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WASHINGTON, D. C., AUGUST 15, 1932

No. 4

STURMIA INCONSPICUA MEIGEN, A TACHINID PARASITE OF THE GIPSY MOTH¹

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INTRODUCTION

Sturmia inconspicua Meigen is recognized as one of the most important parasites of the introduced pine sawfly, *Diprion simile* (Hartig) (*Lophyrus similis* Htg.). As a parasite of the gipsy moth (*Porthetria dispar* L.) it is not so well known, although its attack upon that species was recorded many years ago. As a parasite of *P. dispar* in Europe it compares favorably with other tachinids except *Phorocera agilis* Robineau-Desvoidy and *Sturmia scutellata* Robineau-Desvoidy. In certain localities it has even outranked the latter parasite. Illustrative of the periodic abundance of this species are the rearings made at Rembertow, Poland, in 1927. Approximately 200,000 *P. dispar* larvae were reared for their parasites, and from them were obtained more than 20,000 puparia of *S. inconspicua*.

This increased knowledge of the insect's importance as a gipsy-moth parasite and the establishment in the northeastern part of the United States of one of its favorite hosts, *Diprion simile*, have renewed interest in this species.

SYNONYMY

European authorities do not wholly agree upon the taxonomic status of *Sturmia inconspicua*. According to Bezzi and Stein,³ *inconspicua* Meig. (1830), *flavoscutellata* Zett. (1844), and *curvitans* Rond. (1861) are synonyms of *bimaculata* Htg. (1838). It is not clear why these authors used *bimaculata* when *inconspicua* has priority. Probably it is an instance of common usage. *S. gilva* Htg. (1838) is regarded by them as distinct. In a later work Stein⁴ still holds to his opinion as regards the distinctiveness of the two forms *bimaculata* and *gilva*, but here he recognizes the priority of *inconspicua* over *bimaculata*. Baer,⁵ like Bezzi and Stein,³ uses *bimaculata* in preference to *inconspicua*, but he considers *gilva* a synonym, or at most a variety, of *bimaculata*. In 1926 J. Villeneuve discussed the synonymy of these forms with the writer. According to him, they are all synonymous with *S. inconspicua*, *gilva* being at most a poorly marked variety.

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² In the preparation of this paper the author was materially assisted by the use of data obtained by C. F. W. Muesebeck and his associates, P. B. Dowden and R. C. Brown, of the Budapest laboratory, and by data obtained from the files at the gipsy moth laboratory, Melrose Highlands, Mass. The writer appreciates the assistance given him by C. W. Collins, T. H. Jones, and W. F. Sellers, of the gipsy moth laboratory, and also the kindness of W. R. Thompson, Farnham House laboratory, London, for his criticisms.

³ BEZZI, M., and STEIN, P. KATALOG DER PALÄARKTISCHEN DIPTEREN. Bd. 3, p. 227. Budapest. 1907.

⁴ STEIN, P. DIE VERBREITETSTEN TACHINIDEN MITTELEUROPAS NACH IHREN GATTUNGEN UND ARTEN. Arch. Naturgesch. (A) 90 (6): 57. 1924.

⁵ BAER, W. DIE TACHINEN ALS SCHMAROTZER DER SCHÄDLICHEN INSEKTEN. Ztschr. Angerw. Ent. 6: 242. 1920.

GEOGRAPHICAL DISTRIBUTION

Sturmia inconspicua is common to central Europe and northern Africa. According to Fisk,⁶ who refers to it under the name *Zygothria gilva*, it is more abundant in the Mediterranean countries than in the north. In recent years, however, practically all the material collected has come from northern Europe, especially the area where pine is grown. It is probable that its regional abundance has some connection with the presence of its alternate hosts.

HISTORY OF IMPORTATION AND COLONIZATION

In 1906 the first attempt was made by the State of Massachusetts and the Federal Government to introduce the species into the United States. The colony was small and there is some doubt concerning the point of liberation. Presumably it was in the vicinity of North Saugus, Mass. During 1907-08 but few puparia of this species were received from abroad and no colonies were liberated. In 1909 more than 7,000 puparia were received from France and colonized at Wellesley, Wenham, Stoneham, Byfield, and Melrose Highlands, Mass. In addition 385 puparia were obtained from importations of *Porthetria dispar* from Belgium, Austria, and Germany, and flies were liberated in the same localities. During the following years all attempts to recover the species failed, and it is safe to conclude that the establishment of *inconspicua* from this introduction was unsuccessful.

In recent years another effort has been made to establish the species. During 1923-24 only a small quantity of material was received and no colonization attempted. In 1925, 1,886 puparia were imported from Poland, Hungary, Portugal, and Czechoslovakia. Of this material two colonies, aggregating 1,200 adults, were liberated under unsatisfactory conditions. Less than 60 puparia were received in 1926 and none of the flies was liberated. In 1927 importations totaling 15,607 puparia were received from Poland, Hungary, and Yugoslavia, and approximately 4,798 adults were liberated in Massachusetts, New Hampshire, and Rhode Island. In 1928 nearly 55,000 puparia were received from the same localities, and four colonies, aggregating 28,000 adults, were placed in Massachusetts, New Hampshire, and Rhode Island.

The first recovery of *Sturmia inconspicua* was made during July, 1929, when seven puparia were obtained from *Porthetria dispar* larvae collected at the colony site in Saugus, Mass. This colony was liberated in July, 1927.

DESCRIPTION OF STAGES

The description that follows has been drawn from a large number of specimens of both sexes reared from *Neodiprion dyari* Roh. and *Porthetria dispar* L. at the gipsy moth laboratory. The parent stock was bred from *Lophyrus pini* L. collected at Wloclawek, Poland.

⁶ FISKE, W. F. PARASITES OF THE GIPSY AND BROWN-TAIL MOTHS INTRODUCED INTO MASSACHUSETTS. WHERE THEY COME FROM. WHAT THEY ARE DOING. A GENERAL SURVEY OF THE WORK. p. 39, illus. Boston. 1910.

THE ADULT

Head (fig. 1): Horizontal axis, measured at base of antennae, but little wider than at vibrissae. Front variable; average specimen at widest part measuring, in the male, a little less than and, in the female, a little more than one-third the head width. Eyes bare, bucca from one-eighth to one-fifth the eye height. Front and parafacials usually gray pollinose, the former often with a decided golden tinge that sometimes spreads over the entire face (more pronounced in the females) and bearing, in the male, a row of 10 to 12 and, in the female, from 7 to 9 bristles, the lowest and uppermost ones of which are reclinate, and those of the intermediate region decussate. Outside of and parallel with frontal row, several bristles which in some individuals give the appearance of a double row. These bristles are variable and are sometimes entirely absent in the female. In the male the inner vertical bristle large, the outer vestigial; in the female both the vertical bristles well developed, the outer one less strong. Facial ridges bristly on the lowest fourth; palpi yellow. Antennae usually black, reaching lowest fourth of face, third joint in both sexes from two to two and one-half times length of second. Base of third joint and apex of second sometimes red or yellowish, particularly in the female. Arista tapering from base to apex.

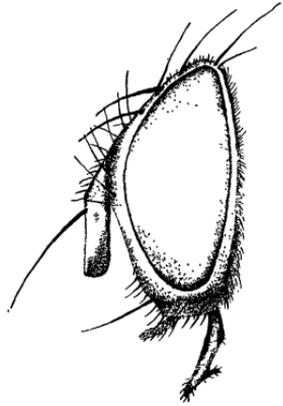


FIGURE 1.—Head of adult female of *Sturmia inconspicua*, lateral view

Thorax black, moderately to thickly gray pollinose and bearing before the suture 3 acrostichal and 3 dorsocentral bristles; behind the suture either 3 or 4 acrostichal (usually 3) and 4 dorsocentral bristles. Scutellum black at base, the apical half brownish and bearing 3 pairs of strong marginal bristles besides the decussate apical pair. Disk thickly beset with fine depressed hairs, from which arises 1 strong pair of widely separated bristles. Sternopleura usually with 4 bristles, sometimes 3 and a weaker one. Pteropleural bristle small.

Abdomen black, at least the basal half of segments II, III, IV, and a good part of the pleural and ventral regions moderately gray pollinose; segment I and the apices of the following segments shining black. Segment I with no macrochaetae; segment II with a marginal pair; segment III with a marginal row; and segment IV wholly covered except at extreme base. Sides of the second segment sometimes reddish. In the male, underneath segment III there is a small dense patch of depressed hairs similar to that found in *Zenillia eudryae* Town. and in several species belonging to the genus *Sturmia*. This character is absent in the female. Mid tibiae with 1 bristle on the outer front side near the middle, 1 on the forward side which often appears as an inner bristle, and 2 hind bristles. Hind tibiae thickly ciliate, with 1 longer bristle.

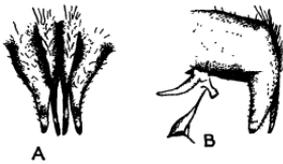


FIGURE 2.—Male hypopygium of *Sturmia inconspicua*: A, Rear view; B, side view

Wings hyaline, third vein usually with one strong bristle at base, sometimes a weaker one present. Apical cell open, ending far from the extreme wing tip.

Genitalia (fig. 2) small, retracted. Inner forceps shining black and tapering to slender points. When viewed from the side they are nearly straight, the basal half densely clothed with fine black hairs which are directed upward; when viewed from behind they

are distinctly separated from base to apex, parallel for one-half of their length and then outwardly bowed. Outer forceps light brown, shining, wide at base, and tapering to blunt, rounded points; outer surface sparsely clothed with light-brown hairs. Anterior claspers elongate, slender, brownish, terminating in fine points; posterior claspers short, knoblike, scarcely three times as long as their apical width.

Length, moderate size flies, usually about 7 mm but sometimes as long as 10 mm.

THE EGG

Length from 0.55 to 0.60 mm, width 0.18 to 0.20 mm, depth about equal to width; transparent; moderately elongate-oval in profile, posteriorly rounded and tapering anteriorly; lower side concave. Viewed from above, surface of egg finely punctate, with distinct reticulation.

THE LARVA

Stage 1 (fig. 3, A).—Size variable. A larva 2 days old measured 1.0 mm in length and 0.33 mm in width; another larva, 3 days old, measured but 0.80 by 0.27 mm. Moderately elongate, tapering anteriorly, posteriorly rounded; skin colorless and transparent; head without spines and bearing 2 conspicuous pairs of rodlike sensory organs. On segment I is an anterior band of spines made up of 3 to 5 irregular rows, which are weakest in the pleural region. The spines of the dorsum are less numerous but stronger than those of the venter and stronger than those of any other segment except the anal segment, where the stigmatic spines are located. There is also a much weaker dorsolateral band of 2 or 3 rows commencing near the posterior border of this segment and merging into the anterior row at the pleural region. All spines directed posteriorly. Segment II banded anteriorly with 3 to 5 irregular rows of spines, posteriorly directed, and somewhat weaker than those of the dorso-anterior border of segment I. Rows more numerous in ventral region. Segments III and IV likewise banded anteriorly with 3 to 5 irregular rows of posteriorly directed spines slightly weaker than those of the preceding segment. Posterior two-thirds of segments II, III, and IV apparently naked. Segments V and VI with anterior bands of 3 to 5 irregular rows of posteriorly directed spines which are weakest in the pleural region. Posterior margins of segments sparsely clothed with incomplete rows of minute

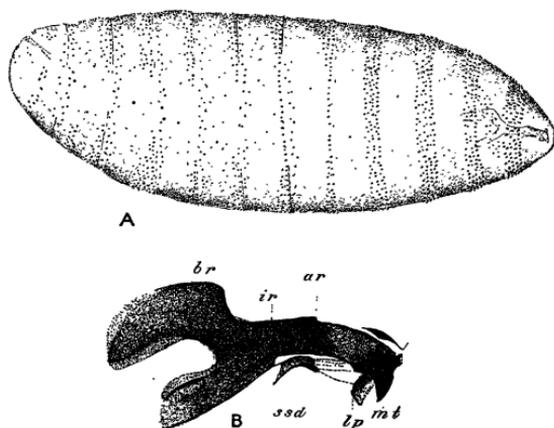


FIGURE 3.—*Sturmia inconspicua*: A, First-stage larva (X 64); B, bucco-pharyngeal armature of same (br, basal region; ir, intermediate region; ar, anterior region; ssd, sclerite of the salivary duct; lp, lateral plates; mt, median tooth)

anteriorly directed spines. Segments VII and VIII with weak anterior bands consisting of from 2 to 4 incomplete rows of posteriorly directed spines which are feeble or missing in the pleural region, also posterior bands of from 2 to 4 rows of anteriorly directed spines which are but narrowly separated from the posteriorly directed spines of the segments which adjoin them. Posterior bands weak along the dorsum. Segments IX and X with incomplete anterior bands of 3 to 5 rows of posteriorly directed spines which are interrupted at the pleural region and strongest at venter. The posterior borders of these segments have more or less complete bands of several rows each of anteriorly directed spines. On segment X the posterior band is broken at venter, but midway to the suture which separates segment IX a short, though well-defined, ventral row of anteriorly directed spines can be observed. Segment XI has no well-marked anterior band of spines, although in some specimens there appears to be a weak, sparsely beset row along the suture that separates segments X and XI. Ventrally, near the middle of segment XI, an irregular row of anteriorly directed spines of varying length, widest at venter and narrowing as they approach the pleural region, where they terminate in a small patch of 5 to 8 strong spines which are of an entirely different character from those which precede them. Region adjacent to posterior spiracles sparsely beset with weak, anteriorly directed spines, inconspicuous in most part, even under high magnification. Anterior to, but directly between, the spiracles there arise 3 to 6 strong, black, anteriorly directed stigmatic spines. Opposite them a somewhat similar posteroventral patch of strong anteriorly directed stigmatic spines. Segment XI further characterized by 2 conspicuous brown sclerotized spots each equal in size to one of the posterior spiracles and situated midway between them and the ventral patch of stigmatal spines. There are also several pairs of papillae on this segment. These papillae are the usual clavate sensorial organs and are about 5 times as long as they are broad.

The first-stage larva is metapneustic, the posterior spiracles opening near the apex of the last segment considerably dorsad of the longitudinal axis. Bucco-

pharyngeal armature without articulations. (Fig. 3, B.) Anterior lateral plates (*lp*) lightly pigmented and irregularly shaped; the sclerite of the salivary duct (*ssd*) large, somewhat shoehorn-shaped with a slender ventral appendage; anterior region (*ar*) with a median tooth (*mt*) directed straight downward, moderately thickened and pointed at tip, bearing on the upper half of its anterior edge a series of 4 or 5 distinct, though minute, accessory teeth. Behind the teeth and arranged in parallel formation are a number of well-defined striae. Basal half of anterior region lightly pigmented. Intermediate region (*ir*) defined on its dorsal anterior edge by a slight hump and on its ventral posterior edge by a marked indentation of the basal region. Upper wing of the basal region (*br*) abruptly curved, at its widest part nearly one and one-half times the width of the intermediate region; lower wing weakly sclerotized at apex and about one-half the size of the upper one.

Stage 2 (fig. 4, A).—Length and width variable. Average measurements 2.0 to 2.5 mm by 0.80 to 1.0 mm. Segment I with dorsal and ventral spinous areas composed, respectively, of 4 and 7 irregular rows of posteriorly directed spines. Pleural region bare. Segments II and III with complete anterior bands composed of 5 to 7 rows of posteriorly directed spines, weakest in pleural region and strongest at venter. Spines of segments I and II stronger than those of any other segments. Posterior borders of segments I and II bare. Segment III with a few weak, scattered spines in the posterior region. Segment IV with a complete anterior band composed of 5 or 6 rows of posteriorly directed spines, also an incomplete ventroposterior band of anteriorly directed spines of the same strength which end in the pleural region. Segment V with an anterior band (sometimes narrowly interrupted at dorsum) of 4 or 5 rows, which are directed posteriorly, and a posterior band of anteriorly directed spines of the same strength, which is also interrupted at dorsum. Segments VI to IX with complete bands of weak spines composed of 5 to 7 rows bordering their anterior and posterior margins. The spines of the ventral region are stronger than those of the dorsum. All spines bordering the anterior edge of segments directed posteriorly, those of posterior edge directed anteriorly. Segment X with weaker and narrower bands of 3 to 5 rows of posteriorly directed spines on its anterior margin. Spine rows of venter more numerous than those of dorsum. Posterior margin of this segment partially banded (interrupted at venter), with numerous irregular rows of anteriorly directed spines much weaker than those of the preceding segments. Segment XI with no well-defined anterior spine bands, but entire dorsum lightly beset with weak spines and the pleural and ventral regions feebly spinose. Posterior region with 5 or 6 irregular rows which vary greatly in strength and arrangement. At venter, between these rows and the suture, a conspicuous ventrolateral patch of weak, anteriorly directed spines. Extreme posterior region bare. Stigmatic spines and sclerites of anal segment, which are characteristic of the first-stage larva, not present in this stage.

Anterior spiracles, if present, inconspicuous and difficult to locate. Posterior spiracles located, as before, on dorsal surface of anal segment and appearing more robust than those of the preceding stage.

The bucco-pharyngeal armature is shown in Figure 4, B. In this stage there is a well-marked joint (*a*), which separates the now paired mandibular hooks from the intermediate section.

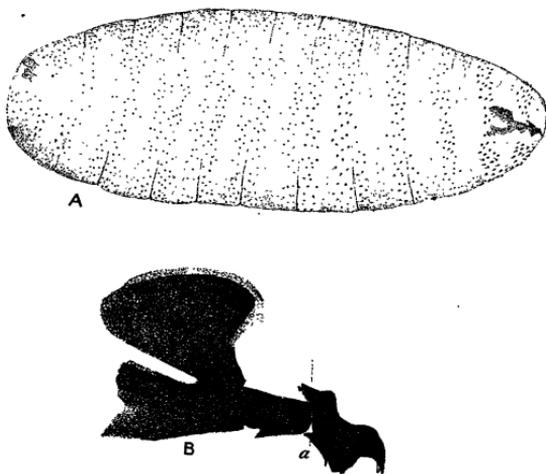


FIGURE 4.—*Sturmia inconspicua*: A, Second-stage larva ($\times 26$); B, bucco-pharyngeal armature of same (*a*, joint separating mandibular hooks from intermediate section)

Stage 3 (fig. 5, A).—Length and width variable. Average measurements 8.0 to 9.0 by 3.0 to 3.5 mm. Head bare except about the mouth, where there is a small patch of posteriorly directed spines. Two pairs of sensory organs conspicuous. Segment I, anterior edge bordered dorsally and ventrally with 6 or 7 irregular rows of short, black, posteriorly directed spines; pleural region weakly spinose (3 or 4 rows); posterior region having few weak spines, in most part outwardly directed. These spines (fig. 5, B) are nearly colorless, unusually long and hairlike, and in decided contrast to those of the anterior border. Segment II, anterior border with 7 or 8 rows of short, black, posteriorly directed spines, strongest in the dorsal and ventral regions; posterior region less thickly clothed with hairlike spines, those nearest the margin, at least, directed anteriorly. Segments III to X with complete anterior bands of 5 or 6 irregular rows of posteriorly directed spines, in most part hairlike, weakest in the pleural regions and strongest ventrally; posterior regions of these segments thickly clothed with the same type of spines, anteriorly directed; intermediate regions less densely spinose. Anal opening situated on posterior margin of segment X, on ventral side.

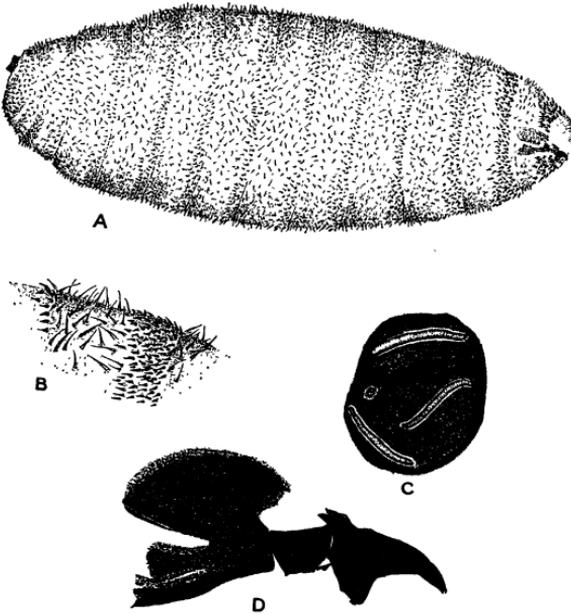


FIGURE 5.—*Sturmia inconspicua*: A. Third-stage larva ($\times 7.5$); B, dorsal view of segment II of same, showing type and arrangement of spines; C, posterior spiracles of same; D, bucco-pharyngeal armature of same

stalks directed obliquely upward, about as long as broad. Each spiracle with three light brownish respiratory slits, varying somewhat in length and arrangement, located on top of well-defined ridges. In the slide mounts it is difficult, because of their irregular elevation, to obtain a good perspective of the posterior spiracles. Usually they appear as in Figure 5, C, although they are frequently distorted so that only two of the slits are visible. Anterior spiracles, if present, inconspicuous and difficult to locate.

The bucco-pharyngeal armature is represented in Figure 5, D. In this stage there are three articulations which can be readily discerned, although in some cases the segmentation between the intermediate and the anterior regions is not clearly defined. Other differences separating this stage from the preceding one are the elongation of the laterally paired mandibular hooks, the subsequent modification of the sharp angles which characterized the anterior region of the second stage, and the very distinct formation of the intermediate section.

THE PUPARIUM (fig. 6)

Length and width variable, specimens as small as 3 by 1 mm and as large as 7 by 3 mm have been noted. Usually opaque brown or black, but sometimes light

around opening, which is as large as that from which one of the posterior spiracles arises, bare and entirely surrounded by black spines. Segment XI with anterior border clothed with several rows of hairlike spines, in most part posteriorly directed. Posterior extremity, ventrad of the spiracles, defined by a weak suture bordered anteriorly by a dense ventropleural band of anteriorly directed spines; immediate region either side of this band less thickly beset with weak, colorless spines. Except for the bare area adjacent to the spiracles, which is broadest ventrally, and the narrow ventral anterior border of the posterior extremity, which is nearly bare, the segment is thickly beset with anteriorly directed, short, black spines, similar to those which form the anterior bands of segments I and II. Posterior spiracles (fig. 5, C) opaque brown or black, protuberant, their

brown and semitransparent, never shining. The long hairs borne on it give a dull appearance and also favor the accumulation of dirt. Posterior spiracles (fig. 6, B and C) located just above the horizontal axis and separated at base by a distance about equal to their width, conspicuously protuberant, the stalk shining black, directed obliquely upward, about as long as broad, each spiracle and three brownish slits each located on top of a well-defined ridge. Button small, located at inner edge of spiracular plate and, in some cases, poorly defined and appearing as a minute shining black dot some distance from the edge. At the base of the tubercles which form the spiracles, below and between them, is a slight elevation with a median depression. Prothoracic spiracles inconspicuous and, if present, extremely difficult to locate on the external surface of the puparium. Anal opening large, located far below the posterior spiracles, near the posterior border of segment X.

SEASONAL HISTORY

In Europe the species passes the winter as a first-stage maggot within the cocooned larva of several species of the old genus *Lophyrus*

(sawflies) and in the overwintering larva of *Dendrolimus pini* L. At the beginning of spring the hibernating maggot develops to maturity and, in the case of a sawfly host, escapes from the cocoon through a circular opening cut at one end. The pupal period is about two weeks long. The adult then issues, mates, and in about another two weeks attacks those hosts which are suitable for its perpetuation. The maggot of the next generation develops rapidly within the parasitized host larva, some individuals completing their larval development in six days. The adults of this generation (summer generation) appear about a month later. They behave as did their parents, mating and later ovipositing upon certain host species which are then available. As a rule it is the progeny of this generation that hibernate, although there are apparently some individuals which emerge, thereby forming a partial third generation. At the Budapest laboratory oviposition by the flies of the summer generation was obtained as late as September 12 on *Porthetria dispar* in which development had been retarded for several weeks. Their progeny did not attempt to hibernate, but completed their development, issued, and gave adults between October 20 and 27—that is, after 38 to 45 days. These adults were then mated and later successfully deposited eggs on *Plusia gamma* L. and *Noctua c-nigrum* L. (*Agrotis c-nigrum* L.).

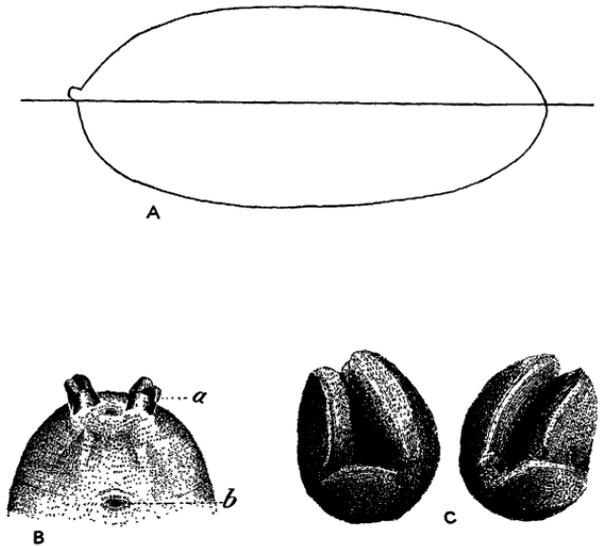


FIGURE 6.—*Sturmia inconspicua*: A, Puparium, lateral view ($\times 8$); B, ventral view of posterior end held at an angle of 45° (a, stigmata; b, anal opening); C, posterior spiracular plates

LIFE HISTORY

MATING

As is usual among the tachinids, the males issue first. Several days elapse between the height of their emergence and that of the females. Mating of the species was readily obtained in cages measuring 14 by 16 by 36 inches. These cages were of wood frame and covered with cloth with the exception of part of the front, which was celluloid. One cage would accommodate 300 flies. In shell vials, 2 by 8 inches, and in smaller containers mating was not so easily obtained.

Usually the females are several days old before mating is effected. In other species instances have been recorded of the males mating with females whose wings were scarcely dried. Of the several thousand flies observed at this laboratory, such an occurrence has not been recorded.

According to observations made at the Budapest laboratory, the mating flies prefer the bright sunlight. It was found that when the flies were moved from the laboratory into the bright out-of-door light mating would take place at once. At the Melrose Highlands, Mass., laboratory, however, the flies apparently mated very well in the semidarkened laboratory.

The pairing of the species is usually preceded by a momentary struggle of the flies; they then settle down and remain more or less stationary for a variable length of time. Ordinarily the flies remain in coitu for several hours, and frequently those taken from the cages during the evening remain so until the following morning. In some cases, however, a pair will separate in less than an hour even though there is no obvious disturbance. Of nine pairs removed from the cages June 8, the time spent in coitu was: $1\frac{1}{4}$ hours for one pair, $4\frac{1}{4}$ hours for four pairs, and more than 5 hours for the remaining pairs.

Males that have mated once will do so a second time and the result of the second union is successful. Females seen in coitu from 15 minutes to 1 hour have been observed to separate and remate after a short time, the second mating continuing for more than 6 hours.

PREOVIPOSITION PERIOD

In 1928 adults began to issue from the first installment of imported material upon its arrival at the laboratory on May 18, and continued issuing until the middle of June.

On May 31 and June 1, 20 pairs of flies (in coitu) were taken from the cages, placed in separate containers, and their behavior noted. Dissection of some females five days after fertilization showed the uterus swollen to many times its original size and packed with minute, elongated maggots each inclosed within a thin membranous eggshell. Occasionally a marked difference in the development of the eggs within the uterus was noted, those at the anterior end being semi-transparent and motionless while those at the posterior end contained fully developed maggots, some of which were active. By actual count there were 97 maggots in the uterus of one female and 102 maggots in that of another.

After the third day of mating, various host larvae were presented to the flies in an attempt to obtain oviposition. This procedure was

continued daily up to the time of oviposition, which usually did not occur until 12 to 14 days after mating. The minimum period for preoviposition was obtained from two females taken in coitu June 8 and separating after two hours. Seven days later these two flies oviposited on the penultimate-stage larvae of the sawfly *Neodiprion dyari*. In every other instance where flies of this age were used the results were negative. They would either appear frightened or show no interest whatever in the caterpillars before them.

OVIPOSITION

Oviposition has been repeatedly observed. The fly faces the host, and, with its ovipositor extended between its legs, calmly proceeds to attach an egg to the skin of the host larva. Often the fly will stand at almost the maximum distance away from the host larva, so that an active larva could easily crawl out of range. This behavior was apparent when the species was confined with *Hyphantria cunea* Drury or *Diacrisia virginica* Fab. Oviposition was frequently attempted on the rapidly moving larvae, but rarely were the flies able to deposit their eggs. As a rule, once a larva escaped, the parasite would not only fail to follow it up, but apparently lost all interest in it. With a less active species of host, especially the tenthredinids, the flies were more persistent and deposited many eggs. In certain species of this family a larva when disturbed raises the anterior portion of its body and jerks its head backwards and sideways until relieved from alarm. This behavior on the part of the species observed was futile, however, so far as *Sturmia inconspicua* was concerned. Such action may have delayed oviposition, but eventually the flies succeeded in their attack and deposited many eggs.

The fertilized female, when given preferred host material, did not exhibit the degree of excitement noted among some other tachinids. This was also true of the females that had been held back after fertilization for experimental purposes. Only rarely did any of the flies exhibit excessive eagerness to oviposit, even under what were considered to be ideal conditions.

Sensing of the host by tapping it with either the front feet or the antennal organs was not a prerequisite to attack, although the flies would often go through with these preliminaries. Motion, even of inanimate material, seemed to supply the necessary stimulus, and occasionally they would attempt oviposition on the forceps or brush as it was being withdrawn from the vial which contained them.

Oviposition was obtained at all hours of the day. Night conditions were simulated as nearly as possible, but the flies that would oviposit by day would not do so in darkness.

Apparently the flies will deposit their eggs on any part of the host. Perhaps the pleural region received the most eggs. If so, it was simply because this region was most accessible. As a rule, the eggs were laid perpendicular to the longitudinal axis of the host larva, although they were frequently found otherwise. Eggs deposited on the head capsule and on the dorsum where the integument is thickest have been noted. When they are laid on the head it is not known to a certainty that the maggots succeed in penetrating. If not, they probably die, for in no instance has any migration of the maggot been observed. A maggot hatching from an egg laid on the dorsum of *Neodiprion dyari*

or *Porthetria dispar* has no difficulty in penetrating. In other species the maggot might experience some difficulty, but no information concerning this point is available. At the Budapest laboratory, when eggs were laid on the proleg of *P. dispar*, the maggots were successful in reaching the body cavity. Eggs deposited on the sides of the thoracic segments have the best chance of survival, as the host larva is then unable to crush them. No data are available, however, which could possibly be interpreted to indicate that the fly was aware of this fact.

In confinement the number of eggs deposited on a single host is governed largely by the fly's eagerness to deposit or by the length of time that the host is subject to attack.

Sturmia inconspicua shows a preference as to its hosts. This is illustrated by the following experiment: Larvae of various stages of *Porthetria dispar*, *Malacosoma americana* Fab., *M. disstria* Hbn., *Hemerocampa leucostigma* A. and S., and *Neodiprion dyari* were placed in a cage with a number of *S. inconspicua* and allowed to remain until the next day. Subsequent examination of this material showed all the larvae free of eggs except the *N. dyari*, which were heavily infested. Other experiments were of a confirmatory nature. For instance, if *inconspicua* were placed in the same cage with *Diprion simile* and *N. dyari*, their interest would eventually center upon the latter. Furthermore, flies actively engaged in attacking *N. dyari* when transferred to *P. dispar* or *Malacosoma* spp. failed to exhibit the same eagerness to oviposit. When these hosts were replaced by *N. dyari*, the flies resumed their former interest.

LONGEVITY

Under laboratory conditions *Sturmia inconspicua* is a hardy species, there being little difficulty in keeping the flies in good condition. Individuals well cared for by daily feeding and cleansing of containers lived for 4 or 5 weeks. An instance was observed in which two females, removed from the mating cages, in coitu with males, on May 31 and used daily in reproduction experiments, lived for 42 days. A case of one female fly living for 112 days has been recorded at the Budapest laboratory.

PARTHENOGENESIS

Virgin females showed little interest in the usual hosts and, although they occasionally attempted oviposition, they were never successful. Furthermore, dissection of the flies revealed no egg development whatever. Parthenogenesis is therefore unlikely. The fact that no infertile eggs were deposited by any of the flies is interesting. In *Carcelia laxifrons* Vill., *Phorocera agilis*, and other tachinids, even though the female is unfertilized, the eggs will descend into the uterus and eventually be deposited.

DEVELOPMENT OF THE LARVA

From egg deposition to the complete disappearance of the maggot within the host is a matter of 5 to 10 minutes only. The maggot hatches immediately from one end of the egg and bores its way into the caterpillar, the chorion of the egg collapsing simultaneously with the exit of the maggot. Its progress is then arrested and it soon

becomes enveloped within an integumental funnel caused by an ingrowth of the body wall of the host. Apparently there is no attachment to any of the tracheae, but the maggot obtains its supply of air directly from the exterior by way of the funnel, in which its posterior stigmata are tightly fitted. This funnel is cone-shaped, the basal portion being highly sclerotized, dark brown to black, and gradually fading out into a lighter shade anteriorly until it becomes hyaline and difficult to see. The entire first and second stages and a part of the third stage are spent in this fixed position. The maggot then leaves its funnel and wanders freely in the body of the caterpillar. It is thought to remain thus for at least a day. This belief is strengthened by the fact that, when nearly mature third-stage maggots are dissected out alive and are allowed to remain on a watch glass with the dead host material, they will feed and complete their development and produce perfect adults. Under such conditions several maggots have lived for more than a day before transforming to pupae.

Sometimes the attack of the parasite does not bring about any definite reaction from the host larva other than a slight contraction of the segments at the moment of oviposition. Certain individuals seem to be totally unaware of the entrance of the maggot and display no apparent discomfort. Others move constantly about, throwing back the head and trying to dislodge the burrowing maggot. A parasitized larva, when exposed to a second attack one to seven days later, behaves precisely as does one suffering its initial attack. Apparently there is no recognition of its enemy.

The time required for the growth of the different larval stages is variable. Over 100 penultimate-stage larvae of *Neodiprion dyari* were parasitized in one day. Dissections of this material, together with that obtained from other host species (*Malacosoma disstria*, *M. americana*, and *Porihetria dispar*), showed a great disparity in larval development. First-stage maggots were found, either alone or in company with more fully developed ones, in larvae that had been parasitized up to 12 days; second-stage maggots were found in material parasitized from 6 to 12 days; and third-stage maggots in material parasitized from 6 to 27 days. The average duration of the larval stages of 104 individuals was 13.9 days. Usually it was not until the sixth day that any stage other than the first was found, although a few individuals reached maturity in this time. There seems to be no extra development of the maggot in the uterus of females that have withheld their eggs for an extended period. Some of the flies were held in reserve and not allowed to oviposit until 27 days after fertilization, but their progeny did not develop any more rapidly than those that were treated normally. From all the available data a mean of 3 to 6 days has been calculated as best suited to the larval development in each stage. These figures will account for at least 90 per cent of the larvae observed. It is not believed that an equal time is spent in each stage; in fact, there is some evidence that the second stage is shorter than either of the other two.

THE PUPAL PERIOD

Rarely does the maggot form its puparium within the host. Usually it cuts its way through the end of the cocoon or, in the case of a lepidopteran, tears its way through the skin of the host larva, crawls

a short distance away, and pupates. In the rearing trays the parasites often formed their puparia in the excrement and other débris. Owing to this habit and also because of the spiny nature of their skin, to which all small particles will adhere, the puparia are often mistaken for other matter and thus are easily overlooked.

The duration of the pupal stage of the summer generation was found to average about 10.5 days. A rare exception was a minimum of 7 days. The maximum time recorded was 18 days, but no doubt this could be extended almost indefinitely by lowering the temperature. The time spent in the puparium seems to depend somewhat on the sex of the individual. Of the 68 flies studied, 32 males averaged 10.9 days and 36 females averaged 11.3 days.

HIBERNATION

Sturmia inconspicua hibernates as a first-stage maggot in the cocooned larva of *Lophyrus pini* and in the overwintering larva of *Dendrolimus pini*. At the Budapest laboratory it has been observed that when the cocoons of *pini* are opened, and the overwintering larvae removed, those which are parasitized may be readily detected by the protuberance caused by the heavily sclerotized breathing funnel of the parasite. Often this structure is surrounded by a dark brown scab, and close examination reveals a minute hole through which the posterior spiracles of the parasite maggot are discernible. Communicating with the outside in this way, the *Sturmia* larva passes the winter in a well-defined sac which is attached to the sides of the funnel.

At the Melrose Highlands laboratory *Sturmia*-infested overwintering hosts (*Diprion simile* and *Neodiprion lecontei* Fitch) were dissected in October and in February of the next year, and without exception first-stage *inconspicua* maggots were found encysted beneath the skin of the host larva at their point of entrance, in a manner as described above.

SUPERPARASITISM

Superparasitism is often encountered in dissection work. Several examples which may be of interest are as follows: One *Porthetria dispar* larva parasitized 6 days contained one second-stage and one third-stage maggot; one larva of *Neodiprion dyari* parasitized 6 days contained one first-stage and four second-stage maggots in various stages of development; one *P. dispar* larva parasitized 10 days contained one second-stage (newly molted) and three third-stage maggots; one *N. dyari* parasitized 12 days contained one first-stage and one third-stage maggot.

This excessive parasitism is not always advantageous to the parasite. Many of the *Neodiprion dyari* larvae were infested with more than one parasite, yet the actual rearing of two parasites from one individual was not recorded. Evidently, in this host at least, it is the one parasite best fitted that survives. From *Porthetria dispar*, *Malacosoma americana*, and *M. distria* several parasites have frequently been obtained from a single individual. From the Budapest laboratory Muesebeck reports three to five parasites from a single *P. dispar* larva as common, and as many as seven have been obtained. With these species it is probable that the number of *inconspicua* in each caterpillar is limited only by the size of the host.

HYPERPARASITES

According to Sitowski,⁷ *Sturmia inconspicua* suffers from two hyperparasites in Poland, (*Hemipenthes*) *Anthrax morio* L. and *Argyramoeba varia* Fab. The parasitism by the former is sometimes severe. At the gypsy moth laboratory there is no record of any secondary parasite having been reared from material imported from Europe.

COMPETITION WITH OTHER PARASITES

This important phase of parasitism has not been studied in this country with sufficient thoroughness to warrant anything more than a general statement. In Europe, at the Budapest laboratory, some of the most interesting observations on the competition occurring between *Sturmia inconspicua* and other parasites have been made by C. F. W. Muesebeck and his assistants. These observations⁸ show that—

* * * *Sturmia inconspicua* is able to complete development more quickly and thus win out in competition with two of the most common of our central European parasites of *Porthetria dispar*. When eggs of *Sturmia* are laid on *dispar* larvae that were parasitized as many as 8 days previously by *Phorocera agilis* or 5 days previously by *Tachina larvarum* L. it is usually the *inconspicua* larvae which first complete development and form puparia. *S. inconspicua*, when developing in otherwise parasite-free stock, requires from 6 to 20 days to form puparia, whether or not more than one *inconspicua* larva is present. *P. agilis* requires from 17 to 26 days and *T. larvarum* from 9 to 20 days under the same conditions. Since the average *P. agilis* larva requires more time than the average *Sturmia*, it is easily understood why *inconspicua* larvae issue first, but the case of *T. larvarum* is different. *T. larvarum*, on an average, requires no more time than *S. inconspicua*, most of its larvae forming puparia on the eleventh day in the laboratory. Nevertheless, *Sturmia* regularly wins over this species in competition, and it seems as if the presence of *inconspicua* larvae must have some retarding influence on those of *T. larvarum*. Later in the season *inconspicua* completes development in the larval stage very much more rapidly than *T. larvarum*. Parasite-free *dispar* larvae attacked by *T. larvarum* on August 30 produced no puparia until October 2, 33 days later, whereas *S. inconspicua* needed but from 9 to 20 days in larvae attacked September 21. In the summer, though, at the regular *dispar* season, the two species develop separately in about the same time. When, on the other hand, 30 *dispar* were attacked first by *S. inconspicua* and later by *P. agilis*, probably only the larvae which would never have produced *inconspicua* puparia or which supported both species produced those of *agilis*. Thirty *inconspicua* puparia were reared from this lot, all but one of which issued before a single one of the *P. agilis* puparia which were obtained.

From the foregoing it is evident that, because of its rapid development, *Sturmia inconspicua* is well able to hold its own even when competing against two of the most important parasites of *Porthetria dispar*.

In the United States *Porthetria dispar* has no native parasites worth mentioning. Of the introduced parasites that have been successfully established, only three, which attack the larger caterpillars, will be of interest here. These are *Compsilura concinnata* Meig., *Sturmia scutellata*, and *Phorocera agilis*, tachinid flies from Europe. The effect on these species of the establishment of *S. inconspicua* is problematical. So far as *Compsilura* is concerned, it is probable that an intensive competition would result in which *Compsilura* would be the loser. Should this prove to be the case, the status of

⁷ SITOWSKI, L. DO BIOLOGJI PASORZYTOW BORECZNIKA (LOPHYRUS LATR.). (SUR LA BIOLOGIE DES PARASITES DE LOPHYRUS IATR.) Roczn. Nauk Rolnicz. 14: 1-25, illus. 1925. [Original in Polish; title in both Polish and French. Summary in German, Zur Biologie der Lophyrusparasiten, p. 22-25.]

⁸ Unpublished notes at the Budapest laboratory.

Compsilura would not be materially affected because of its extraordinary ability to adapt itself to other hosts. On the other hand, *S. scutellata* and *P. agilis* are peculiar to *P. dispar*; moreover, their development is comparatively slow. For these reasons it is probable that on occasions of periodic abundance of *inconspicua* they would indeed suffer. It has often been stated that the natural control of *P. dispar* in the European forests is due, in part, to the large number of species that are parasitic upon it. Here the struggle for supremacy, or perhaps for the perpetuation, of the parasitic species themselves, is as acute as in the United States, if not more so, and yet these species persist. It is safe to predict that the establishment of *inconspicua* in this country would in no way interfere with the continuance of the other species.

The parasites of *Diprion simile* have been recorded by Middleton.⁹ Mention is made of seven hymenopterous parasites and one tachinid, *Phorocera claripennis* Macq. (*Exorista petiolata* Coq.). Two species of Hymenoptera, *Monodontomerus dentipes* Boheman and *Ephialtes (Itoplectis) conquisitor* Say, and two tachinids, *Phorocera claripennis* Macq. and *Winthemia quadripustulata* Fab., have been reared at the gipsy moth laboratory. In no case were these parasites abundant. From collections of approximately 1,000 larvae only five individuals were parasitized, and it seems unlikely that *inconspicua* would find much competition in the United States as regards this host.

It is difficult to conceive of any instance in which the native parasites would suffer because of *Sturmia inconspicua*. Certainly other species besides *Porthetria dispar* and *Diprion simile* will be attacked, and the parasites peculiar to them must suffer the competition of *inconspicua*. It is by no means certain, however, that such competition would jeopardize the species so much as do numerous other factors which exert their influence entirely independent of host or parasite. The author knows of no instance in which a foreign tachinid has usurped the position of a native one. *Compsilura concinnata* is a far more adaptable species than *S. inconspicua*; yet, with all its reputed aggressiveness, there is little indication that its presence has in any way proved detrimental to its native competitors.

HOSTS

A list of the European hosts of *Sturmia bimaculata* Htg. (= *S. inconspicua* Meig.) prepared by Baer¹⁰ includes the following species: *Dendrolimus pini* L., *Lymantria* (= *Porthetria*) *dispar* L., *L. monacha* L., *Panolis griseovariegata* Goeze, *Stauropus fagi* L., *Lophyrus pini* L., *L. similis* Htg., *L. pallidus* Klug, *L. virens* Klug, *L. frutetorum* Fab., *L. socius* Klug, *L. rufus* Klug, *L. polytomus* Htg., and *L. laricis* Jurine.

At the Budapest laboratory *Sturmia inconspicua* has been reared from several additional hosts, which are as follows: *Trichiocampus viminalis* Fall., *Pygaera pigra* Hufn., *Plusia gamma* L., *Agrotis c-nigrum* L., and from two unidentified tenthredinids.

Other host species, exclusive of *Porthetria dispar* and *Diprion simile* Htg., which have been reared at the Melrose Highlands laboratory

⁹ MIDDLETON, W. THE IMPORTED PINE SAWFLY. U. S. Dept. Agr. Bul. 1182, p. 16, illus. 1923.

¹⁰ BAER, W. Op. cit.

are *Malacosoma americana* Fab., *M. disstria* Hbn., *Hemerocampa leucostigma* A. and S., *Hydria undulata* L., *Alypia octomaculata* Fab., *Neodiprion dyari* Roh., and *Neodiprion lecontei* Fitch.

SUMMARY AND CONCLUSIONS

Sturmia inconspicua Meigen is an effective European parasite of the gipsy moth, *Porthetria dispar* L. It is also the most important European tachinid parasite of the introduced pine sawfly, *Diprion simile* Htg., and because of the recent introduction of this species in the Northeastern States the establishment of *S. inconspicua* should prove of decided benefit.

European authorities do not wholly agree upon the taxonomic status of *Sturmia inconspicua*, but according to J. Villeneuve the form treated in this paper is that species.

Sturmia inconspicua is indigenous to central Europe and is commonly found in northern Africa. The first attempt to colonize the species in the northeastern part of the United States was in 1906. Between 1907 and 1910 other introductions were made, but during the following years all attempts to recover the species failed. In more recent years (1923 to 1925, inclusive) large colonies were liberated and in 1929 the first recovery was made.

Superficially, the adult bears a general resemblance to the common house fly, but on critical examination it will be found to possess certain characters that are typical of the genus *Sturmia*, family Tachinidae. The eggs are grayish and about 0.5 mm in length. The first-stage larva is white, more or less spinose, and characterized chiefly by the presence of stigmatic spines and sclerotized areas on the posterior segment. The bucco-pharyngeal armature is without articulation. The second-stage larva appears less spinose and lacks the two principal characteristics of the preceding stage. The bucco-pharyngeal armature has one articulation. The third-stage larva is characterized by a clothing of spines and long hairs and protuberant posterior spiracles. The bucco-pharyngeal armature has two articulations. The puparium is brownish black, averaging 4 or 5 mm in length, and has tuberculate spiracles each furnished with three spiracular slits.

The species passes the winter as a first-stage maggot within the cocooned larvae of several species of sawflies of the old genus *Lophyrus* and possibly in some lepidopterous pupae. Completing its development in the spring of the year, the maggot issues, forms its puparium, and in about two weeks the adult emerges. There is a second generation, the species being able to develop on a number of hosts. It is the progeny of this generation which hibernate.

The species will readily mate in confinement. Ordinarily the flies remain in coitu several hours. Males frequently remate and the result of the second union is successful.

The preoviposition period is variable, 12 to 14 days usually being required.

The fly attaches its eggs to the skin of the host larva. In confinement the number of eggs deposited on a single caterpillar is governed largely by the eagerness of the individual to oviposit or by the length of time that the host is subject to attack.

Under laboratory conditions the flies will live for 4 or 5 weeks. An instance of one female living for 112 days has been recorded.

The species is believed not to be parthenogenetic.

The average duration of the entire larval stage is about 13.9 days, although certain individuals will mature in 6 or 7 days. The duration of the pupal stage averages about 10 days.

Superparasitism is frequent, as many as seven individuals having been obtained from a single caterpillar.

In Europe two species of hyperparasites attacking *S. inconspicua* are known, but none has been recorded from the United States.

Competition with other parasites is certain to occur, but because of the rapid development of *S. inconspicua* it will probably not suffer in this respect.

In addition to *Porthetria dispar* and *Diprion simile*, *Sturmia inconspicua* has been reared from many other host species, seven of which are native to the United States.