; 3, tergosternal; 4, the two median external dorsals; 7, median external ventral; 8, lateral external ventral; 9, 10, lateral; 13, tergosternal. *SecZ*, zone of wax secretion; *ctZ*, *itZ*, *ltZ*, central, intermediate and lateral zones; *Sp*, spiracle; III T, III S, third tergite and third sternite of the abdomen.



Head of fourth-instar larva of *P. impexus:* A, dorsal view; B, ventral view: *Lm*, labrum; *Md*, mandible; *FrCpl*, fronto-clypeal area; *Plpm*, maxillary palpi; *Ant*, antenna; *Plpl*, labial palpi; *Mx*, maxillae; *Mt*, mentum; *St*, stipes; *Cd*, cardo; *Smt*, submentum; *Gu*, gula; *oc*, ocelli; *fs*, frontal suture.



Fourth-instar larva of *P. impexus:* A, claw and adhesive setae, lateral view; B, maxillary palpus, dorsal view; C, mandible, dorsal view; D, antenna, dorsal view: *Cl*, claw; *ads*, adhesive setae; *TbTar*, tibio-tarsus; *m*, molar part of the mandible; *Bmb*, basal membrane; *SeAp*, sensorial appendage; *oc*, ocellus; 1, 2, 3, first, second and third sclerotised rings.

fig. 1 & Pl. XIX). On the abdominal tergite of this zone one can perceive a slight inflection of the skin in the centre of each segment. This inflection is caused by two small median external dorsal muscles arising from the posterior segmental suture and converging at the centre of the segment, and by the superior cone-shaped portion of the heart-ostium, the vertex of which is attached to the tergum (InHt + 4, Pl. XVI, fig. 1; 4, text fig. 2). On each abdominal sternite the two transverse folds result from the presence of two pairs of small (median and lateral external ventral) muscles also arising from the posterior margin of the segment.

The intermediate zone (itZ) is regular in all the tergites and in the abdominal sternites. It is separated from the lateral one by a very deep fold (A, B, Pl. XVI, fig. 1; 11, 12, Pl. XVI, fig. 2). The lateral zone (ltZ) and the sternal region of the thorax are folded the most. The points of attachment of the two ventral muscle complexes to the skin (5, 6, Pl. XVI, fig. 2) are evident in the thoracic sternal region.

The mesothoracic plates form an angle of about 45° with the median line whereas the metathoracic plates form a slightly wider angle (Pl. XIX).

The dorsal and dorsolateral strumae (fig. 2) are each provided with two setae, the smaller one set nearer the median body line. The frontal suture (Pl. XVII) is V-shaped, diverging to the base of the antennae where it becomes less distinct. The epicranial suture is absent. The apex of the mandibles is simple (Pl. XVIII). The molar part is prominent and in the shape of a process with hair-like asperities. The second segment of the labial palpi (Pl. XVII) is well developed, much longer than wide and conically truncate. The first segment is very short and ring-shaped. The antenna (Pl. XVIII) is evidently three-segmented, the second segment as long as the first. The sclerotised ring of the second segment of the maxillary palpi (Pl. XVIII) is about twice as long on the outer surface as on the inner one, twice as wide as long on the outer surface and much longer than that of the first segment.

It would be useful to look for other characters in the larva allowing a better definition of the several genera and the determination of species. Perhaps a detailed study of the head chaetotaxy of many related species would offer characters of systematic value.

Distribution and Specificity of *P. impexus*.

In the present work, carried out in Europe, the predator was always found in association with *Adelges piceae*. In Switzerland *P. impexus* was collected in large numbers at Seegraeben near Zurich in 1950 and 1951 and in smaller numbers on the Pfannenstiel, at Winterthur, Aathal, Ottenhausen, St. Gallen, Binz and Wil. At Aathal and Winterthur *P. impexus* was abundant in 1952 only and in Naenikon in 1950 only (spring). The predator was observed in France at Ribeauvillé (Ht. Rhin) by Mr. H. G. Wylie. In Germany it was observed in the south, particularly in Bavaria, by Dr. J. Franz. It is apparently absent from northern Germany since it was not found at Flensburg, near the Danish frontier, where our most northern observation point was located.

According to Korschefsky (1931) *P. impexus* has a wide distribution extending from central Europe to north Africa. Dr. F. Capra, of the Museum of Natural History, Genoa, states that *P. impexus* has been found in Piedmont (northern Italy), there being specimens in the museum from the following localities:—Val Sesia, 28.viii.1922 (F. Solari); Val Pesio (F. Baudi). Baudi (1889) states that *Scymnus abietis* Payk. may be found in quantity by beating the branches of *Abies pectinata* in the Maritime Alps, but Dr. Capra, upon re-examination of the Baudi collection, found *impexus* under the name of *abietis*, originating from Val Pesio. Therefore he indicates that the quotation from Baudi's catalogue refers partly at least to *P. impexus*. Luigioni (1929) found *impexus* in Italy in the Maritime Alps, Tuscany and Lazio. From Tuscany there are also specimens of the predator in the Museum of Natural History, Genoa, from the following localities:—near Pistoia, 1906 and 1922 (F. Solari); Mount Argentaro, 1907 (F. Solari); Vallombrosa, 1930 (A. Gagliardi). Two specimens of *impexus* were found by the author on 29th June 1952, in the *Abies alba* forest of Vallombrosa, where no infestation of *A. piceae* exists. Schatzmayr (1943) has collected *impexus* "in series" on Mount Pollino, on the boundary between Lucania and Calabria, in southern Italy. M. Rungs, of the Service for Plant Protection, Rabat (Morocco), states that *impexus* does not occur in the African region, where *A. piceae* does not exist and *Abies alba* is very rare. M. D'Aguilar, of the National Institute of Agricultural Research, Versailles, informed me that the *impexus* in the Gruardet collection were collected from the Vosges, and those in the Sicard collection from both the Vosges and the Basses-Alpes. Sainte-Claire Deville (1935–38) states that the Coccinellid is to be found in the Vosges, in the subalpine zone of the Basses-Alpes, in the Alpes-maritimes and also in the Pyrenees, especially on *Abies*. Dr. Beier, of the Museum of Natural History, Vienna, informed me that the *impexus* specimens in that Museum originated in Calabria (southern Italy), southern France, the environs of Vienna, from Maehren and also from Hungary.

Thus the distribution of *impexus* in Europe extends southward beyond that of *A. piceae*. In the southern regions of Europe the Coccinellid might have adapted itself to a diet different from the one observed in the present work in the more northerly regions of the Swiss Alps. This is supposition, however, for the exact distribution of the Aphid is not known with certainty. For this reason the degree of specificity of the predator is still unknown. Since in the areas studied *P. impexus* has been always found in the *Adelges piceae* infestations, it must be closely related to this host, due in part to the environment of the Aphid. In captivity *impexus* larvae develop normally on *A. nordmannianae* (Eckstein) (*nüsslini* (C.B.)) as well as on *A. piceae*, whereas in nature pure infestations of *A. nordmannianae* are always free from the predator.

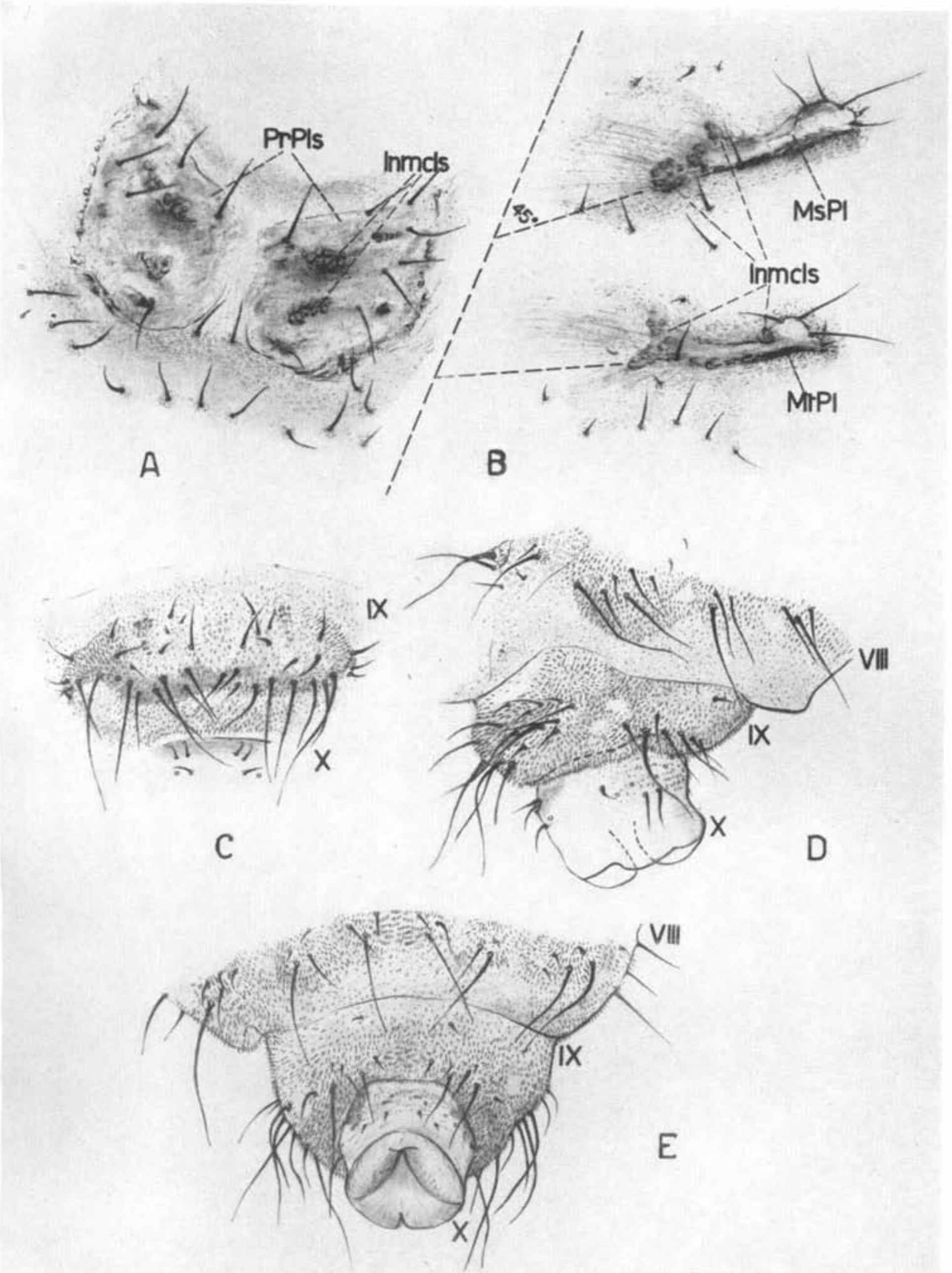
Biology.

Adult.

The longevity of *P. impexus* adults is estimated at 12–13 months. Individuals of the preceding generation are to be found until the end of June on the *Adelges* infestation together with the fresh adults emerging towards the end of May or during June. The adults of the old generation are generally recognisable by the darker colour of the thoracic and the first abdominal sternites.

The adults emerging at the end of May and beginning of June remain on the *Adelges* infestation (spring generation) which is starting to decline. By the beginning of July they are seen less frequently and during this month those remaining change their activity period and become crepuscular. During the day they remain hidden, possibly due to the rather high temperature (28–30°C.). In this period copulation either does not take place or is very rare, and activity is restricted to feeding. At this time the ovaries are developing and maturing in preparation for oviposition in August.

The autumn generation of *Adelges* appears rapidly in August and within a week may change the aspect of the infestation area, as it did at Seegraeben in 1950. Coincident with this rapid increase in the *Adelges* population is the gradual increase in numbers of the adult predators. Copulation occurs followed by heavy oviposition. The highest point of this threefold activity is attained in September (observations at Seegraeben, Pfannenstiel, Aathal and Winterthur). In early October, when the temperature is dropping, the adults gradually



Anatomical details of the larval body of *P. impexus:* A, plates of the prothorax; B, plates of meso- and metathorax; C, D, E, last abdominal segment, dorsal, lateral and ventral views: *PrPls*, prothoracic plates; *MsPl*, *MtPl*, meso- and metathoracic plates; *Inmcls*, insertion of the muscles; VIII, IX, X, 8th, 9th, 10th abdominal segments.

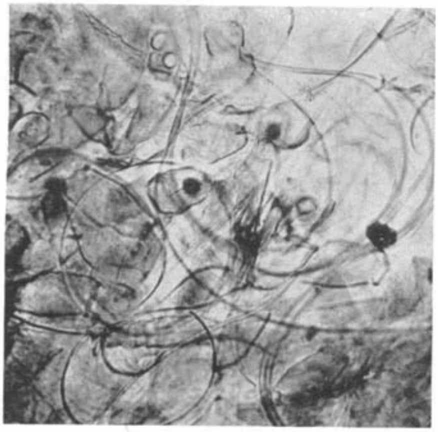


FIG. 1. Residues of sistentes found in the mesenteron of adults of *P. impexus*.

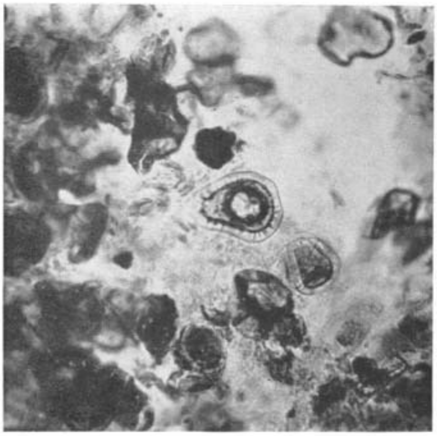


FIG. 2. Fungal spores from the mesenteron of adults of *P. impexus*.

FIG. 3. Egg of *P. impexus* deposited in the *Adelges* wax of the spring generation at Naenikon in 1950.

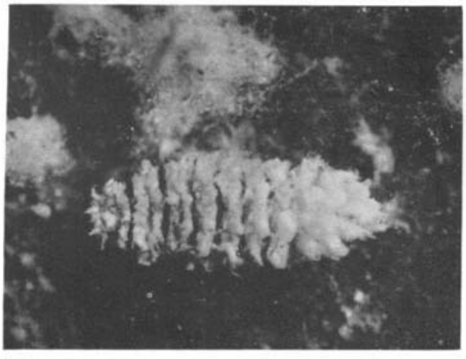


FIG. 4. Fourth-instar larva of *P. impexus*.

FIG. 5. Five mature larvae of *P. impexus* feeding on *Adelges*-infested tree. Photo. Dr. J. Franz.

disappear until none are to be seen towards the middle of the month (observations at Seegraeben, in 1950). Probably this gradual diminution of the numbers of adults begins when the daily temperature reaches 10°C. and is complete when the temperature drops below 5°C. The adults seek their hiding places when the nights become colder in October and remain in these winter quarters until the following spring.

Hibernation of the adults lasts about six months and usually takes place in the crevices of the bark near old knots on infested trees. *P. impexus* leaves its hibernation place in the first sunny days of spring (25th March 1951, at Seegraeben), and returns to hiding at any noticeable drop in temperature. It is usually permanently out of hiding by the time the first-instar larvae appear; this is generally during the first or second fortnight of April. Oviposition is resumed in April and in May. During the last period of its life the adult remains on the *Adelges* infestation, copulating frequently and preying on the Aphid population.

The activity of the adults in relation to that of the Aphid seems to be entirely conditioned by temperature. The adult becomes torpid when exposed to a temperature lower than 10–15°C. A drop in temperature in spring and autumn has a very marked effect and the adults remain motionless, and without feeding, on the infested trees. Activity begins again as soon as the temperature rises. The adults are most active against the *Adelges* population during their main oviposition period in autumn and in the three spring months. They show a very reduced activity between these two periods and remain dormant for about 6 months.

The most important period for the development of the population of the predator is the main oviposition period, which takes place during the autumn generation of *A. piceae*, but both the spring and the autumn seasons are equally important with respect to biological control. The scarcity of food in the month of July and part of August is probably responsible for some dispersal of the predator. Up to the present time no experiments have been conducted to investigate the importance of dispersion. Weise (1884) found *P. impexus* adults in July on *Picea excelsa* in Germany. The supposition of aestivation is not readily acceptable since some individuals are present all summer on the trees attacked by the Aphid. On the other hand it is thought possible that some of the *P. impexus* adults return to the *A. piceae* infestation about the middle of the summer, especially if we compare the number of individuals that remain on the trees in July with the number found later, in September.

A few observations seem to indicate that the adults, having once reached the infested tree, do not show any particular sensitiveness. They do not appear to be able to distinguish a heavily from a lightly infested tree, and their search for food appears to be a random one. Flying was observed very infrequently and consisted of flights of a few metres only.

Diet: *P. impexus* feeds on eggs and sistentes of every instar. Residues of food are found in the mid-gut (Pl. XX, fig. 1). Some dissections have shown the mesenteron to contain at times large numbers of fungal spores (Pl. XX, fig. 2), introduced perhaps with the usual food. It is not known whether any supplementary food is ingested by the predators.

It is difficult to estimate the quantity of food ingested by the adult. This is, of course, dependent upon the season, being greater in the two periods coinciding with spring and autumn generations of *Adelges*. The adults seldom feed when the weather is bad. The density of the Aphid population and that of the population of the other predators present (Diptera, Coleoptera, Neuroptera) on the infestation also has a marked influence on the food consumed. The adult *P. impexus* does not feed at night.

Some information on the voracity of the adults and therefore their value from the standpoint of biological control was collected. The larval activity in the third and fourth instars is considered aggressive, disorganising and rapid, whereas the adult activity is slow but continuous. The following data was assembled during the autumn infestation of *Adelges*.

—An adult feeding for a day at the end of July (24th–27th) consumed on the average 5·3 neosistentes;

—an adult destroyed in one day at the beginning of August (10th–12th) 5·75 neosistentes;

—an adult fed in one day (12th–13th August) on 11 neosistentes;

—in the course of 7 afternoon hours (14th–15th August) an adult fed on 6 neosistentes;

—in 17 hours (the night included) between 14th–15th August, an adult consumed on the average 8 neosistentes and 3 sistentes II;

—in 39 hours (two nights included) between 16th–18th August, an adult destroyed an average of 12 neosistentes and 3 sistentes II;

—in 4 hours (14th August) 5 adults destroyed 10 neosistentes, 70 sistentes II and one sistens IV with 19 eggs.

It is very difficult to express mathematically the average voracity of adults of *P. impexus*, owing to the varying behaviour of each individual in a given time. From the preceding and following data we may learn more about the behaviour of the adults than if we attempt to formulate any opinion concerning their average voracity. The sistentes III and IV are never completely consumed by *P. impexus* adults. The dead or slightly sucked Aphids may be greater in number than those totally devoured and this fact is of particular importance. Generally a waste of food is observed, chiefly when the *Adelges* population is dense.

—In 60 hours (26th–29th August) two adults devoured 7 sistentes III and 9 sistentes IV;

—in 59 hours (26th–29th August) an adult destroyed an average of 3·6 adult Aphids per day;

—in 74 hours (26th–29th August) two adults destroyed 6 sistentes II, 15 sistentes III, 13 sistentes IV with almost all the eggs of the broods;

—in 59 hours (27th–30th August) an adult consumed an average of 3·4 sistentes per day;

—in 48 hours (27th–29th August) two adults destroyed 33 eggs;

—in 50 hours (27th–29th August) two adults devoured 34 sistentes III and 31 sistentes IV with 65 eggs;

—in 48 hours (27th–29th August) three adults devoured 34 sistentes III, 27 sistentes IV with almost all the eggs of their broods;

—in 47 hours (29th–31st August) an adult destroyed an average of 8 Aphids per day;

—in 10 days (27th August–6th September) an adult destroyed 17 sistentes III and 47 sistentes IV with eggs in great numbers;

—in 72 hours at the end August two adults devoured 6 sistentes II, 15 sistentes III and 13 sistentes IV (without eggs);

—in 120 hours (1st–5th September) male and female together fed on 204 eggs;

—in 120 hours (1st–5th September) single adults destroyed an average of 17 sistentes IV with their broods;

—in 120 hours (1st–5th September) an adult fed upon 156 *Adelges* eggs.

The behaviour of one adult in a given time was observed. The adult was placed into a rearing tube with a sistens and its 18 eggs, at a temperature of 22°C. For eight minutes the adult was seen running up and down the tube, passing near the Aphid three times before finally settling at the eggs. Remaining in its normal position, it destroyed one egg after the other, until after the lapse of

6 minutes 21 seconds it attacked the sistens and fed upon it for a period of 6 min. 14 sec. The next egg was devoured during 1 min. 16 sec., it then searched for the other eggs and ate them in 10 min. 23 sec., after which it cleaned its tarsi and mouth parts for one minute. Again it fed on eggs for 2 min. 57 sec., cleaned its tarsi and mouth parts, fed, cleaned again and departed. Altogether the *P. impexus* adult took about 40 minutes to destroy an Aphid with 17 eggs, spending about a third of its time cleaning itself and searching for food. It failed to attack one egg only, perhaps because the feeding behaviour is connected with the touching of prey.

In relation to lack of food, an experiment was set up at the laboratory (at 20°C.) with material collected at Winterthur on 28th August, 1952. Among the adults of *P. impexus* left in the rearing tubes without *A. piceae* for food, mortality was observed on the fifth day of starvation and reached its maximum on the ninth day. The last of the adults died on 11th September. In an experiment performed in Munich beginning on 13th September with material collected at Laimbach, at a temperature varying between 12° and 20°C., Dr. J. Franz noted that mortality among the adults was lower and only 50 per cent. of the insects died in September. The last of the survivors died on 5th October.

Egg and oviposition period.

a. Time and place of oviposition.—Eggs are deposited in nature in protected places or are hidden in the residues of the wax secreted by the Aphids of the spring generation (Pl. XX, fig. 3), especially where the *Adelges* infestation has been intense as at Naenikon in 1950. They are also found in the moss partially covering the trunk of infested *A. alba*, in crevices of the bark and frequently in the crevices of the knots (the most favoured place), in the empty puparia of *Cremifania nigrocellulata* and of *Leucopomyia obscura*, in the pupal exuviae of *Aphidecta obliterata* and in the larval exuviae of *Laricobius erichsoni*. In only one instance was an egg of *P. impexus* found unprotected on the smooth bark.

The location of the eggs on the trees is random, depending upon the conformation of the hiding place and on the position required by the female for oviposition. The eggs may be deposited in a horizontal, vertical or an oblique position on the tree. Probably no fluid is secreted for fixing the egg to the substrate and perhaps the fluid substance covering the egg as it leaves the genital chamber is sufficient. The eggs are generally deposited singly. In the crevice of one knot four eggs were found, separated from one another and perhaps laid by different females. Two eggs close together and laid by the same female were seldom observed. According to Dr. Wichmann the deposition of an egg takes 3 to 4 minutes.

Generally, oviposition begins in August. At Spoeck (Bavaria), in 1950 a female of *P. impexus* was observed by Dr. Wichmann to lay the first egg on 21st July in a rearing tube. In Switzerland the first eggs were found in nature on 20th August 1950, at Seegraeben. The oviposition period extends to the first cool autumn days, generally until October, when the adults seek their winter quarters. The eggs do not hatch till the spring.

Oviposition is practically limited to the period mentioned above. After hibernation, however, the adults continue laying eggs on the infested trees in April and May, and freshly deposited eggs may be observed at the time when the first pupae of the new generation are to be seen (field and laboratory, 1952). Samples of these spring eggs never hatched during the next few months. They were kept in the laboratory from May till October, some at a constant temperature of 20°C., some at temperatures ranging from 20° to 7°C., and a beginning of embryonic development was to be observed in August. It is possible, therefore, that these eggs attain the same embryonic development in autumn as that of the autumnal eggs. Some spring eggs were noticed on the trees in September 1952. Although rare, they were easy to distinguish from the freshly deposited autumn ones.

In July 1951, when all the adults of the new generation had emerged, a third-instar larva was noticed on an infestation in Germany. According to Dr. Franz, the same thing happened in the previous year. Such an exceptional case suggests the possibility of an abnormal hatching of an autumnal egg rather than the hatching of an egg laid in the spring. Even if late egg-hatching (which very seldom happens) could be associated in nature with the spring oviposition, these isolated cases are of no importance from the biological control point of view. The larvae emerging from overwintered eggs provide the only successful action against the *Adelges* infestation.

b. *Fecundity*.—The results of ten experiments carried out simultaneously in the laboratory and lasting three days are given here. They were investigated at a constant temperature of 20°C. at the end of August 1952.

TABLE I.

Oviposition in captivity and degree of parasitism of adults of *P. impexus*.

Rearing tube no. ..	1	2	3	4	5	6	7	8	9	10
Adults per tube ..	19	19	19	18	19	18	20	20	19	20
Females per tube ..	12	4	8	6	10	10	10	11	5	8
No. of eggs laid (3 days)	37	19	23	38	32	42	19	45	16	16
Adults parasitised by *Centistes scymni* ..	2	3	6	3	—	3	7	3	8	10
Females parasitised by *Centistes scymni* ..	2	—	3	—	—	1	4	2	2	5
Laying females ..	10	4	5	6	10	9	6	9	3	3

Material collected at Winterthur, August 1952.

From this Table we infer that 65 females deposited 287 eggs in three days; an average of three eggs per female every other day. If it be considered that the autumn oviposition period lasts from two and a half months to three months, then a female will deposit from 80 to 100 eggs. It must be kept in mind that towards the end of the period (October) the weather is not as favourable as it is in August or September.

From the Table it is seen that account was taken only of the first three days of oviposition in captivity since the number of eggs deposited diminishes considerably in the subsequent days, and after the sixth day mortality among adult males and females was observed. In rearing tube no. 8 the number of the eggs fell from 45 to 4 in the second series of three days, and remained at 4 in the third series; in tube no. 6 the number of eggs fell from 42 to 9 and in the third series to 8.

c. *Development of the eggs*.—The embryonic development was studied in collaboration with Dr. G. Krause of Munich during the winter 1950–51, using material collected both in Switzerland and in Germany. In nature, during the winter, eggs of *P. impexus* go through a latent life stage during embryonic development from the moment when the abdominal extremity of the embryo reaches the dorsal mid-point of the egg to the moment when its abdomen shortens (so that its extremity reaches the posterior pole of the egg) and the eye pigmentation appears. The period of latency does not occupy a very definite period. It has been generally observed that this stage is reached in September, as was the case at Seegraeben in 1950, and such embryos may be found as late as in February. It is therefore possible that the eggs deposited in the period August–September develop rather rapidly until they reach a certain embryonic stage and in this condition they remain until the end of the winter.

The eggs kept in the laboratory (Munich) for the winter hatched in April and did not develop more rapidly than in the field. This suggests that room temperatures with very little fluctuation do not affect the length of the embryonic life. According to Dr. Franz, eggs left under natural winter conditions until 20th December at Laimbach, and then taken to room temperatures did develop faster, one specimen hatching in January as a normal larva. It is therefore possible for the embryo to develop from the moment it reaches its latent stage, and further development may be caused by a considerable change of temperature.

d. Vitality and mortality of the eggs.—*P. impexus* eggs collected at Seegraeben and on the Pfannenstiel (near Feldmeilen) were put on filter paper in petri-dishes covered with muslin (organdie) and kept at the meteorological station on the Pfannenstiel (850 m.) until 10th December. The temperature dropped to a minimum of −6°C. on 5th December. Thirty eggs were held for three consecutive weeks at −12°, −25°, −12°C., respectively, and thirty eggs for three weeks at −12°C. without interruption. They were then returned to natural winter conditions, where the temperature reached −8°C. only once at the end of February (1951). All the eggs held for three weeks at −12°C. hatched simultaneously on 21st April. Eighty per cent. of the eggs held at −25°C. hatched on 21st April, 15 per cent. hatched during the next three days and the mortality was 5 per cent. The eggs overwintered on the Pfannenstiel (winter minimum −9°C.) also hatched simultaneously on 21st April and a mortality of 3 per cent. was noted.

From these few experiments on the resistance to winter temperatures in Europe it seems probable that any eggs deposited in Canada would survive the extremes of weather to be encountered there.

It is difficult to evaluate the mortality of eggs deposited in nature, since they are present at the end of summer along with numerous larvae of *C. nigrocellulata*, *C. latitarsis*, *L. obscura*, *A. thompsoni*, *C. ventralis*, etc. All these predators probably destroy eggs of *P. impexus*. In addition there are mites living gregariously in the same overwintering places as the eggs and perhaps feeding upon them. Without the activity of the above-mentioned predators, it is thought that the egg mortality of *P. impexus*, from climatic extremes, would be very low or non-existent.

e. The egg and its hatching.—The egg (Pl. XX, fig. 3) is oval in shape, rather stocky and orange in colour. It measures 0·6–0·7 mm. in length and is twice as long as broad. The egg becomes lighter in colour at the end of the winter. At the end of its embryonic development it loses its gloss and just before hatching it is possible to see the segmentation of the mature embryo. At the right time the embryo breaks the chorion (by means of one of the egg-bursters) causing a short longitudinal split. Afterwards, the embryo presses its thorax against the opening and with longitudinal movements it succeeds in cutting the chorion with the next egg-burster. With movements of expansion and contraction and pressure against the chorion, the embryo extends the two slits and breaks the connection between. The hatching process lasts about 45 minutes.

In nature the time of hatching of overwintered eggs in any particular locality and year is fairly restricted. Nevertheless some variation of a few days exists due to the position of the tree in the infested zone and to the position of the egg on the tree. On the Pfannenstiel (near Feldmeilen) in 1950 the eggs hatched almost simultaneously between 1st and 3rd May and in the next year on 21st April. At Seegraeben they hatched in 1951 between 15th and 20th April, at Laimbach near Munich some days later. In 1952 egg-hatching took place at the beginning of April at Aathal and Winterthur$_1$ ("Försterhütte") and in the second half of the month at Winterthur$_2$ (fig. 3).

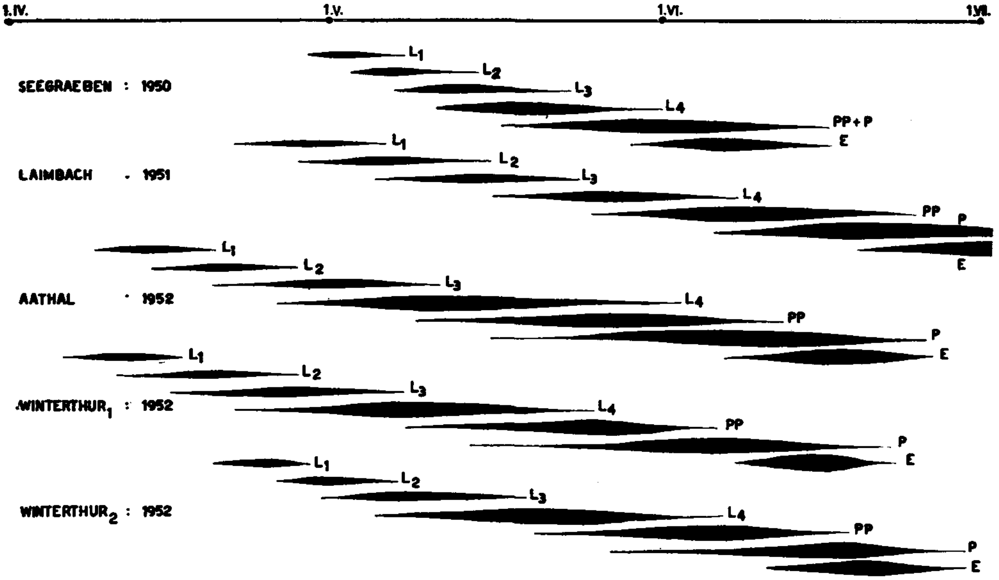


Fig. 3.—Development of the pre-imaginal instars of *P. impexus* in different localities and in different years.

Larval development.

a. The first-instar larva.—The newly hatched larva is orange with brown ocelli and brown egg-bursters and leaves the chorion without feeding on it. On the *Adelges*-infested trunks the newly hatched larvae are moving about near the old knots, near the crevices or on the moss, where the eggs had been deposited. At first they live more or less gregariously, then they disperse among the Aphid population. On the Pfannenstiel on 3rd May 1950, 130 larvae were gathered around the knots in a space of 80 cm. of trunk at 3 m. from the ground. First-instar larvae were found at Seegraeben from the end of April to 2nd–3rd May 1950 (fig. 3), having hatched after a cold period lasting for nearly all the second half of April. In 1952 at Aathal first-instar larvae were observed between 8th and 19th April, at Winterthur$_1$ between 5th and 14th April, and at Winterthur$_2$ between 19th and 28th April (fig. 3).

At a laboratory temperature of about 17°C. the first larval instar lasts five days.

Diet: The first-instar larva feeds on eggs and Aphids. The Aphids are attacked on their tergal region and the larva sinks its mouth parts into the wound. No haemolymph oozes from the wound since the predatory larva has such strong sucking power. The feeding activity of the larva is rather slow and requires from 5 to 10 minutes to suck an egg of *Adelges*. The larva sinks its mandibles into the chorion and slowly sucks the egg contents. Beneath the anterior fronto-clypeal region of the head the movements of the internal mouth parts may be observed. The egg is emptied slowly, flattens, then is generally filled and emptied over and over again with a dark violet-coloured liquid originating in the mesenteron. The chorion of the egg is not consumed. The mid-gut liquid injection occurs when feeding on the Aphids as well, but is less visible.

The first-instar larva seldom feeds upon eggs or Aphids isolated on the bark. It prefers to plunge its head into a little heap of eggs near an egg-laying sistens and destroys many eggs without changing position.

b. The second-instar larva.—In nature the second-instar larvae of *P. impexus* were observed at Seegraeben in the first 10 days of May 1950, in 1951 at the end of April and at Laimbach during the first half of May. In 1952 they were noted at Aathal and Winterthur$_1$ at the end of April and at Winterthur$_2$ at the end of April–beginning of May (fig. 3).

At a laboratory temperature of about 17°C. the second larval instar requires four days for completion.

The feeding activity of the second-instar larva is more rapid than in the preceding instar. A newly moulted larva devoured 19 eggs and 4 sistentes IV in an hour in the laboratory. A single egg can be sucked in 30–90 seconds. It was noted that in this larval stage injection of the mid-gut liquid into the prey is a continuous process and the reabsorption of the injected liquid which is an intermittent process appears related to slight larval body movements. The destruction of a sistens IV takes longer, about 3–5 minutes. The Aphid is attacked and sucked so that it appears to have only about half of its initial volume remaining. The mid-gut liquids are then injected and the Aphid is refilled. The liquid injection is so violent at times that the Aphid may have a volume larger than its initial one. A larva of *P. impexus* of this stage that was left four days on 10 cm^2. of densely infested bark, devoured practically everything, leaving behind very few eggs and Aphids.

c. The third-instar larva.—In the first half of May 1950 the third-instar larvae were observed at the same time in Seegraeben in Switzerland and at Spoek in Bavaria (observed by Dr. Wichmann). In 1951 they were seen at Seegraeben at the beginning of May and in Laimbach for two weeks in the same month. At Aathal and Winterthur$_1$ the larvae of this stage were present in the infestation at the end of April–beginning of May 1952, and at Winterthur$_2$ in the first fortnight of May (fig. 3).

The third larval stage lasts four days at the usual temperature of about 17°C.

The voracity and the mobility of these larvae on the tree increases considerably as compared with that of second instar. The larva III is able to destroy an egg in 20–50 seconds, and a sistens IV in 1–3 minutes. Its voracity was recorded as follows:

Larva III, two days after moult, observed in captivity during a given time at Laimbach near Munich at laboratory temperature 17° C.

In 30 seconds 1 *Adelges* egg destroyed, mid-gut liquid twice injected,
75 seconds 1 *Adelges* egg destroyed, mid-gut liquid 4 times injected,
15 seconds food search,
45 seconds 1 *Adelges* egg destroyed, mid-gut liquid 3 times injected,
15 seconds 1 *Adelges* egg destroyed, mid-gut liquid twice injected,
45 seconds 1 *Adelges* egg destroyed, mid-gut liquid twice injected,
15 seconds food search,
90 seconds 1 *Adelges* egg destroyed, no injection,
15 seconds food search,
75 seconds 1 *Adelges* egg destroyed, no injection,
120 seconds food search,
120 seconds 1 *Adelges* egg destroyed, no injection,
30 seconds food search,
30 seconds 1 *Adelges* egg destroyed, no injection,
20 seconds food search,
70 seconds 1 *Adelges* egg destroyed, no injection,

10 seconds food search,
40 seconds 1 *Adelges* egg destroyed, no injection,
20 seconds food search,
50 seconds 1 *Adelges* egg destroyed, once injected,
150 seconds food search,
60 seconds 1 *Adelges* egg destroyed, mid-gut liquid twice injected,
120 seconds 1 *Adelges* egg destroyed, no injection,
60 seconds food search,
60 seconds 1 egg punctured, slightly sucked and then left. It contained an Aphid embryo.

The *P. impexus* larva destroyed 15 *Adelges* eggs in a rearing tube in 23 minutes. The eggs belonged to two broods only. After eating the 15th egg, roving began on the bark without any further egg destruction.

The following test with a larva starved for two hours indicates larval voracity:

Larva observed for two hours, laboratory temperature 25° C.

Larva feeds on 1 egg ;	39 sec. —	searches for food ; 11 sec. ;
„ „ „ 1 egg ;	54 sec. —	„ „ „ 32 sec. ;
„ „ „ 1 Aphid ;	2 min. 7 sec. —	„ „ „ 21 sec. ;
„ attacks a sistens but leaves it after 36 sec. ;		
rest time ;		
larva feeds on 1 Aphid ;	3 min. 14 sec. —	searches for food ; 35 sec. ;
„ „ „ 1 Aphid ;	1 min. 2 sec. —	„ „ „ 4 sec. ;
„ „ „ 1 Aphid ;	29 sec. —	„ „ „ 2 sec. ;
„ „ „ 1 Aphid ;	25 sec. —	„ „ „ 12 sec. ;
„ „ „ 1 egg ;	1 min. 48 sec. —	„ „ „ 15 sec. ;
„ „ „ 1 egg ;	1 min. 15 sec. —	„ „ „ 21 sec. ;
„ „ „ 1 egg ;	50 sec. —	„ „ „ 6 sec. ;
„ „ „ 1 egg ;	54 sec. —	„ „ „ 5 sec. ;
„ „ „ 1 Aphid ;	1 min. 36 sec. —	„ „ „ 6 sec. ;
„ „ „ 1 egg ;	27 sec. —	„ „ „ 2 sec. ;
„ „ „ 1 egg ;	2 min. 4 sec. —	„ „ „ 3 sec. ;
„ „ „ 1 egg ;	1 min. 1 sec. —	
rest time ;		
larva feeds on 1 egg 49 sec., egg not entirely devoured ;		
rest time ;		
larva feeds on 1 egg ;	1 min. 15 sec. —	searches for food ; 3 sec. ;
„ „ „ 1 Aphid ;	1 min. 29 sec. —	„ „ „ 2 sec. ;
„ „ „ 1 egg ;	29 sec. —	„ „ „ 11 sec. ;
„ „ „ 1 egg ;	1 min. 17 sec. —	„ „ „ 3 sec. ;
„ „ „ 1 Aphid ;	7 min. 55 sec. —	„ „ „ 13 sec. ;
„ „ „ 1 egg ;	2 sec. (only punctured)	searches for food ; 36 sec.;
„ „ „ 1 egg ;	1 min. 12 sec.	
rest time ;		
larva feeds on 1 Aphid ;	4 min. 6 sec. —	searches for food; 7 sec. ;
„ „ „ the same Aphid again ;	9 sec.	
rest time ;		
larva feeds on 1 egg ; 7 sec., egg not entirely devoured ;		
rest time ; searches for food 7 sec. ; rest time ;		
larva feeds on 1 egg ;	59 sec. —	searches for food ; 35 sec. ;
„ „ „ 1 egg ;	1 min. 16 sec. —	„ „ „ 1 min. 3 sec. ;
„ „ „ 1 egg ;	1 min. 12 sec. —	„ „ „ 24 sec. ;
„ „ „ 1 egg ;	47 sec. —	

In two hours of observation the larva III fed upon 20 eggs and ten sistentes.

d. The mature larva.—Mature larvae (Pl. XX, figs. 4 & 5) have been observed at Seegraeben in 1950 during the last 20 days of May, in great number at Naenikon between 9th and 20th May where the density of fourth-instar larvae of *P. impexus* reached 25–30 individuals per dm^2., at Binz near Zurich until the beginning of June and at Kalberstein in Bavaria (observed by Dr. Wichmann) until 28th May. In 1951 mature larvae were found at Seegraeben from 6th May, at Laimbach from 15th May until the first ten days of June and at Berchtesgaden a little later. In 1952 at Aathal and Winterthur, larvae IV were present on the infestation from the end of April and during whole May, at Winterthur$_2$ during May until beginning of June (fig. 3).

At a laboratory temperature of about 17°C. the fourth larval stage lasts 17 days, the first half with normal larval activity on the *Adelges* infestation and the second half corresponding to the prepupal period. On the chart (fig. 3) this second period has been described separately since sufficient data were collected at Laimbach, Aathal and Winterthur.

The mature larvae are particularly voracious. They sink their heads into the *Adelges* broods with particular violence, break them up and destroy them. Sometimes the destruction of an egg does not require more than ten seconds and one larva destroys whole broods in rapid succession. These fourth-instar larvae seem to specialise in egg destruction rather than in killing Aphids. Considering the short developmental time of the larva IV, limited to 5–7 days, among the *Adelges* population, its efficiency is very great. The increase of the body volume of the larva in the first four days after the moult (fig. 4) is a good measure of estimating the larval voracity. Such an increase in size does not occur during other larval stages.

At Naenikon the Aphid population on 9th May 1950 entirely covered the trunk of *A. alba*, making them whitish. The population was almost completely destroyed in ten days time by a population of fourth-instar larvae of *P. impexus* estimated at 3,500–4,000 larvae for each infested tree. In this infested locality together with *P. impexus* there existed only a few specimens of other predatory species, such as *L. obscura*, *C. ventralis*, *L. erichsoni* and *A. thompsoni*. The

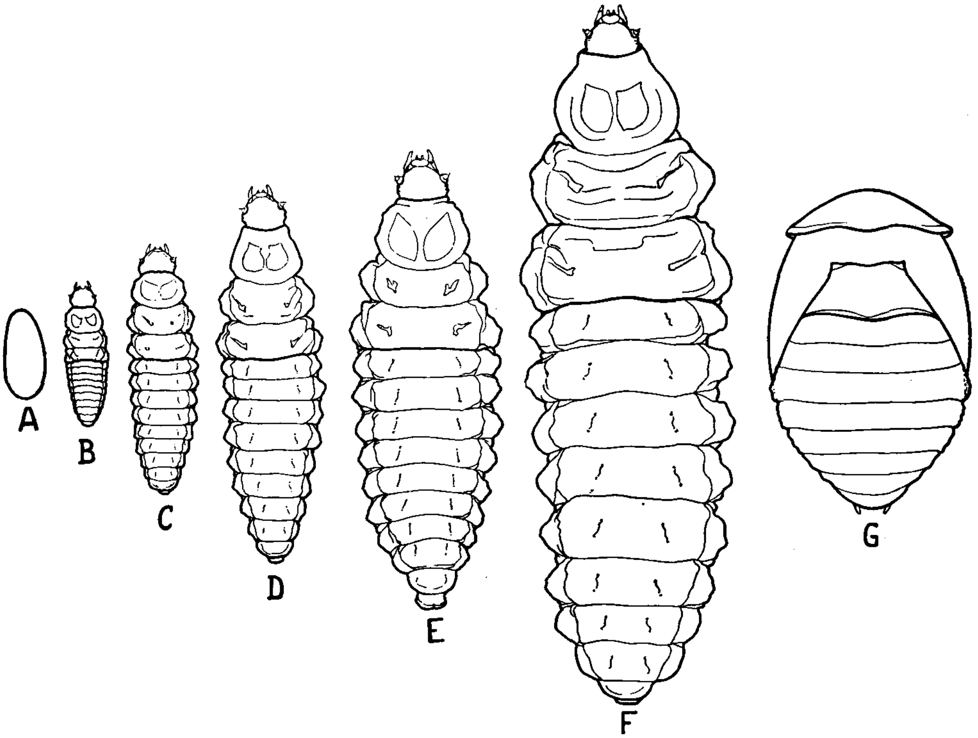


Fig. 4.—Increase of the body volume during the larval time: A, egg; B, first-instar larva after hatching; C, D, E, 2nd-, 3rd- and 4th-instar larva, respectively, after moult; F, four-day-old mature larva; G, pupa.

destruction of the *Adelges* population was effected for all practical purposes by the *impexus* larvae only.

It is a striking and conspicuous fact that mature larvae descend from the upper to the lower part of the infested tree a few days before the prepupal period is beginning. This behaviour was noticed at Aathal early in May 1952. Every day the *P. impexus* larvae were collected from the lower portion of the tree (about 3 m. of trunk) for rearing in cages, and every day, for many days, on the same portion of the tree mature larvae were found by tens and sometimes by hundreds. Beneath the moss covering the basal portion on an infested tree at Winterthur 700 pupae were collected on 6th June 1952. In the last ten days of May a concentration of mature larvae was noticed here on the lower part of the trees. The results of collecting of pupae has always been very poor on those portions of the trees situated above 3 m. from the ground.

e. General considerations on the larval stages.—The newly hatched larva of *P. impexus* measures a little more than 1 mm. and is light orange in colour. The mean maximum width of the head is 0·204 mm., varying between 0·189 and 0·216 mm. The larva is easy to recognise, having on its prothoracic plates the characteristic egg-bursters, strongly chitinised and standing out on the orange-coloured body. To separate the subsequent instars the head-capsules must be measured. The measurements were taken from a hundred individuals in each stage collected at different localities. The maximum head width for the second-instar larva averages 0·252 mm., varying between 0·229 and 0·270 mm.; for the third-instar larva it averages 0·309 mm., varying between 0·297 and 0·324 and for the mature larva has a value of 0·386 mm., varying between 0·364 and 0·405 mm. (fig. 5). The colour of the second-, third- and fourth-instar larva, as well as that of first-instar after a short period of feeding, is darker orange than the newly hatched one or those immediately after a moult.

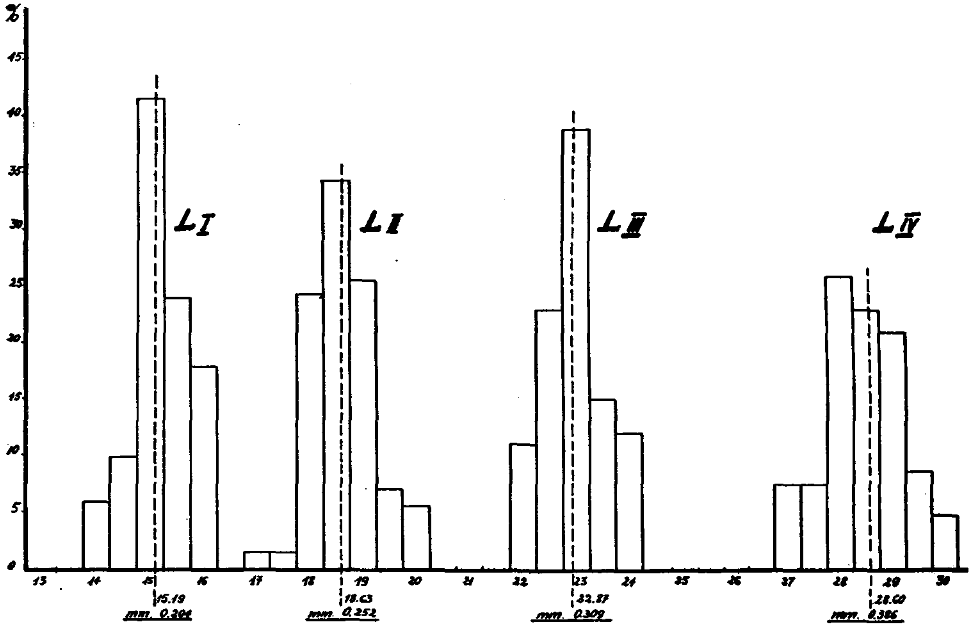


Fig. 5.—Maximum head width in each larval stage. The actual measurements of head width are shown in micrometer units, the mean for each instar being converted into mm.

The remarkable increase of the body volume from the first to the fourth

FIG. 1. Fourth-instar larva of *P. impexus* immediately after the moult.

FIG. 2. A prepupa of *P. impexus* in the spun network on the bark.

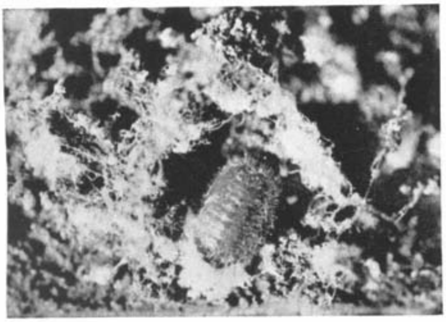


FIG. 3. A pupa of *P. impexus* in the spun network on infested bark.

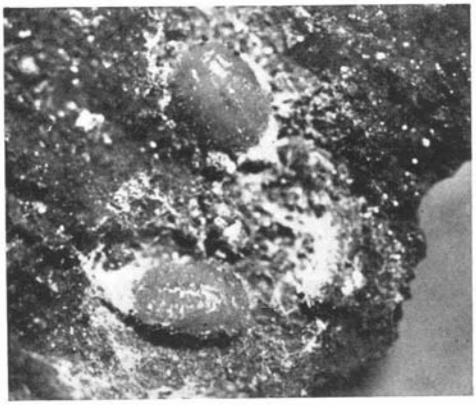


FIG. 4. Pupae of *P. impexus* on the bark without spun network.

instar is shown in fig. 4. This increase is particularly evident during the last instar from the moult to the prepupal period. The length-ratio between the head, thorax and abdomen of larva I is 6 : 15·5 : 19, of the mature larva after the moult 12 : 40 : 65 and of the four-day-old mature larva 12 : 67 : 105. The increase in body volume of the mature larva during the first four days is more or less equal to the increase in the first three stages combined. The importance of the larva IV is therefore evident from the biological control standpoint. The thoracic and almost the whole of the abdominal cavity are occupied by the mid-gut only. The four-day-old mature larva measures about 5 mm. in length, after the third moult 3·2 mm., the early third-instar larva after the second moult measures 2·5 mm. and the second-instar larva after the first moult measures 1·75 mm.

The exuviae of larvae of *P. impexus* are not generally found among the Adelgid population since moulting (Pl. XXI, fig. 1) usually takes place in protected bark areas (old knots). In the laboratory rearing tubes the larvae moult beneath the bark or in a dark corner. The moulting process is rapid and the wax secretion starts at once.

Prepupa and pupa.

The pupal stage begins after a prepupal period of 8 to 9 days. In previously described hiding places on the bark surface (see p. 262) the fourth-instar larva spins a kind of " cocoon " composed of silk filaments (Pl. XXI, figs. 2, 3). The mature larva in the laboratory rearing tube moves to the darkest corner and the spun network composing the " cocoon " has no definite arrangement. The base of the network in contact with the bark consists of intertwined vertical and horizontal filaments joining the floor of the hiding place to the overhead covering. In this irregular cocoon network may be found residual *Adelges* wax, wax of the larva left from the spinning process, dead crawlers and residues of sistentes IV and of eggs, etc. The threads are fixed to the substrate with a brown-coloured secretion. The network looks closely woven and probably is an aid in preventing the entrance of predators. When the overhead covering of the hiding place is removed the whole network collapses (Pl. XXI, fig. 3). The filaments extend farther than the immediate surroundings of the prepupa, indicating that the spinning movements are irregular and therefore do not fit any set pattern. Not every mature larva spins this network (Pl. XXI, fig. 4). During the prepupal period the mature larva gets considerably shorter, looks withered (Pl. XXI, fig. 2) and the wax covering all the tergites appears disorderly. The moult then begins and the next stage lasts about ten days at a laboratory temperature of 20°C.

The larval stages of *P. impexus* are synchronised with the *Adelges* population, especially the fourth-instar larva which seems to be closely related to the most active time in the *Adelges* population development. The pupal period on the other hand is present during the decline of the host population.

Pupae were found at Seegraeben in 1950 from 15th May onwards, at Naenikon from 20th May onwards, and at Winterthur on 2nd June. In 1951, at Seegraeben the first pupae were collected in the first fortnight of May, at Laimbach near Munich at the beginning of June only, at Tussenhausen (Bavaria) on 17th June. At Aathal and Winterthur$_1$ the first pupae were noted on 14th–15th May 1952, and at Winterthur$_2$ a little later (fig. 3).

General considerations of the life cycle of P. impexus *in Switzerland and in Germany.*

From the observations described above it is concluded that *P. impexus* has only one generation a year. The complete cycle from the hatching of the egg to the emergence of the adult takes about six weeks. Eggs deposited on the infested trees in the late summer and the beginning of the autumn produce larvae in April after a slow embryonic development during the winter. The hatching of the larvae coincides with the start of the *Adelges* infestation and the larval development coincides with the most active time of the spring generation of the Aphid. *Thus the mature larvae achieve the greatest value from the viewpoint of biological control.* The imagines, on the contrary, although they are present from spring to autumn have a *slow but persistent* influence and do not succeed in changing the degree of infestation of the autumn generation.

Factors limiting the Development of the Population of *P. impexus*.

In addition to the influence of the host, *A. piceae*, on the development of the population of *P. impexus* there are other factors of environmental resistance in the form of parasites. These parasites are the two new species, *Scymnophagus mesnili* and *Centistes scymni*, described below. *C. scymni* is by far the more effective, parasitising an average of from 25 to 30 per cent. of the females of the new generation (22·8 per cent. at Winterthur (see Table I); 32 per cent. at Aathal). This results in the loss of a third or even a half of the *P. impexus* larvae, which would otherwise be present on the infested trees the next spring. *S. mesnili* attacks a rather small percentage of pupae and therefore has no great influence on the numerical status of the Coccinellid population.

Scymnophagus mesnili.

S. mesnili is a new species of the palearctic region, the specific name for which was proposed by Dr. Ch. Ferrière in 1950, and he has kindly allowed his original description of the species to be published in this paper.

a. Description by Dr. Ch. Ferrière.

" *Scymnophagus mesnili*, n.sp. (Pteromalidae, Pteromalinae):

" Female: body dark bluish-green, the scutellum more aeneous, the abdomen " shining green at the base and along the sides. Antennae brown, scape and " flagellum below yellowish. Legs with the coxae greenish-brown, the femora " light brown, the tibiae and tarsi yellow, with very faint brownish lines on " middle and hind tibiae. Head finely shagreened, narrowed behind the eyes; " ocelli forming a very low triangle, the lateral ocelli not much farther distant " from each other than from the eye-margins; eyes short oval; temples very " narrow in the middle; cheeks straight, converging towards the mouth; front " margin of clypeus excavated in the middle; both mandibles with four teeth. " Antennae inserted in middle of the face, short; scape reaching to the level of " the front ocellus, pedicel longer than broad, three anelli very small, the five " funicle joints subquadrate, subequal in length and in breadth, club three-" jointed, not broader than the funicle and about as long as three preceding " joints together. Thorax very finely reticulate, the reticulation a little broader " on the mesonotum than on the scutellum; parapsidal furrows very short; " scutellum with a narrow transverse furrow; propodeum without median carina, " but with a rounded nucha, which is more strongly punctate than the rest of " the propodeum. Wings hyaline; marginal vein somewhat thickened, shorter " than the postmarginal vein and about as long as the narrow stigmal vein. " Legs relatively short and narrow. Abdomen about as long and as broad as " the thorax, the first visible tergite as long as the third of the abdomen; " ovipositor scarcely protruding. Length 1·2 mm.

" Male unknown.

" Type deposited at the British Museum (Natural History), London; several " females have been obtained at the laboratory of Prof. L. P. Mesnil, to whom " I have the pleasure to dedicate this species.

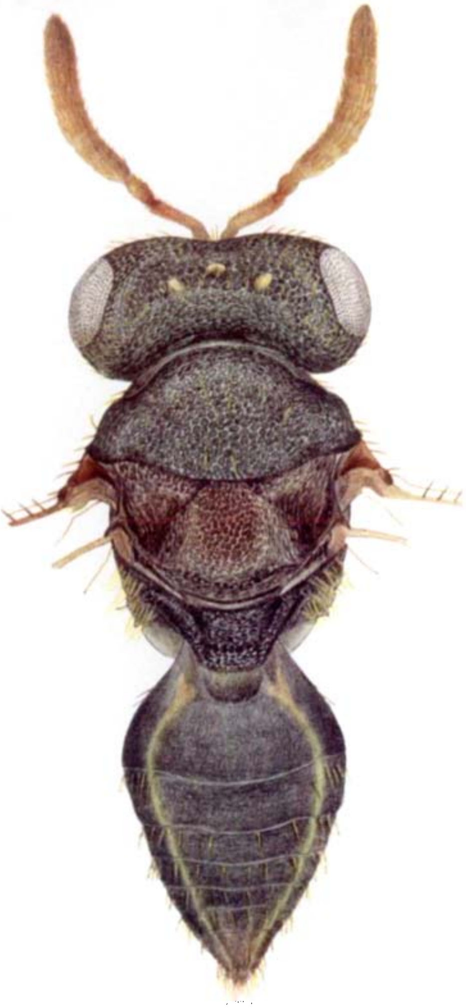


FIG. 1. *Scymnophagus mesnili*, sp.n., dorsal view.

FIG. 2. *Scymnophagus mesnili*, sp.n., lateral view.

" This is the first representative of the genus in Europe, but it is very " closely related to the North American species *S. townsendi* Ashm. Mr. A. B. " Gahan kindly sent us specimens of this species from the United States and " from Japan, which were obtained from Scymnid pupae. Compared with our " European species, they can be distinguished as follows:

" *S. townsendi*: body black, scarcely dark bluish on the face only, greenish " at the base of the abdomen; abdomen and legs more yellow; head larger, " distinctly broader than the thorax; abdomen narrower than the thorax, more " pointed behind; propodeum as strongly punctate at base as on the nucha;

" *S. mesnili*: body dark green; antennae and legs more brownish, the coxae " more or less dark metallic green; head scarcely broader and abdomen not " narrower than the thorax; propodeum with punctation smaller at the base " than on the nucha.

" The specimens from Japan are similar to the American species in the black " body and the relative size of head, thorax and abdomen, but have darker " coxae. Another species, *S. secundus* Crawford 1912 (*Proc. U.S. nat. Mus.*, " **43**, p. 172) was obtained in East Africa, Uganda, from a *Scymnus* sp. or allied " genus; specimens of that species from Kenya, bred from the Coccinellid " *Hyperaspis senegalensis* (Muls.) are in the British Museum. This species is " also much similar to *S. townsendi*, but differs, according to Crawford, by the " more distinctly differentiated furrow on the scutellum and the less distinct " sculpture of the propodeum laterad of the lateral folds.' A fourth species, " *Xenocrepis mexicana* Girault 1916 (*Ent. News*, **27**, p. 223), parasite of a " Coccinellid predator of *Saissetia oleae* (Bern.) in Mexico is probably also a " *Scymnophagus*.

" The genera *Scymnophagus* Ashm. and *Xenocrepis* Foerst. are very closely " related and very similar in the more or less broadened marginal vein and the " short antennae with three anelli and five funicle joints. They cannot be " synonymised however since they differ mainly by the form of the propodeum, " which in *Scymnophagus* has a distinct punctate nucha and no median carina, " whereas in *Xenocrepis* there is no nucha but a distinct median carina and well " marked lateral folds.

" *Xenocrepis* Foerst. is a valid genus the type of which, based on Foerster's " specimens, should be *X. pura* Mayr. It was a confusion of names which " induced Ashmead to synonymise *Xenocrepis* Foerst. and *Caenocrepis* Ths., " two quite different genera. *Xenocrepis pura* Mayr has five funicle joints and " is a real PTEROMALINAE, whereas *Caenocrepis arenicola* Ths. has six funicle " joints and belongs to the METASTENINAE, with two spurs on the hind tibiae."

b. Source of the material.—The first adults of *S. mesnili* (Pl. XXII, figs. 1, 2; text fig. 6) emerged in the laboratory at Feldmeilen from pupae of *P. impexus* collected at Seegraeben between 16th and 25th June 1950. In Germany Dr. J. Franz observed adult emergence between 28th June and 7th July in Spoeck (Bavaria). In the spring of 1951, at the German substation of our laboratory (Munich) some examples emerged from pupae of *P. impexus* which had remained, because of parasitism, in the pupal stage from the preceding spring. The parasite was also observed in 1951, in two Bavarian localities (Tussenhausen and Laimbach) infested with *A. piceae*. In the Swiss localities Naenikon, Pfannenstiel and Winterthur the Coccinellid pupae were found free from parasites.

c. Life history of S. mesnili.—The life history of this Pteromalid is not yet completely known. From parasitised pupae of *P. impexus* collected in June 1950 at Seegraeben all the parasites emerged in the laboratory within ten days (Pl. XXIII, figs. 1, 2). From parasitised pupae collected at Spoeck (Bavaria) on 6th June of the same year, the emergence of the parasites was *partial* and a number of *Scymnophagus* remained in larval diapause until the next spring, *i.e.* for a period of ten months. It is not yet known what happens to the parasites which emerge in June and July without having gone through a diapause period. Possibly a secondary host in which *S. mesnili* is able to develop further generations exists. This would allow the parasites to emerge the next spring.

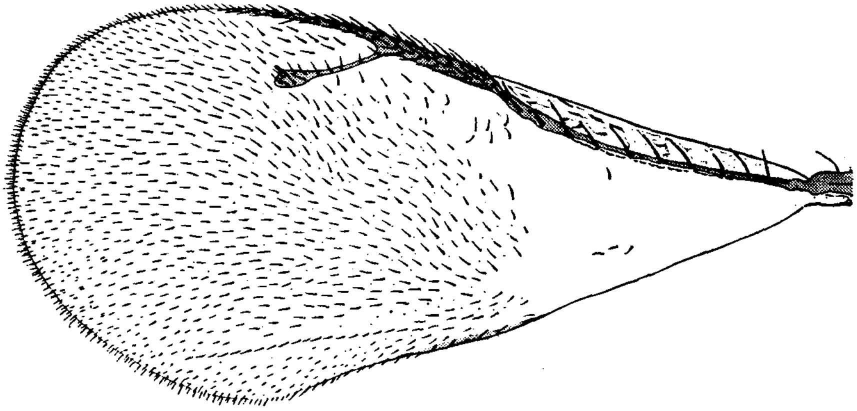


Fig. 6.—Left fore wing of *S. mesnili.*

Scymnophagus has not emerged from any other predators of *A. piceae* in the laboratory and the diagram of the life history as shown in fig. 7 corresponds to the data at present available. The parasite attacks the pupae of *P. impexus.*

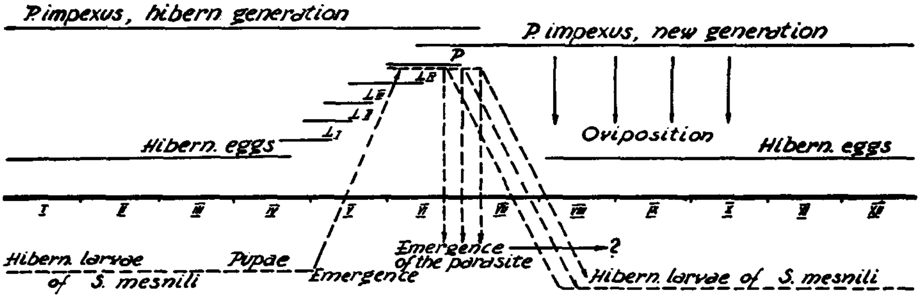


Fig. 7.—Life history of *S. mesnili* in relation to that of *P. impexus.*

The degree of parasitism by *S. mesnili* was not very high in the past few years. Out of 1,000 pupae of *P. impexus* collected at Tussenhausen (Bavaria) on 17th June 1951, 126 were parasitised; out of 1,124 pupae collected at Laimbach, near Munich, in the first days of June, 61 (5·4 per cent.) contained parasites; out of 1,200 pupae collected at Aathal (Switzerland) in May 1952, only ten proved to be parasitised.

The parasitised pupae of *P. impexus* are easy to distinguish by their light brown colour, which differs from the reddish brown of the healthy ones. Each Coccinellid pupa usually contains two individuals of *S. mesnili* lying face to face (Pl. XXIII, fig. 1) in their pupal stage. The parasitised pupae are to be found in the spots where *P. impexus* normally spends its pupal period.

FIG. 1. Two pupae of *S. mesnili* in a pupa of *P. impexus*; Seegraeben, June 1950.

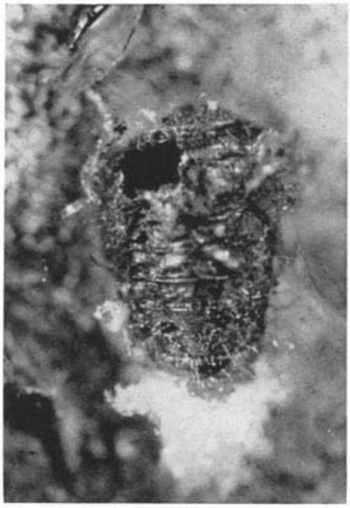


FIG. 2. Hole in the thorax of a pupa of *P. impexus* after the emergence of the parasites (*S. mesnili*); Seegraeben, July 1950.

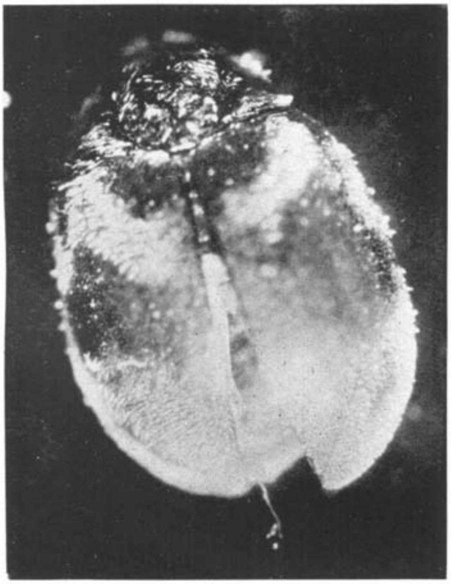


FIG. 3. Normal appearance of adult of *P. impexus* after emergence of larva of *C. scymni*.

FIG. 4. Cocoon of *S. scymni* on the infested bark of *Abies alba*.

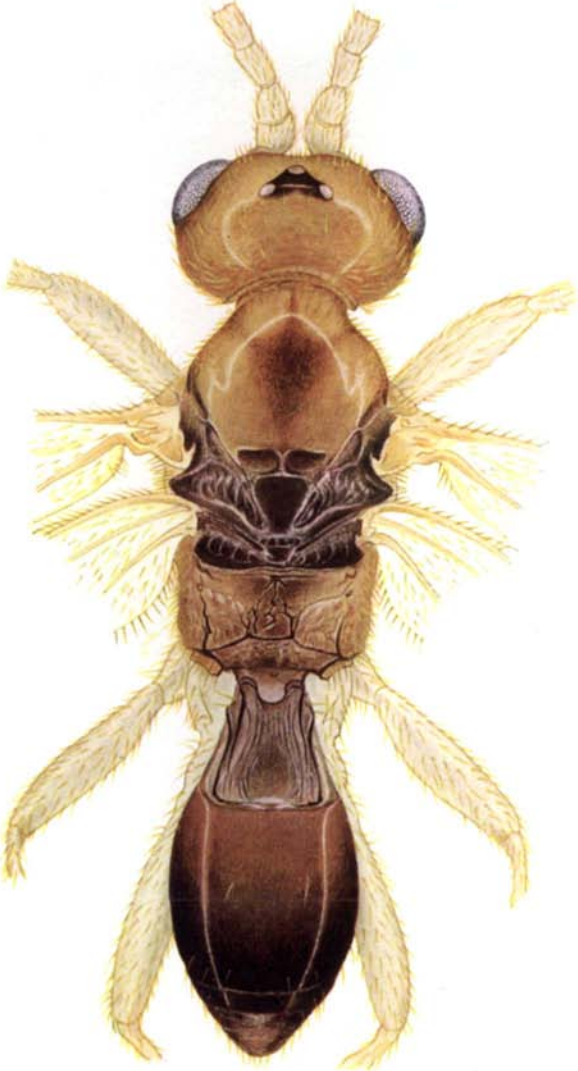


FIG. 1. *Centistes scymni*, sp.n., dorsal view.

FIG. 2. *Centistes scymni*, sp.n., anterior and posterior wings.

Centistes scymni.

The original description of this species, drawn up by Dr. Ch. Ferrière, is, with his permission, included below.

a. Description by Dr. Ch. Ferrière.

" *Centistes scymni*, n.sp. (Braconidae, Leiophroninae):

" Female: head orange-yellow, only the stemmaticum blackish; the clypeus " and mandibles lighter yellow. Thorax and abdomen black, the propleurae, " mesopleurae and metapleurae reddish, as are also the first abdominal segment " and the sides of the second. Antennae brown, the three first joints yellow. " Legs entirely yellow, coxae included. Stigma and veins in the wings brown.

" Head smooth, narrowed behind the eyes, ocelli forming a small regular " triangle, the lateral ocelli twice closer to each other than to the eye-margin; " seen from in front, the head is rounded, the vertex arched, the cheeks short; " clypeus well separated from the face; mandibles with the upper tooth longer " and more pointed than the lower tooth. Antennae with 22 joints, almost as " long as the body, inserted in the middle of the face, the points of insertion " more distant from each other than from the eyes; first joint short, about twice " as long as broad, the second rounded, the third a little longer than the first, " the following joints all longer than broad, but gradually shorter and narrower. " Thorax smooth, only the propodeum more or less finely rugulose; mesonotum " without parapsidal furrows; scutellum small; propodeum with a distinct arched " transversal carina in the middle, the supero-median area faintly marked. " Wings large, as long as the body, the stigma broad, triangular, the first " abscissa of the radial vein very short, about three times shorter than the " breadth of the stigma, the second abscissa curved, the radial cell closed; two " cubital cells, the first separated from the discoidal by a distinct vein; recurrent " vein interstitial, shorter than the transverse-cubital vein; anulus postfurcal; " parallel vein inserted near the base of the brachial cell, where this cell is open; " nervellus not broken. Legs relatively strong, with short ciliae. Abdomen " shorter and narrower than the thorax, the first segment a little longer than " broad, finely striate, the following segments smooth, slightly compressed from " the sides. Ovipositor curved like a scythe and directed under the abdomen " towards the thorax, reaching beyond the middle of the abdomen. Length " 2 mm.

" Male unknown.

" Type deposited at the British Museum (Natural History), London.

" Although some Leiophroninae have been described from different parts of " the world, the members of this subfamily are still rare and not well known. " Only two species of *Centistes* had been found in Europe, both described by " Nees. *C. fuscipes* Nees is distinguished by its short antennae with 19 joints, " its short ovipositor, as long as the fourth of the abdomen and its brown legs; " *C. lucidator* Nees, more common, has long antennae with 24 joints, ovipositor " as long as the first segment, and is entirely shining black with only mandibles " and clypeus testaceous; *C. scymni* is easily distinguished by its entirely yellow " head, reddish sides of the thorax, antennae with 22 joints and longer ovipositor, " which is longer than half the length of the abdomen.

" Nothing is known about the biology of the two older species. In De " Gaulle's catalogue, *C. fuscipes* is given as the parasite of an *Elachista*, " probably by error. The Leiophroninae are all probably parasites of small " Coleoptera as are *C. scymni* and the few *Leiophron* spp. of which the hosts " are known."

b. Source of the material.—This parasite (Pl. XXIV, figs. 1, 2) was found in five localities: at Seegraeben (Switzerland) and Spoeck (Bavaria) in 1950, at Laimbach (Bavaria) in 1951 and at Aathal and Winterthur (Switzerland) in 1952. In other localities checked by this laboratory the parasite was not found in the three-year period. Mature larvae issued on 15th May 1950 and on 16th and 17th May 1952 from adults of *P. impexus* placed in rearing tubes at the Feldmeilen laboratory. From the resultant cocoons adults of *C. scymni* emerged at the end of May, and on 1st and 2nd June, respectively (temp. 20°C.).

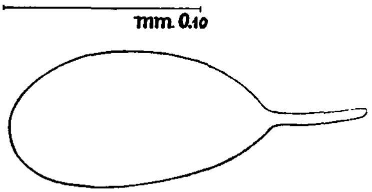


Fig. 8.—Egg of *C. scymni.*

c. Life history of the parasite.—*C. scymni* was present in 1950 on the *Adelges* infestations in June; it attacks *P. impexus* adults of the new generation. The parasite generally emerges from its cocoon after the appearance of the first new adults of *P. impexus* (laboratory checks). It attacks the host from the side, thrusting an egg (fig. 8) through the pleura into the abdomen. The eggs deposited in adults confined in rearing tubes were always arranged along the sides of the abdomen extending from the thorax to the genital opening. The stalk is always turned inwards. In the rearing tubes adults of *P. impexus* were found containing 3–5 parasite eggs in their abdominal cavities. Only one of them develops into a normal larva. The embryonic development takes place in June and July and the first-instar larva hibernates in the thoracic-abdominal cavity. The larva resumes development at the beginning of the spring and on maturing leaves the host through a hole cut between the 5th and 6th abdominal tergites (Pl. XXIII, fig. 3). Emergence is usually near the middle of May (observations at Seegraeben in 1950 and at Aathal in 1952). The mature larva issuing from the host measures about 3 mm. in length, is rose coloured and very active. It spins a white silken cocoon 2–2·5 mm. long (Pl. XXIII, fig. 4) and after a two-week pupal period (laboratory temperature of 20°C.) the adult emerges and attacks *P. impexus* of the new generation (fig. 9).

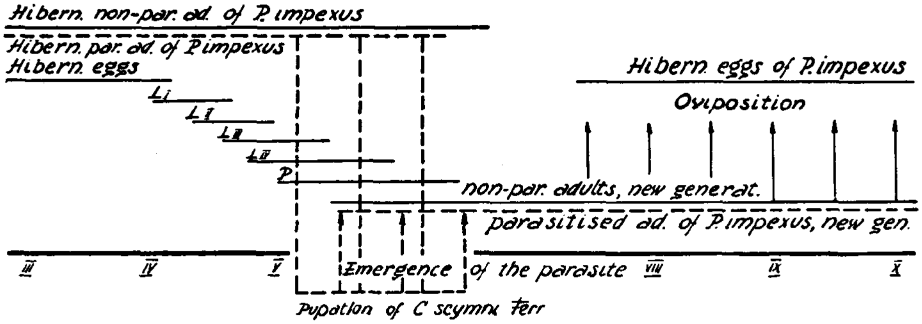
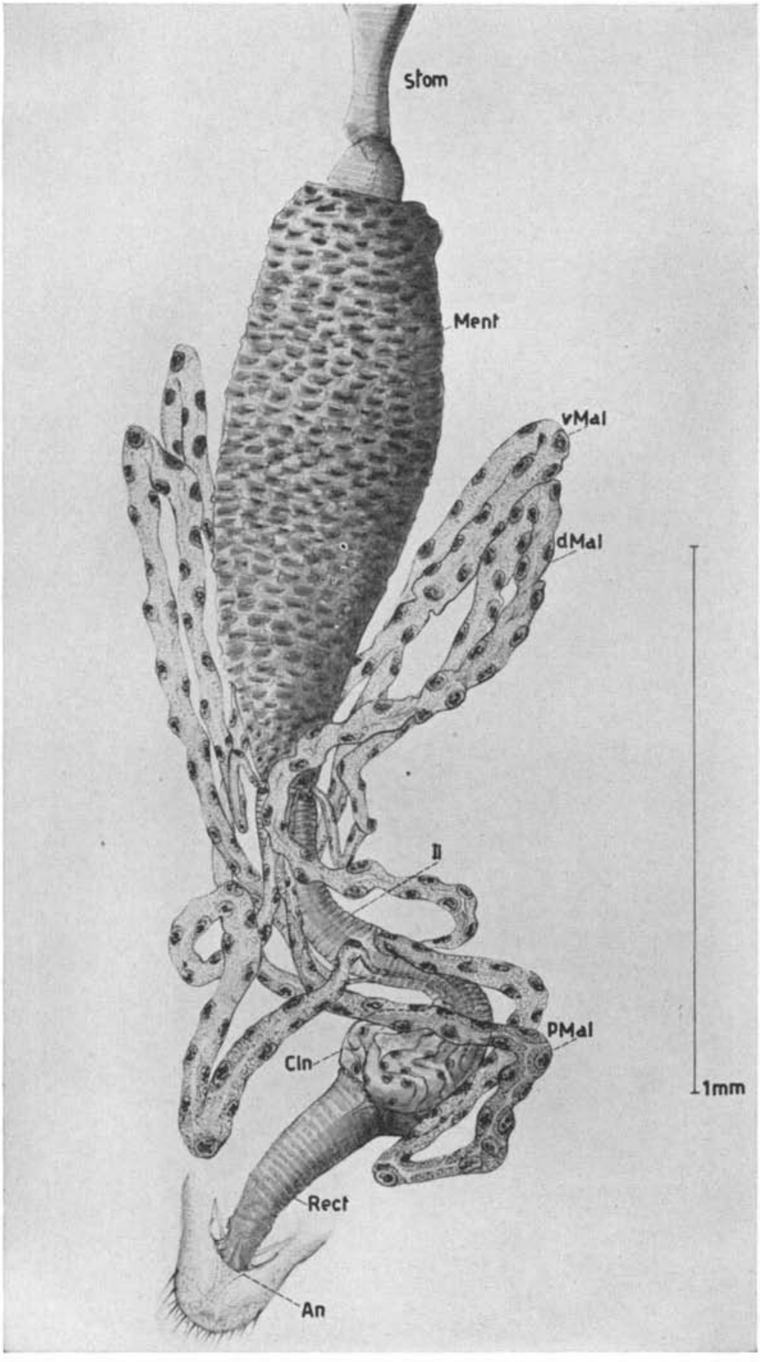


Fig. 9.—Life history of *C. scymni* in relation to that of *P. impexus*.

d. Effect of the parasite and reaction of the host.—The growth of the parasite in the body of the host causes at first a strong inhibition of the development of the reproductive organs both in the male and in the female. From the practical point of view the parasite action on the male is of no significance. On the other hand the effect it has on the female of *P. impexus* is important, inasmuch as the inhibition of ovarian development (fig. 10) prevents oviposition during the



Digestive tract of *P. impexus* adult: *Stom*, stomodaeum; *Ment*, mesenteron; *Il*, ileum; *Cln*, colon; *Rect*, rectum; *An*, anus; *d-*, *v-*, *pMal*, dorsal, ventral and posterior Malpighian tubes.

summer and the beginning of autumn. In the spring, the hibernated first-instar larva continues its growth and matures in a 6- to 8-week period. At this time it slowly consumes all the abdominal contents except the sclerotised parts. The parasitised adults of *P. impexus* live normally until the parasite larva emerges. The host reaction to the inhibition of ovarian development is marked by an abnormal production of adipose tissue which eventually fills the abdominal cavity.

The degree of parasitism by *C. scymni* is difficult to estimate, since a large

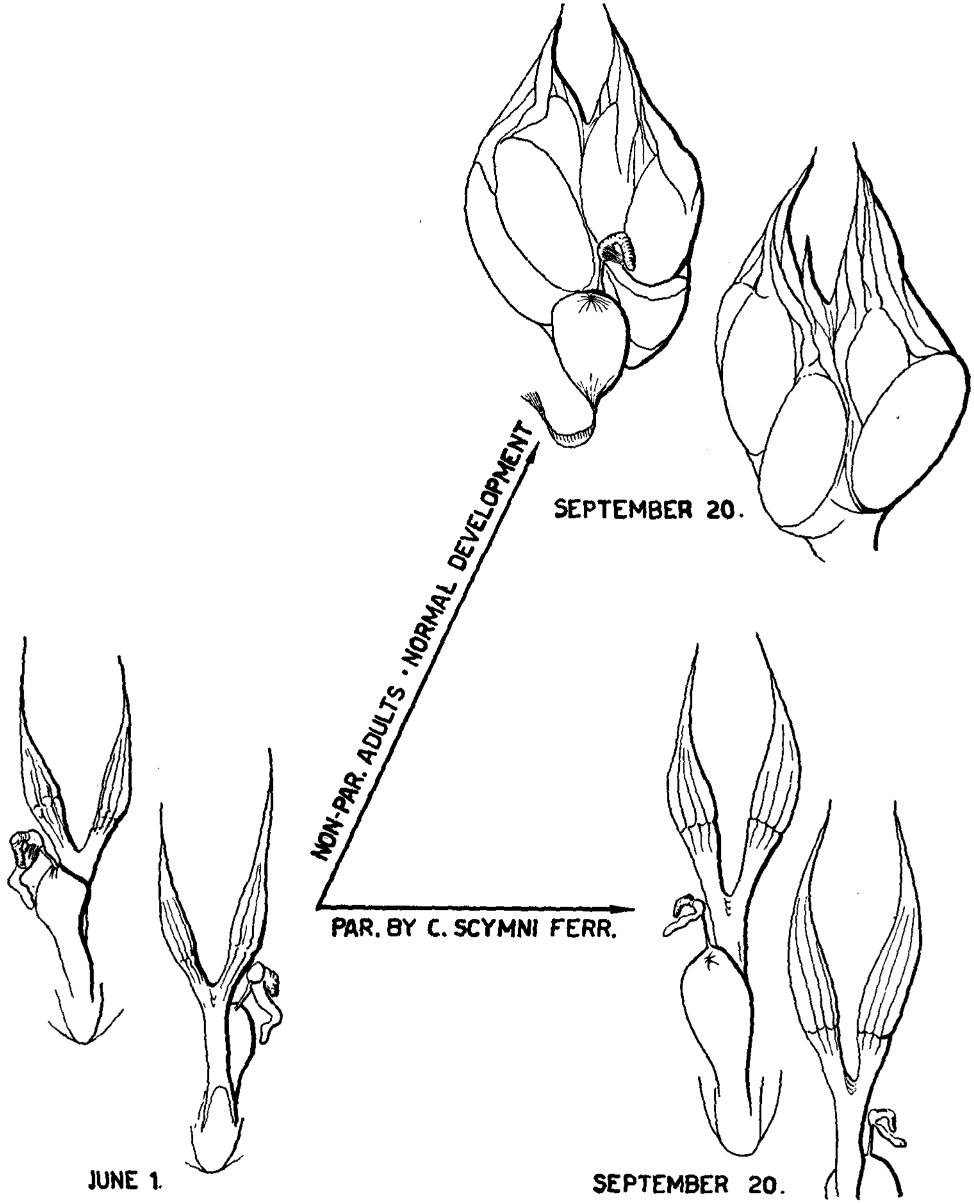


Fig. 10.—Inhibition of ovarian development caused by *C. scymni*, compared with the normal development of ovaries in non-parasitised adults of *P. impexus*.

sample of adults of *P. impexus* should be taken in the autumn and in the spring. This is practically impossible for the adults are never observed in great number on the infestations of *A. piceae.* At the end of August 1952 it was possible to collect 191 adults of *P. impexus* at Winterthur. Forty-five of these were parasitised (23·5 per cent.). Of 130 adults of *P. impexus* collected at Aathal on 5th September 1952, 38·5 per cent. were parasitised. In both localities it was noticed that the degree of parasitism was higher in the males of *P. impexus* than in the females, with the result that 64 per cent. of the adults parasitised were males at Aathal, as were 58 per cent. of the parasitised adults at Winterthur (see Table I). At Seegraeben, the percentage parasitism in September 1950 amounted to 30 per cent., whereas in the preceding spring (from 6th to 13th May) 67 per cent. of the adults collected were parasitised. The percentage parasitism in spring appears high compared with that among insects collected in the autumn, possibly because non-parasitised adults die before or during the cold winter period. In the rearings a slight mortality occurred in September after the sixth day of captivity, but among the dead insects there were none which had been parasitised. On the other hand, the fat reserve with which the parasitised adults of *Pullus* are provided before hibernation might be the necessary requirement for survival.

Gregarines.

a. Source of the material.—In the mesenteron of both sexes of *P. impexus* (Pl. XXV) collected from spring to autumn in 1950 at Seegraeben and in 1951 at Laimbach, some Sporozoa belonging to the Gregarinida, group Cephalina (Steinhaus, 1947, 1949) were found. The body consisted of two compartments, the smaller being the protomerite and the larger the deutomerite which contains the nucleus. These cephaline gregarines were never found in larvae of *P. impexus* and are supposedly specific for the adults.

b. Notes on the life history and morphology of the known stages.—Though many dissections of mesenteron were made from adults collected during the whole year, it was possible to find only the stages composing the first part of the gregarine's normal cycle, that is from the sporozoite to the sporont. The remaining portion of the cycle is unknown and it is not yet possible to advance any satisfactory hypothesis.

The sporozoites (Pl. XXVI, figs. 1, 2) are to be found in the mesenteron of individuals in oviposition. They are mixed with gregarines of older stages corresponding probably to the sporonts. The sporozoites are elongate in shape, slightly arched, and consisting of a posterior more or less oval part and of a small conical anterior one. The dimensions are about 4–5 μ × 1 μ. The sporozoite fixes itself on an epithelial cell and grows at its expense. On the host cell the sporozoite develops into a trophozoite (Pl. XXVI, figs. 3, 4), which attains the dimensions of about 20–23 μ × 7–8 μ. The deutomerite of the trophozoite is rather stocky, more or less cylindrical in shape and its nucleus is evident. The trophozoite remains attached to the host cell by an organelle of attachment called the epimerite. In cross-section it is crescentic in shape and shorter but broader than the protomerite. At the proper developmental time the trophozoite leaves the epithelial cell of the host and becomes a sporont (Pl. XXVI, figs. 5, 6). The sporonts move about in the lumen of the mid-gut. They are pear shaped or rounded, with maximum dimensions of 0·15 mm. The gregarines in this stage fill the mid-gut of *P. impexus* in autumn, although some of the forms previously described may be present. The sporonts are still present in the spring (Pl. XXVI, fig. 5) in hibernated adults. The deutomerite contains a large nucleus (Pl. XXVII, fig. 2) in this stage. The nucleus is smaller than the protomerite, the cytoplasm is granular (Pl. XXVII, figs. 1, 2) and the epicyte

FIG. 1. Sporozoites free in the lumen of the mid-gut.

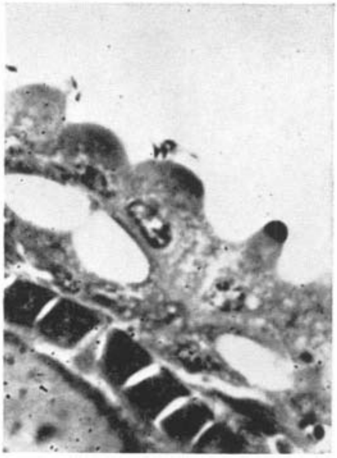


FIG. 2. Sporozoites fixed on an epithelial cell.

FIG. 3. Trophozoite attached to a cell near the nucleus.

FIG. 4. More than one trophozoite attached to the same epithelial cell.

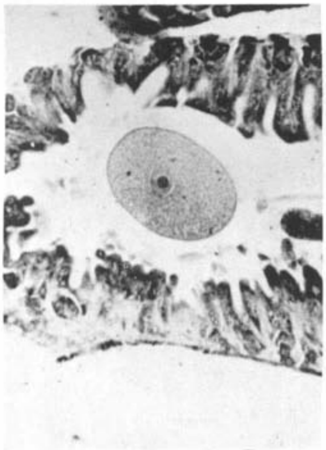


FIG. 5. Sporont in mid-gut of adult collected in the spring.

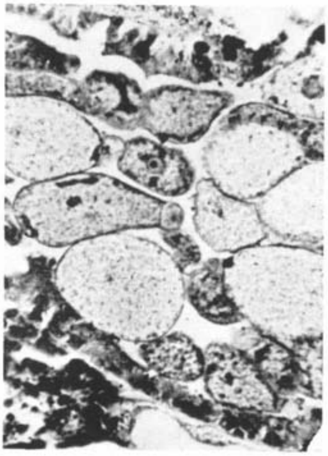


FIG. 6. Sporonts fill the mesenteron cavity of *P. impexus* adult collected in the autumn.

GREGARINES FROM MESENTERON OF *P. IMPEXUS*.

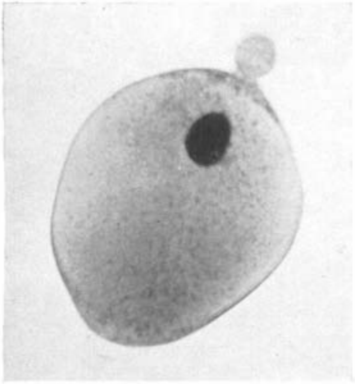


FIG. 1. Sporont rounded in shape, showing the granular cytoplasm and the relative sizes of protomerite, deutomerite and nucleus.

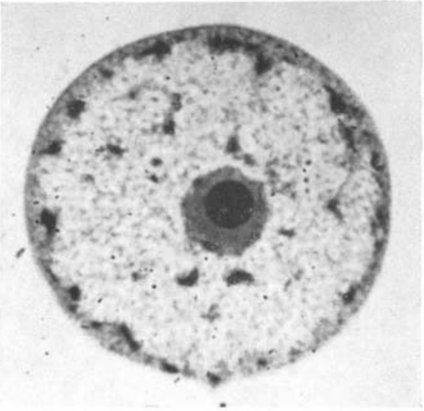


FIG. 2. Cross-section of a sporont showing the granular cytoplasm and the thinly furrowed epicyte.

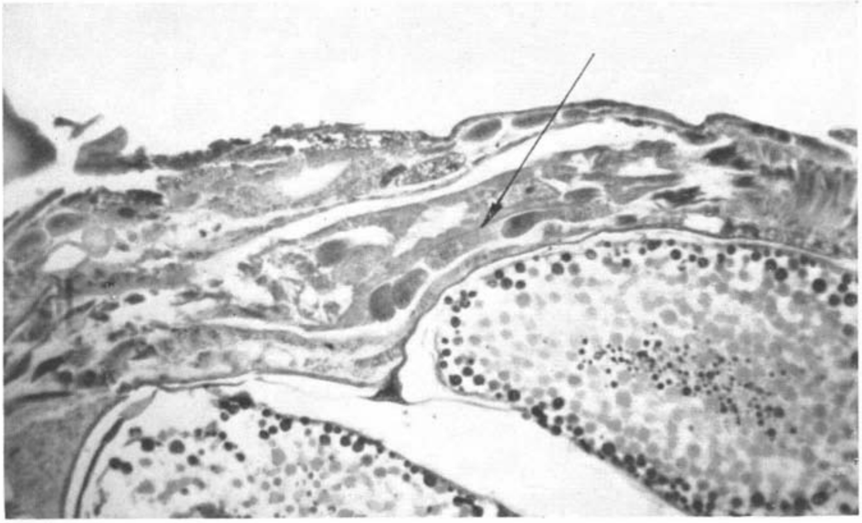


FIG. 3. Sporonts passing through the ileum of an adult of *P. impexus*.

GREGARINES FROM MESENTERON OF *P. IMPEXUS*.

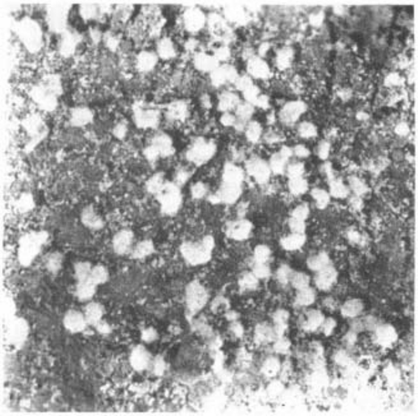


FIG. 4. Autumn infestation of *A. piceae* at Seegraeben 29th August 1950, after the action of predators in presence of their parasites and diseases.

FIG. 5. Light autumn infestation at Naenikon, at the same time, after the action of a population of *P. impexus* almost free from other predators and parasites.

ACTIVITY OF PREDATORS IN TWO DIFFERENT LOCALITIES.

(Pl. XXVII, fig. 2) is very thinly furrowed. The natural colour of the gregarines is whitish.

The succeeding stages of the life cycle are not known. Forms identical with the sporonts contained in the mid-gut have frequently been observed in the ileum (Pl. XXVII, fig. 3) and rectum. These, however, had probably been evacuated from the mid-gut because of the large number present there.

c. Effect on the host and number of gregarines.—The gregarines are looked upon as parasites inasmuch as they are able to derive their nourishment from the host's organs. Their parasitic life begins with the trophozoite attached to the epithelial cell through its epimerite. The trophozoite increases its body volume considerably. The epithelial cell seems to be disintegrated by the effect of the trophozoite. The sporonts floating freely in the lumen of the mid-gut no doubt derive a considerable quantity of nutrient material through absorption. The increase in their body volume during this stage is evident.

The relationship of the gregarines to their hosts is not yet known. From the standpoint of biological control it would be important to establish whether the presence of gregarines reduces the ability of the adults of *P. impexus* to deposit eggs before winter.

The number of gregarines in the mid-gut of adults of *P. impexus* varies from season to season. Sporozoites in large numbers are found in late summer, a few months after the beginning of the new generation, but in this period of sporozoite formation it is possible to see a great number of forms of the two subsequent stages and often the sporonts fill the lumen. In the spring we generally find a few gregarines round in shape with a diameter of approximately 0·15 mm.

Nematodes.

A roundworm was found in the body of an adult collected at Seegraeben on 8th October 1950. This was the only example found during the period of the study. According to Dr. Menzel, of Wadenswil, the worm might belong to either of the genera *Mermis* or *Hexamermis*. It is difficult to determine because it is sexually immature. This is probably the first instance on record of Coccinellids being parasitised by Mermithids.

The worm, dissected from the body of a female of *P. impexus*, filled the abdomen and partially filled the thoracic cavity. It was wound around the digestive tract three times, with one end in a Malpighian tubule. The ileum of the host was longer than under normal conditions and the mesenteron more flattened. There was no trace of ovaries; however, the genital chamber and sclerotised parts of the genitalia remained.

This parasitism by a nematode has no importance, since only a single case has been observed. It could presumably assume a different aspect in biological control if the degree of parasitism should increase and so limit to some extent the oviposition of *P. impexus*.

Predators of P. impexus.

When there is a scarcity of the normal food, the predators of *Adelges* may easily prey upon one another. At Naenikon, in May 1950, some larvae of *Chrysopa ventralis* were observed destroying mature larvae of *P. impexus*; at Winterthur, on 2nd June 1950, mature larvae of *Cnemodon latitarsis* were seen feeding on pupae of *P. impexus* hidden in crevices of the bark; at Aathal, in May 1952, a mature larva of *Syrphus arcuatus* was sucking a larva IV of *P. impexus* and the numerous larvae of this Syrphid decimated the larvae and the prepupae in the rearing cages.

These occurrences are not frequent in nature and happen only when the *Adelges* population has been strongly reduced by the predators or when the population of a predacious species (as in the case of *P. impexus* at Naenikon) becomes very numerous and therefore undergoes the action of other predators. Predators of predators are generally the largest ones such as *Chrysopa, Syrphus, Cnemodon* and *Aphidecta.* In Germany, Dr. Franz observed the habits of the bird *Certhia familiaris* L. which in a quarter of an hour filled its bill three times with predatory larvae, particularly of *P. impexus.*

Estimate of the Controlling Value of *P. impexus.*

It is difficult to estimate the predatory activity of the single species *P. impexus* in its relations to *A. piceae.* It is even more difficult to express its value in relation to that of other predatory species living together with it.

The evaluation of *P. impexus* was not established on the basis of statistical data, from field experiments, but rather on facts observed in nature during the years 1950 to 1952. As to this Coccinellid, the localities from which the largest quantity of interesting observations were made were Seegraeben/Aathal and Naenikon.

At Seegraeben/Aathal, the site of an old *Adelges* infestation with many trees damaged in 1934, it was possible to find the greatest complex of control factors on *A. piceae.* Predator species and parasites and diseases of predators were all present. In this locality the *Adelges* infestation was present every spring and autumn, although the intensity was variable. Here the fluctuations of the number of each insect species were never extreme, but were always present and readily visible. At Seegraeben/Aathal we observed the action of every parasite species and disease, and the way it prevented excessive multiplication of the predator population. This often resulted in a more or less heavy *Adelges* infestation (Pl. XXVII, fig. 4). It is impossible to express the value of *P. impexus* at Seegraeben/Aathal, because it is difficult to separate or orient the the action of any one predatory species.

At Naenikon, a relatively newly established infestation was located on the border of the woods. In May 1950 the trunks of *A. alba* were completely covered with white *Adelges* wax. At this time a very heavy population of *P. impexus,* estimated at 25/30 larvae per dm^2. existed in close relation to some predatory species which were weakly represented numerically. It is believed that the population of *P. impexus* had reached, in relation to that of the *Adelges,* its highest point, for during the three or four week larval period it destroyed the Aphid infestation almost completely. At Naenikon neither *S. mesnili* nor *C. scymni* were found in numbers capable of reducing the predator action. Naenikon is one of the most important and rare instances showing the value of a predatory species. With the mass multiplication of the prey we observed the mass increase in number of the predator and with the mass destruction of the prey we found the predators almost completely dispersed (Pl. XXVII, fig. 5).

From the observations at Naenikon, where no important parasites limited the mass increase of *P. impexus,* it may be concluded that it would be advisable *to introduce this predator without its parasites to Canadian conditions.*

Rearing *P. impexus* and Shipment to Canada.

General plan of the work.

From the preliminary study carried out by this Laboratory in 1950, it was possible to plan the mass-rearing and shipping of *P. impexus* adults to Canada without their parasites. The importance of preliminary research as the basis of every biological control problem is evident. It is particularly important to screen and remove parasites and any disease organisms which might cause heavy mortality among the beneficial insects. During the mass-rearing in 1951, these

FIG. 1. Method of cage-rearing of *P. impexus* on infested tree .

Photo. Dr. J. Franz.

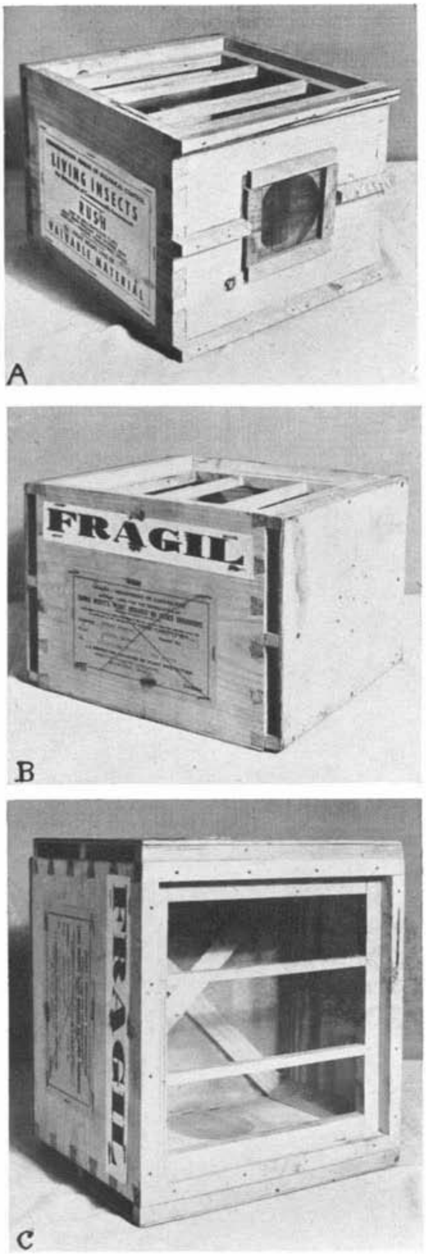


FIG. 2. Case used to ship *P. impexus* and other predators of *A. piceae* to Canada.

A, B, C. Different aspects of the case to show its special construction.

facts were not emphasised sufficiently and it is possible that the gregarines were introduced to Canada. In the mass-rearing technique three points require special attention:

a. To avoid the presence of *Scymnophagus mesnili* in the pupae of *P. impexus*, no shipping should be made of pupae collected in nature;

b. To avoid the presence of *Centistes scymni*, a very dangerous adult parasite, no shipping should be made of adults collected in nature;

c. To avoid any shipment of *P. impexus* adults containing gregarines, no shipment of individuals fed with *Adelges*-infested bark should be made.

The mass-rearing work was undertaken in 1951 in Germany with Dr. Franz, and in 1952 in Switzerland with the following instructions by Prof. L. P. Mesnil:

a. Building of cages in the infested forest of Laimbach (1951) and Aathal (1952) around the infested trees. The cages to be large enough to confine a considerable number of larvae of *P. impexus* of different instars, preferably of the fourth. These larvae should be collected in the immediate vicinity.

b. Removing the pupae from the rearing cages and separating the parasitised ones from the unparasitised ones.

c. Collecting pupae in other localities and separating as above.

d. Rearing pupae of *P. impexus* at the Laboratory to prevent parasitism by *C. scymni*.

e. Feeding newly emerged adults with nutritive solution until a sufficient number are accumulated to be sent to Canada. The danger of gregarines is thus avoided.

f. Shipment by air mail in special boxes.

Rearing cage.

The rearing cages in the field were built around the infested trunks to reduce the amount of work. No time was lost in feeding of larvae in cages. The cages prevented any activity by the parasite *S. mesnili* and assembled the pupae in one place so that the adults could be collected at the right time.

The cages (Pl. XXVIII, fig. 1) were raised from the ground 4–5 m. and fastened to the trunks so that they would not be disturbed. They are made of muslin (organdie) held away from the trunk by means of an upper and lower iron ring with four bars driven horizontally into the bark at equal distance from one another. Above and below the two iron rings the muslin is fitted to the tree. The muslin is provided with a zip fastener allowing free access to the cage. The muslin is brown in colour (1951) and blended well with the background. A black cloth was fastened around the trunk in the lower portion of the cage. This offered a convenient place for pupation. The cage was designed together with Dr. Franz. In 1952 the black cloth strip was replaced by a strip of corrugated cardboard held to the trunk with iron wire.

From 500 to 800 larvae of *P. impexus* were introduced into each cage in 1951. Of 3,050 larvae put in the cage at Laimbach between 13th and 26th May 1951, 80 per cent. were removed in the pupal stage between 11th and 16th June. The pupae were then taken to Munich and reared in tubes until the adults emerged. Between 17th and 23rd June 1951, more than 1,000 pupae were collected at Laimbach and 1,000 pupae at Tussenhausen. The adults which emerged were fed with agar-honey-sugar solution (Parker, 1948) and supplemented with *Adelges*, thus they may have contained Gregarines. The 4,050 adults were sent by air mail to Belleville (Dominion Parasite Laboratory) in special boxes containing from 500 to 850 individuals each.

In 1952 the number of larvae of *P. impexus* for each cage was increased to 800–1,000. From 11,000 larvae (see *, Table II) collected between 28th April and 6th May at Aathal, Horgen and Winterthur, and put into cages, 42 per cent. were destroyed by *Syrphus arcuatus* larvae present on the *A. piceae* infestations of eastern Switzerland. Unknowingly while the cages were being built on the trees, *S. arcuatus* eggs were enclosed and larvae penetrated under the corrugated cardboard. In some cages the predacious action of the *Syrphus* was so heavy that 90 per cent. of the *P. impexus* were destroyed. The cages were taken from the trees between 3rd and 11th June, when it was noticed that some Coccinellids were emerging and at the same time pupae were collected at Horgen, Aathal and Winterthur (Table II).

TABLE II.

Mass-rearing of *P. impexus* in Switzerland in 1952.

Locality	Larvae collected	Pupae collected	Adults emerged	Mortality of pupae in rearing tubes, incl. parasitism	% of mortality of pupae, incl. parasitism
Horgen	700 } 11000*	700	600	100	14·30
Aathal .. .. (wood)	9800	1200	700	500	41·70
Aathal .. .. (cages)		6350	6300	50	0·78
Winterthur ..	500	4200	4000	200	4·76
Total ..		12450	11600	850	Mean 6·83

The pupae collected in nature, or taken from the cages, were reared in tubes at a temperature of 20°C. until emergence. Each tube contained 500 pupae in a moist air current of 80 per cent. R.H. for the whole period. The 11,600 adults were shipped directly to Belleville without supplementary feeding, between 9th and 18th June, in boxes containing up to 1,300 adults each.

The high pupal mortality recorded in the last column of the Table is due to improper handling during collection. The mortality was highest at Aathal, since the collecting began there.

Shipping box.

The box employed for shipments of the predator is a slight modification of the one already used by this Laboratory in 1949 to send parasites to Australia. In the shipments of *P. impexus* to Canada in the spring of 1951, employing the new boxes, the mortality was 6 per cent.; in 1952 the mortality of *P. impexus* in the boxes sent to Canada was only 0·6 per cent.

The box (Pl. XXVIII, fig. 2) is built in such a way that it needs no particular care during shipment other than a temperature check. It is 24·5 × 24·5 × 20 cm. Two opposite walls have a hole in the centre 7–8 cm. in diameter which is covered on the inside with muslin (organdie), and on the outside with a brass-wire screen. The screen is further protected by a thin board of the same dimensions as the wall of the box itself. This board is fixed to battens so that it is 1·5 cm. from the net and permits air circulation. The board is also supplied with holes opposite the hole covered with the net. After adding these two boards the length of the box measures 28 cm. The interior of the box is provided, on the top, with a frame 1·5 cm. below the cover (cover not shown in Pl. XXVIII), to which a rather thick cellophane sheet is glued. This frame is held by four reinforcers at the corners. The cellophane is left in water for half an hour, then dried and applied directly to the frame. It permits customs inspection. Approximately 4 cm. from the bottom there is a wooden structure consisting of two small crossed boards fixed to the corner reinforcers. A square of organdie is glued to them. The space between the organdie and the box bottom is filled with moist sterilised sphagnum to maintain a constant relative humidity above 90 per cent. The organdie prevents the smallest insects from entering the sphagnum.

For the shipment of insects the inside of the box was provided, in 1951, with a wet sponge, wrapped in filter paper and fixed vertically at one corner of the box. This sponge was not included in the boxes in 1952. For food, the solution of Parker (1948) in drops on cardboard was placed on the inside of the box.

Before any insects were shipped to Canada, laboratory experiments were undertaken to determine their behaviour and survival in all stages and under varying conditions within the shipping boxes. Each insect species reacted differently and the mortality varied even for different stages of the same species. For the most part, the investigations were carried out at a temperature of 15°C. The relative humidity was varied, using sphagnum moss with different moisture contents and the insects were also tested both with and without the presence of artificial food.

Summary.

The biology of *Pullus impexus* (Muls.), a Coccinellid beetle predacious on *Adelges piceae* (Ratz.) in Switzerland, Germany and France, was studied during 1950–1952. The present work is a part of the research on the complex problem of factors in the control of the Balsam Woolly Aphid in Canada.

The morphology of both the larva and the adult has been studied. Some information has been provided on the probable distribution of the species.

P. impexus has only one generation a year. The eggs are deposited during the late summer or early autumn on infested trees and the larvae hatch in April. The larvae develop and adults appear in May. The adults of the new generation are to be found in June together with adults of the old generation. In the biology, particular attention has been directed to the diet of the insect in each of its stages, in order to establish the value of the species from the standpoint of biological control.

Two new species of Hymenopterous parasites were found in Switzerland and in Germany, *Scymnophagus mesnili* Ferr., a parasite of pupae, and *Centistes scymni* Ferr., a parasite of the imagines. The life history of these species has been briefly studied. A cephaline gregarine species was noted in the mesenteron of adults of *P. impexus* and a nematode in the abdominal cavity of a female. The two Hymenopterous species provide an important limiting factor in the increase of the population of *P. impexus*.

Chrysopa ventralis Curt., *Syrphus arcuatus* (Fall.) and *Cnemodon latitarsis* Egg. are mentioned, acting as predators of *P. impexus* larvae and pupae.

The organisation of the mass-rearing of *P. impexus* in Europe as well as the shipping of the insects to Canada in special wooden boxes completes the study.

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