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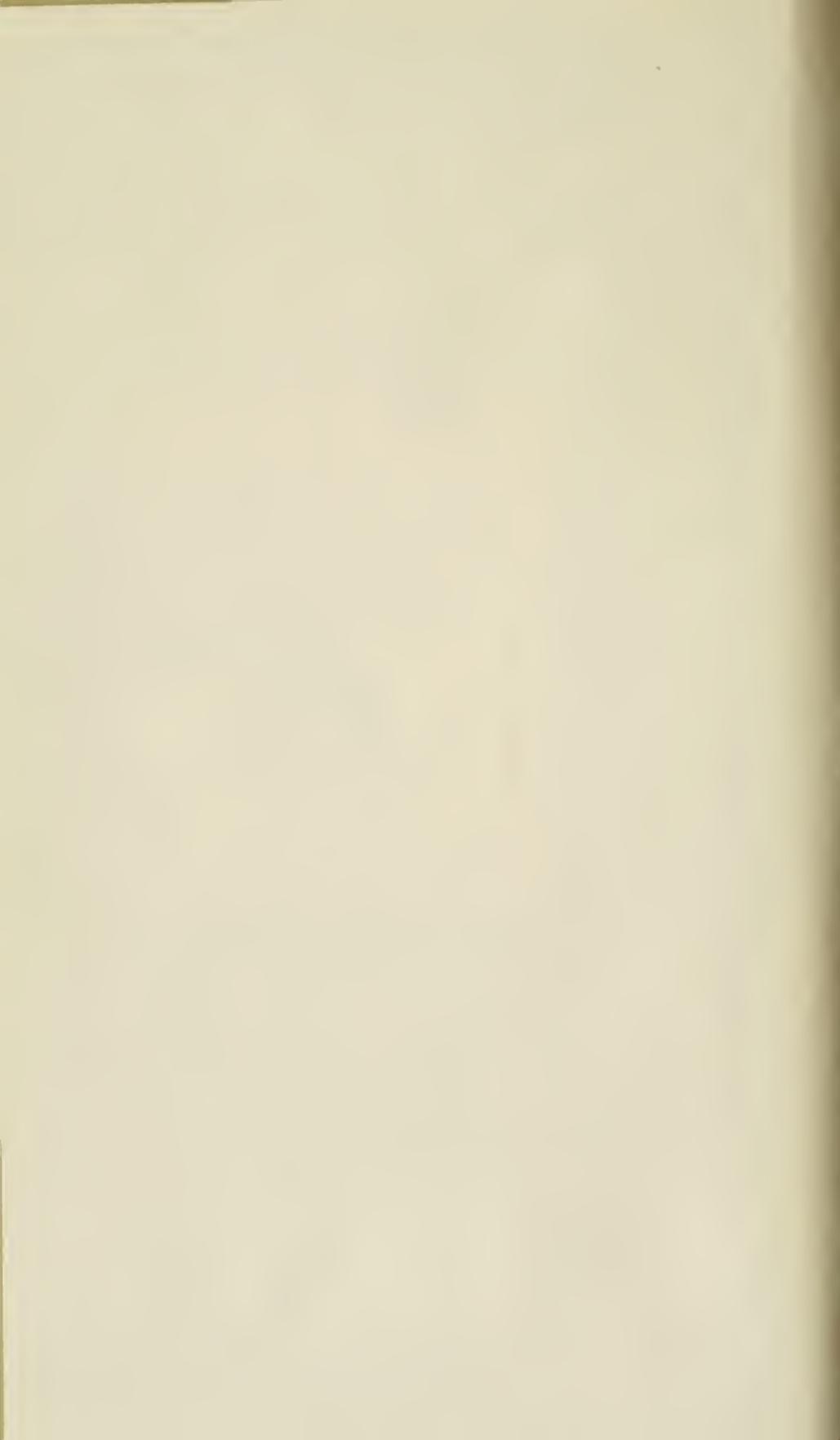
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UNITED STATES DEPARTMENT OF AGRICULTURE



DEPARTMENT BULLETIN No. 1423



Washington, D. C.



October, 1926

PROGRESS OF REINDEER GRAZING INVESTIGATIONS IN ALASKA

By

LAWRENCE J. PALMER

Biologist in Charge of Reindeer Grazing Investigations
Bureau of Biological Survey

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WASHINGTON
GOVERNMENT PRINTING OFFICE

1926

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GROWTH OF THE REINDEER INDUSTRY

The reindeer industry in Alaska, though still in its infancy, promises with proper guidance to become an important factor in the future development of the Territory (pl. 1 and pl. 2, fig. 1). It is comparatively a recent undertaking, and as a commercial enterprise dates back only a few years. From the original stock of 1,280 animals imported from Siberia over the period of 10 years up to 1902, the reindeer in Alaska have increased to about 350,000 head, distributed in 110 herds, all but 6 of which are along the coasts of Bering Sea and the Arctic Ocean. The main grazing at present is

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GROWTH OF THE REINDEER INDUSTRY

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about four chief centers: (1) The Kotzebue Sound country, (2) Seward Peninsula, (3) about Norton Sound, and (4) in the Kuskokwim River basin.

In addition to the numbers in present herds, it is estimated that about 125,000 have been killed for food and clothing. The average gross increase per annum is between 33 and 45 per cent, and the average fawn crop runs between 50 and 60 per cent, although the better-handled herds often attain 70 per cent and sometimes as



FIG. 1.—Distribution of reindeer herds and available range in Alaska, the figures indicating the approximate number of reindeer in each section. Occupied areas are usually less than one-third stocked

much as 90 per cent. The location of herds and the distribution of reindeer and range in Alaska are shown on the accompanying map. (Fig. 1.)

Several small refrigerating plants (pl. 2, fig. 2) and two cold-storage barges were operating on the coast in 1924, and since 1918 shipments of carcasses have been made every year from Alaska to the States. The natural cold-storage facilities of Alaska have been availed of to some extent, and during the winter of 1924-25 one chamber large enough to hold 100 carcasses was excavated in the

underground ice. In areas adjoining the Arctic coast solid ice is reached within 3 or 4 feet of the surface and extends downward to great depths. In the spring of 1925 the carcasses thus stored were removed in excellent condition for shipping.

During the period 1918-1925 more than 1,875,000 pounds of reindeer was shipped from Alaska, the total for 1923 being nearly 200,000 pounds, for 1924 about 375,000 pounds, and for 1925 approximately 680,000 pounds. With continued development, there promises to be a steady increase in the output. Steers for butchering sell (1925) at \$10 to \$12 a head. Breeding stock is valued at \$18 to \$30 a head. The average cost of production for each animal is about \$1 a year. At Nome and St. Michael reindeer meat retails at 15 to 20 cents a pound.

Scientific investigation of reindeer grazing by the Biological Survey were first begun in 1920, when a reindeer experiment station was established by the bureau at Unalakleet; this was subsequently (1922) moved to Nome, and in 1925 was transferred to its present location at Fairbanks. During the progress of the investigations the conditions, both as to class of livestock and their environment, have constantly developed new problems. One of the more fundamental of these has to do with the relation of lichens to grazing. Improved methods in the control and management of the herds and the range are essential to the development of a well-grounded industry. The present publication constitutes a second report on the reindeer investigations being conducted by the Biological Survey and treats particularly the forage and range management phases. The first report¹ dealt also with the biology of the reindeer and the diseases and parasites of the animals.

Plans for future work contemplate studies chiefly along the following lines: (1) The development of interior ranges; (2) conditions governing forage and range management; (3) the various relations of lichens to grazing; (4) relative carrying capacity of lichen and nonlichen ranges; (5) methods of feeding and their effects; and (6) breed improvement of reindeer and the control of the diseases and parasites to which the animals are subject. In view of the fact that conditions in Alaska are so different from those in the States as regards the kind of animal under consideration, the nature of the forage, and the climate, it is particularly important that thorough studies be made.

HERD OWNERS

In addition to the Lapps, who were brought to Alaska to care for the original stock of reindeer and to teach the Eskimos reindeer herding, and who in some cases have since acquired large herds of their own, there are three general classes of reindeer owners in the Territory: (1) Eskimos, (2) white men married to native women, and (3) other white men. The Lapp is by heritage and training a reindeer herder, but is conservative and not inclined to discontinue methods to which he has become accustomed. The white man married to an Eskimo woman differs from others of his kind, so far as

¹ Hadwen, Seymour, and Lawrence J. Palmer, REINDEER IN ALASKA. U. S. Dept. Agr. Bul. 1089, 74 pp., illus. September, 1922.

ownership of reindeer is concerned, in having the privileges of both the Eskimo and the white man. The native Eskimo rates high in intelligence, but is somewhat lacking in initiative and managerial ability. Moreover, since reindeer grazing to him is often merely of secondary consideration to hunting or fishing, as a grazier he requires constant and direct supervision. If the reindeer industry depended upon the unaided efforts of the Eskimo it would be limited in scope. To obtain the best results in range and livestock management and to perfect a desirable grazing scheme and develop the industry on a large scale calls not only for capital but for business ability of a higher order.

A recent count indicates that about a third of the reindeer are owned by white men, including several Lapps, and the remainder by Eskimos. One large incorporated company at Nome owns between 45,000 and 50,000 animals in six herds. Through this white ownership definite efforts have been made during the past few years to place the industry on a commercial basis.

REINDEER AS GRAZING ANIMALS

Reindeer on the range most closely resemble cattle, but band together more like sheep. Like horses they trample over much range in nervous feeding, but, unlike horses, usually travel against the wind. In winter they paw through the snow with the forefeet to reach lichens and other forage. During the summer they move about considerably over the range, and at times cover distances of 15 or 20 miles against the wind. In winter they graze over a comparatively small area, and remain for the most part in one general locality. At fawning time the herd divides, the does grouping by themselves and the bucks, steers, and some of the yearlings banding together elsewhere.

Reindeer become attached to their accustomed haunts, and once well located on a range will unerringly return to it if moved away. In one case, several adult animals were transferred from one herd to another over a distance of 200 miles, and the next year were found back in the original herd, in spite of the fact that there were five other herds between the two places. Unless restrained the reindeer instinctively seek successively their favorite fall, winter, or summer pastures. Such reindeer pests as mosquitoes, horseflies, and warble flies are an important factor in the choice of summer pasture, as they cause the reindeer to resort to the wind-swept areas along the coast, or the ridges and mountain tops of the interior.

Reindeer are excellent swimmers and take readily to water. In Norway it is commonly reported that herds are made to swim as far as 8 or 10 miles from the mainland to some island for summer pasturage. They graze well on the wettest ground and frequently may be seen wading out into ponds to feed on the pond vegetation. In Alaska the typical summer range of the coast is often a wet tundra of hummocky ground (niggerheads) with many ponds and sloughs, and over range of this character the reindeer graze with apparent ease. They are fleet of foot and seem to travel as readily over the niggerheads as over ground more level and firm.



B242911

FIG. 1.—REINDEER GRAZING AT THE NORTHERNMOST POINT OF ALASKA

Part of one of the reindeer herds at Point Barrow, with the hospital and Bureau of Education buildings in the background. September, 1923



B26364

FIG. 2.—REINDEER GRAZING IN THE KUSKOKWIM SECTION

Portion of a reindeer herd at Goodnews Bay, August 1, 1922. Excellent range and fat stock



FIG. 1. MODERN REINDEER STATION

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Summer headquarters cabin of the Buckland reindeer herd on the Arctic coast

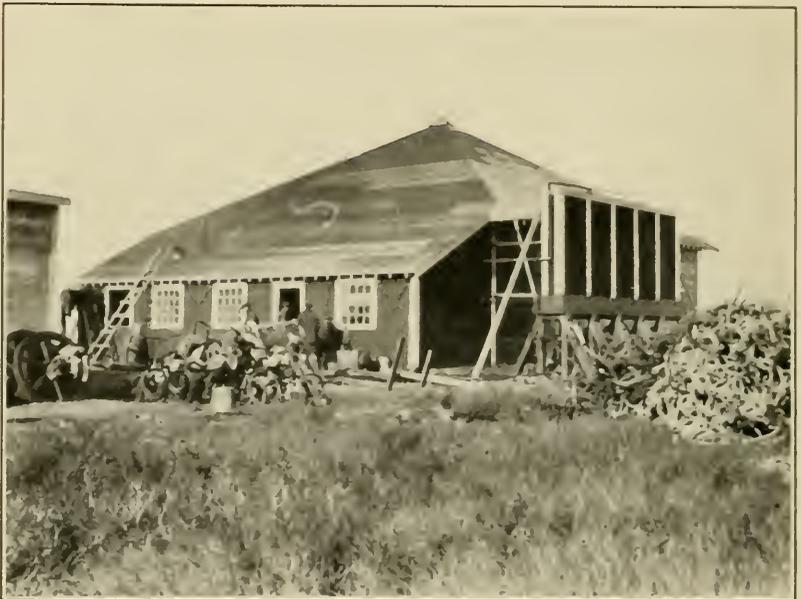


FIG. 2.—REINDEER COLD-STORAGE PLANT

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The capacity of this plant, at Golovin, is 1,000 carcasses. There are now a number of these small refrigerating places along the Bering Sea coast

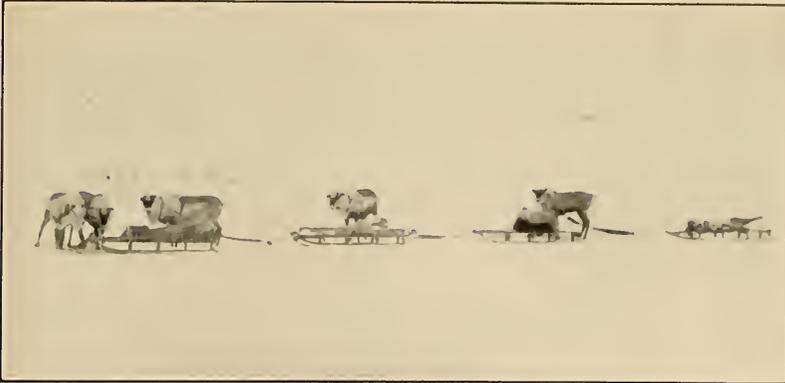


FIG. 1.—REINDEER TRAIN

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A double team in the lead and several single reindeer strung out behind, each drawing a heavy load



FIG. 2.—SLED REINDEER

B28744

Geared with a single-tug type of reindeer harness



FIG. 3.—SLED REINDEER

B28518

Driven with a double-tug type of reindeer harness



FIG. 1.—REINDEER OF THE SHORT, STOCKY TYPE

B24350

In good winter condition. The body is short and thick and the horns flattened and irregularly shaped



FIG. 2.—REINDEER OF THE LONG, RANGY TYPE

B25515

The two adult animals in the middle foreground, in excellent summer condition, are good examples of this type, which has slender, symmetrically shaped horns

BREEDS AND TYPES OF REINDEER

In the Alaska herds there are two general types of reindeer—a long, rangy, big-framed animal and a short, stocky one (pl. 4). The longer, rangy type has finer, longer, more symmetrically branched and harder horns; the shorter has stockier, broader horns, wide at the base and often irregularly branched at the tips. The rangy type of reindeer usually averages heavier and is therefore better for the production of meat.

The average full-grown reindeer in Alaska stands 10½ to 11 hands high, and measures 5½ to 6 feet from nose to tip of tail. The maximum measurements are 12 hands high and 7 feet long. The average dressed weight is about 150 pounds and the maximum 300 pounds. The offal averages 35.1 per cent and the skin 6.4 per cent of the dressed weight, a total of about 41.5 per cent; and the meat or dressed carcass averages 58.5 per cent of the live weight.

With a view to the production of a heavier type of reindeer than at present in the herds, experiments in crossing with the large native caribou are being begun on Nunivak Island, where 10 bull caribou have been introduced into the herd of about 500 reindeer held there. Similar experiments will later be carried on at the reindeer station at Fairbanks. The 10 caribou for the Nunivak experiment were captured in the fall of 1924 at Kokrines, on the upper Yukon, where they were staked out for the winter, and the following spring were transported after many hazardous experiences by barge down the Yukon and transhipped to a schooner for the trip to Nunivak.

The numerous measurements and weights of reindeer indicate that the animals may be most profitably slaughtered at 3 years of age. The big gains in growth are made from the time of birth to this age, particularly as fawns and yearlings. A fair gain is made between the ages of 2 and 3 years, but while some is made between 3 and 4 it is so slight as to be negligible. Consequently, though not considered fully mature until the age of 4 or 5, reindeer are so nearly full-grown at 3 years that they should be slaughtered for marketing at this age rather than held for a longer period.

Observations and measurements also show a color difference depending upon the size of reindeer. The dark colors are superior to the lighter ones, and even in spotted animals reindeer of predominantly darker spots show a superiority over those of lighter shades. White animals are clearly inferior and should be promptly disposed of. The distinctly steel-gray animals, however, seem to be fully as large and strong as the dark-colored ones.

Use of the standard of excellence in Table 1 (p. 6), tentatively adopted by the Bureau of Animal Industry and the Bureau of Biological Survey, will, it is believed, be of value to reindeer breeders in the improvement of their herds.

SLED REINDEER

In Department Bulletin 1089, "Reindeer in Alaska," the present method of handling sled reindeer was described and the suggestion made that if the animals were given some form of grain with the lichens, they would endure more hardships without losing so much

TABLE 1.—*Standard of excellence for reindeer*

	Points considered	Standard
I. Weight and size, according to age (<i>15 per cent</i>)	-----	15
II. Breed-type and color (<i>10 per cent</i>): Representative type dark brown in summer, lighter in winter	-----	10
III. Form, deep, broad throughout (<i>50 per cent</i>):		
(a) Head and neck (<i>10 per cent</i>)—		
1. Masculinity in male and femininity in female	-----	2
2. Antlers flattened and triangular, curving upward and forward	-----	1
3. Muzzle wide; nostrils large, wide, and open	-----	2
4. Eyes clear and bright, indicative of quiet temperament and docile disposition	-----	1
5. Face short; jaws strong	-----	1
6. Forehead broad	-----	1
7. Ears small, well covered with hair	-----	1
8. Neck short, full, blending smoothly into shoulder	-----	1
(b) Fore quarters (<i>10 per cent</i>)—		
1. Shoulders smooth, thickly fleshed, compact	-----	3
2. Brisket wide and full, trim	-----	2
3. Legs wide apart, straight, medium short; dewclaws large; toes spreading; hoofs large	-----	5
(c) Body (<i>15 per cent</i>)—		
1. Chest full, deep, wide, large girth	-----	5
2. Ribs long and well arched, smoothly covered	-----	3
3. Back and loin broad, straight, deeply covered	-----	5
4. Flank full, underline straight	-----	2
(d) Hind quarters (<i>15 per cent</i>)—		
1. Hips and rump full, broad, and smooth	-----	5
2. Thighs deep, full, muscular	-----	5
3. Legs strong, dense, smooth boned; hoofs large; toes well spread	-----	5
IV. Quality (<i>15 per cent</i>):		
1. Pelage heavy, fine texture	-----	5
2. Hide pliable, medium thickness	-----	5
3. Bone dense, smooth, strong	-----	5
V. Condition (<i>10 per cent</i>):		
Sufficient natural flesh to indicate vigor	-----	10
Total	-----	100

flesh and strength. Under the crude handling now practiced the animals are neither trained nor cared for properly and the usual procedure is to drive them until they show signs of exhaustion and then to turn them loose and take fresh ones.

TYPE OF ANIMAL

In selecting reindeer to be broken to harness, attention must first be paid to type. An animal showing a docile nature, as indicated by a wide muzzle and clear, bright eyes, large, wide, and open nostrils, and a broad forehead, is the type that may be easily trained and will make the best sled reindeer.

BREAKING

The Lapps state that with a few tame animals to lead they can sufficiently break a string of 10 or 15 reindeer in two or three days to make a trip with each animal pulling 100 pounds on a sled. But great care and patience must be taken in the process not to frighten or injure the animals. With gentle handling, they learn quickly

and are easily broken to drive. On a trip, the Lapps drive a double team ahead and lead a long string of single reindeer behind, each pulling a sled. (Pl. 3, fig. 1.) Ordinarily reindeer work better in company, and double driving is preferable to single.

In experiments with a sled reindeer conducted while the reindeer experiment station was at Nome, training was begun by haltering the animal and permitting it to drag a rope about the barn inclosure for a couple of days. Then each day for three or four days the haltered animal was coaxed to lead a little. Finally it was harnessed, gently but firmly, and hitched with a second trained reindeer to a sled and driven 2 or 3 miles. It was then returned to the barn, with the harness left on over night. The next morning the harness was removed; two days later the animal was again harnessed, hitched to a sled, and driven behind a trained sled reindeer about $\frac{1}{4}$ miles. To make the start, the animal had to be led by the halter a short distance until it would follow the other sled reindeer, and then it was off at a run. After a few sudden stops and starts, it finally settled down and pulled its sled willingly. The next day it was hitched to a loaded sled and successfully driven double for a while, and then single for about 10 miles; thereafter the reindeer was steadily worked for a period with entire satisfaction.

HARNESS

Two types of harness are used in driving sled reindeer, one with a single pulling tug fastened under the chest and running between the hind legs, and the other with two tugs and a singletree, as used with a horse or dog (pl. 3, figs. 2 and 3). In the first case the tug is usually made of a strip of reindeer skin, since this is less apt to chafe the legs of the animal. Both kinds of harness are satisfactory. A wooden collar is used, made in two pieces to fit around the neck, the ends fastened together by thongs. To this collar are fastened the side-straps leading to a body-band, which encircles the animal just back of the forelegs. When the singletree is used, the tugs, one on each side, are fastened to the body-band and are continuations of the straps leading from the collar. In the single-tug type, the tug is fastened to the harness and to the sled by means of a wooden toggle inserted into a loop.

For guiding sled reindeer two driving lines attached to the halter are used. The animal is started by flipping one of the lines across the back and over the root of the tail, and is guided to the right or left by jerking one line or the other.

WORK ABILITY

To determine the value of feeding grain in the use of sled reindeer, a cross-country trip of 527 miles was made over a period of 42 days, 23 of which were spent in actual travel. In addition to the lichen roughage, grain was fed regularly during the entire period. For comparison, a dog team also was driven on the trip, and it was found that as a draft animal a reindeer performs the work of about three dogs.

The sled reindeer made the trip very successfully, and demonstrated that when fed grain to keep up strength, they may be worked steadily

and driven over long distances. The average distance covered was 23 miles a day, and the maximum, on a fair trail with a load, was 35 miles, whereas on a poor trail it was 20. With an empty sled and carrying only the driver, the daily average would undoubtedly be greater.

The maximum load for a sled reindeer for continuous travel and on grain was 250 to 300 pounds on a good trail and 100 to 150 pounds on a poor one. With the driver riding half the time, on an average trail a full load for each sled reindeer was 100 to 150 pounds, aside from the driver.

FEEDING

During the 42-day experiment the sled reindeer was fed 170 pounds of grain at the rate of 4 pounds a day. Rolled oats were fed morning, noon, and night, the main feeding being at night. Lichens were gathered each day en route just before going into camp, a simple matter toward the end of the day, so that the animal could be fed in camp rather than staked out. By keeping the animal in camp, it could be cared for more conveniently. The practice was also followed, when passing through sections of little moss, of carrying half a sack of it on the sled for occasional feeding en route, especially at noon. On the trail it was necessary to stop the animal three or four times during the day, including the noon stop, to give it a bite of reindeer moss. When passing through country of good lichen growth the animal would pick its own food along the trail, so that it was unnecessary to carry a supply. The reindeer consumed two sacks of the lichens (reindeer moss) daily—about 20 to 30 pounds, air-dry weight. (The wet weight is usually three times the air-dry weight.) It displayed an enormous appetite and consumed about twice as much roughage a day as one would when fed in a barn and not worked.

When hungry, the sled reindeer ate all the lichens offered, irrespective of species, and took also some of the sedge and browse forage, especially Labrador tea, cranberry, and willows. When the first sharp edge of hunger had been allayed, it fed choicely on the lichens only, seeking as much variety as possible. It seemed especially fond of *Cetraria cucullata* and of all light-colored forms of *Cladonia*. When fed grain at night or noon, the reindeer would eat first a few oats and then abandon these for lichens. When fully satisfied on the lichen roughage, it would return and eat a full ration of oats.

USE OF SLED REINDEER

The use of sled reindeer is not so common in Alaska as it should be under proper handling of the herds. The dog team is better suited for main trails and coast travel, but for cross-country travel and for use with the herd, the sled reindeer is cheaper and more practical. For each thousand animals in the herd there should be at least 10 well-trained sled reindeer. They can be used effectively in traveling over the range, hauling supplies to camps, following up the herd or making drives, and in corralling. As they feed on the open range, it is not necessary to carry feed for them, except a small quantity of grain when on long trips or when used continuously. Aside from

this, the presence of several tame sled reindeer in the herd is of greater value in the better domestication of the herd than is commonly supposed.

REINDEER MEAT

Many persons still seem to be under the impression that the reindeer is a game animal and that the meat is venison. This is not the case. The reindeer has been developed from the wild caribou of northern Europe and Asia through countless generations of breeding, and as the breeding up has been without particular direction, the present type is perhaps not far removed from the original. There is some difference, however, in conformation and general coloration² between reindeer of Siberian descent and the caribou of Alaska and Canada, and considerable difference in the temperament of the animals and in range habits.

Reindeer meat, when properly produced and handled, compares favorably with beef. It is fine grained, contains a good, palatable fat, and when fresh is exceptionally juicy and tender. C. F. Langworthy, of the Bureau of Home Economics, comments upon reindeer meat as a food, in a memorandum to the Biological Survey, as follows:

Many studies have been made of the composition of different sorts of meat, of cooking qualities, and of thoroughness of digestion. Judging by available data, meat from different animals used as food is very similar in its general composition.

Besides the considerable amount of water present, meats contain protein or nitrogenous material, fats in varying amounts, minute proportions of glycogen or animal sugar, and some ash constituents. The percentage of fat varies very greatly with feed and other matters.

Some cuts are considered better flavored and some more tender than others, but, generally speaking, meats of different kinds and cuts are very similar in their food value and digestibility, meat protein like other complete protein being used for the building and repair of body tissue, and the fat of meat, like other fats, as body fuel. This applies in a general way to game also.

To understand the place of meats (including reindeer meat) and other foods in the diet, one should remember that in order to be well balanced the diet, week in and week out, should provide: (1) Vegetables and fruit, valuable for ash and vitamin constituents; (2) meat, milk, eggs, fish, and other foods that supply "complete" protein; (3) cereal grains and their products, as sources of carbohydrate for energy or body fuel; (4) sugar and other sweets, as flavor foods and sources of body fuel; and (5) fat, as a source of body fuel, which in some cases, as in butter and cream, is accompanied by vitamin. Reindeer meat is well fitted to take its place with other meats.

Reindeer have been bred for food purposes for centuries in northern Asia, which is clear indication of their fitness for food. The flavor is excellent, the food value compares well with other meats, and the meat is wholesome and can be prepared for the table in a variety of ways.

FEEDING EXPERIMENTS

FEEDING PREFERENCES OF REINDEER

Reindeer are herbivorous and ruminant animals, feeding chiefly on sedges, grasses, and browse plants in summer and on lichens in winter. They are known at times also to eat mice, dried fish, and ptarmigans and their eggs, a habit that probably may be attributed to a craving for certain mineral substances. The value of the differ-

² U. S. Dept. Agr. Bul. 1089, pp. 9 and 10.

ent kinds of range forage plants grazed varies greatly with the stage of growth, and probably to some extent with the tastes of individual animals. As a rule reindeer prefer a variety of green and fresh growths. In spring they seek the earliest vegetation, and feed on green growth throughout the summer. In fall and winter they feed on lichens and grasses and on dry vegetation of various kinds. They prefer, however, the lichens known as reindeer moss which have made new growth and attained greater moisture in fall and consequently are fresher and probably more palatable. Though the lichens represent principally the winter forage of reindeer, they are taken also in summer to the extent of about 15 per cent of their food.

TESTS WITH CULTIVATED GRAINS AND GRASSES

Reindeer are fattest in fall, following the summer grazing on green feed, and during the winter months gradually lose in condition on the lichen feed. It has been commonly stated or supposed that reindeer fatten on the lichen forage and that it is necessary for their maintenance; but feeding experiments have demonstrated that this is not the case, and that reindeer can be fed and fattened on cultivated growth as well as can other classes of livestock. Under experimental winter feeding reindeer have been successfully weaned from a lichen diet and fed on hay and grain. In experiments conducted under the direction of the writer the animals were kept under shelter and handled much as are domestic cattle. The feeds used were timothy, alfalfa, native hay, linseed meal, rolled oats, and chopped corn feed, which included cracked corn, rolled oats, and rolled barley. Check animals were fed on a full ration of mixed lichens and native hay.

It took about 7 days to wean the younger stock from a lichen feed and to get them to eat hay and grain readily, and about twice as long to wean the adult stock fully from the lichen diet. On a lichen ration the check animal ate 10 to 15 pounds of lichens (air-dry weight) and 2 pounds of native hay a day; and on hay and grain the individual reindeer consumed about 4 pounds of hay (alfalfa or timothy) and 4 pounds of grain a day. To make the change from lichens to hay and grain, a mixture of lichens and grain or of lichens and hay was first fed and the quantity of lichens gradually reduced until entirely eliminated.

In experiments in feeding 10 yearling and 2-year-old caribou bulls during a 23-day journey from Kokrines to Nunivak Island, the animals with no lichens supplied took readily to a hay-and-grain diet in three or four days. Each one was fed about 7 pounds of hay and 4.5 pounds of grain daily, but as they consume only the leaves and finer parts, the actual hay eaten by each did not exceed 5 pounds.

IMPORTANCE OF LICHEN FORAGE

In 60 and 90 day station tests on hay and grain the animals made gains of two or three times that of check animals on lichens, varying from half to two-thirds of a pound a day. The check animal made a slight daily gain. Under range conditions, however, reindeer will generally hold their own on a lichen feed and make slight gains where sheltered and where plenty of feed is to be easily obtained, but they lose in condition if unsheltered and forced to rustle extensively for their food.

Lichens are not necessary for reindeer feeding because of any natural or nutritive qualities; but, because they present a readily accessible winter forage, they are the chief factor that makes reindeer grazing possible in Alaska. Without this ready source of food for winter use the reindeer could not be maintained on the coast range successfully, and, consequently, the industry would not exist. The lichen forage crop in Alaska should therefore be carefully guarded in order to continue the yield.

EFFECT ON QUALITY OF MEAT

Feeding reindeer on cultivated crops has an important effect on the meat. An animal fed on alfalfa hay and grain (rolled oats and cracked corn) was slaughtered when fat and the meat tested. As compared with range stock, the meat from this reindeer proved firmer, finer grained, and drier, and the fat generally occurred scattered through the meat rather than being localized. The texture and quality of reindeer meat apparently is affected by the kind of food eaten, and probably varies directly with the quality.

ANALYSIS OF FEEDS

Table 2 (p. 12) shows the analysis of lichens and other range plants and cultivated crops. Generally, in comparison with range and field crops, the lichens show a lower percentage of protein and a higher percentage of starch.

Of the lichens listed in Table 2, those of forage value in Alaska, in the order of their importance, are *Cladonia*, *Cetraria*, and *Stereocaulon*. The species of *Parmelia* are of little economic value because of their scattering occurrence and inferior size. When this is taken into consideration, the difference in protein content of the lichens, as compared with other feeds, is found to be even greater.

NATURE OF GRAZING USE

The nature of the reindeer industry in Alaska was described in detail in Department Bulletin 1089. As bearing directly on the problem of proper range management, however, it may be well to outline briefly the nature of the grazing use in Alaska in order to incorporate information which has resulted from later studies and observations.

No cultivated forage crops are raised and no feeding is done in connection with reindeer grazing in Alaska. The animals are grazed yearlong on the open range, and from six to six and a half months of this they are on winter forage. Each herd is confined to an individual area, which is a piece of range usually fairly well defined within a natural topographic unit. Major features of topography, as large streams and main ridges, divide the various grazing areas. Each unit includes summer and winter ranges and fawning grounds, and each has its own buildings, corrals, and other improvements necessary for the individual herd. (See map, fig. 1, page 2.)

Unlike much of the reindeer grazing conducted by the Lapps in northern Sweden and Norway, where a nomadic existence is common, reindeer grazing in Alaska is more centralized and tends toward permanent ranches. This difference is largely due to the abundance

TABLE 2.—Analysis of food value of lichens, other forage plants, and cultivated grains and grasses¹

Species	Moisture	Ash	Fat	Protein	Starch	Cellulose
	<i>Per cent</i>					
Lichens:						
<i>Cetraria islandica</i>	14.50	1.15	2.10	2.80	74.50	4.55
<i>Cetraria nivalis</i>	15.00	1.40	3.55	1.60	76.00	2.45
<i>Cladonia rangiferina</i>	15.00	.90	2.15	2.05	49.40	30.50
<i>Stereocaulon paschale</i>	15.00	1.85	1.75	6.35	56.00	18.45
<i>Parmelia encrustata</i>	15.00	8.05	2.25	6.10	51.25	17.35
<i>Parmelia saxatilis</i>	15.00	10.70	14.75	5.30	47.15	7.10
Average.....	14.92	4.01	4.42	4.03	59.22	13.40
Browse:						
<i>Salix hastata</i>	15.00	4.40	3.00	14.80	51.10	11.70
<i>Salix lapponicum</i>	15.00	3.60	2.65	14.00	47.00	17.75
<i>Salix glauca</i>	15.00	5.50	4.00	12.85	47.75	14.90
<i>Salix herbacea</i>	15.00	3.85	2.75	14.85	47.30	16.25
Average.....	15.00	4.34	3.10	14.12	48.29	15.15
Grasses:						
<i>Poa alpina</i>	15.00	3.90	2.30	11.60	41.85	25.35
<i>Aira flexuosa montana</i>	15.00	4.70	2.80	10.15	44.00	23.35
Average.....	15.00	4.30	2.55	10.88	42.92	24.35
Grains:						
Corn.....	11.30	1.40	5.00	10.50	70.10	1.70
Barley.....	10.90	2.40	1.80	12.40	69.80	2.70
Oats.....	11.00	3.00	5.00	11.80	59.70	9.50
Average.....	11.07	2.27	3.93	11.57	66.53	4.63
Meal:						
Cottonseed meal.....	8.20	7.20	13.10	42.30	23.60	5.60
Linseed meal.....	9.20	5.70	7.90	32.90	35.40	8.90
Oat meal.....	7.90	2.00	7.10	14.70	67.40	.90
Average.....	8.43	4.97	9.37	29.97	42.13	5.13
Hay:						
Timothy.....	13.20	1.40	2.50	5.90	45.00	29.00
Alfalfa.....	8.40	7.40	2.20	14.30	42.70	25.00
Average.....	10.80	5.90	2.35	10.10	43.85	27.00

¹ The analysis of lichens, grasses, and browse for this table was obtained from a translation of the Norwegian "Report of Grazing Committee on the Use of the Harang Section—Lands Department" (Indstilling fra Fjeldbeitekomiteen om Hardangerviddens utnyttelse—Landbruksdepartementet), Kristiania (Oslo), 1911. The comparable figures for grains, meal, and hay were obtained from "Profitable Stock Feeding," by H. R. Smith, 1913.

of forage in Alaska and to the presence of large natural grazing areas capable of being divided into individual grazing allotments, each complete in itself. The nomadic habit of the Lapp requires that he handle his reindeer under a close-herding practice; but in Alaska, to obtain the best results under a fixed-allotment system, open herding must be practiced.

SIZE OF HERDS

The reindeer are now run in herds of from less than 400 up to 8,000 head, and in one case 12,000, with the average about 2,500. Because of the large natural grazing units, the impracticability of dividing the range among numerous small herds, and the fact that reindeer on the range are not so amenable to control as are sheep but must be handled more like cattle, the future tendency will be toward the larger herds. The number of animals to which each herd may increase is limited by the carrying capacity of the individual allotment. The size of an allotment is governed, of course, by its natural



FIG. 1.—IMPROVED REINDEER CORRAL

B28732

A herd of about 5,000 animals is being driven into the main corral of the Golovin herd. The pen in the background is for holding stock cut out for butchering



FIG. 2.—REINDEER ROUND-UP

B26306

The herders at Pastolik are preparing to cut off and drive a bunch of reindeer into the pens leading to the chute. The animals are still in winter coat, July 4, 1922



FIG. 1.—HANDLING REINDEER AT END OF CORRAL CHUTE

B28790

Each one is caught by the horns, passed through the gate at the end of the chute, and thrown to the ground for marking or castration



FIG. 2.—THROWING A YEARLING REINDEER

B26460

The animal is grasped by the horns and thrown by twisting the head



FIG. 1.—BRANDING REINDEER

B26443

Branding with a hot iron, usually on the flank, when carefully performed has proved sufficiently satisfactory to warrant adoption



FIG. 2.—A SUCCESSFUL BRAND

B26716

A broken circle brand on the left flank one year after branding. Branding with a hot iron is now being practiced in six of the Alaskan herds



FIG. 1.—PERMANENT CABIN CAMP

B25775

Herding cabins, especially on winter range, are preferable to tents. Several of these camps variously located over the range are needed on every growing allotment



FIG. 2.—TEMPORARY TENT CAMP

B25781

Tents are resorted to by the reindeer herders when cabins are not provided. They serve solely as temporary shelter and are not so satisfactory as cabins

boundaries, but most of the units will have a carrying capacity of 5,000 to 10,000 reindeer. Accordingly, the future herds in Alaska will run from 5,000 to 10,000 heads, or an average of 7,500.

Large grazing allotments will make possible the establishment of cooperative herds among numerous small owners, and this will result in the formation of many cooperative reindeer associations, or livestock companies, especially among the Eskimos.

HERDING

Reindeer are now herded almost entirely on foot, mainly by natives and Lapps, commonly aided by dogs. One or two herders go out each day from a central camp to watch the herd, sometimes remaining out over night. Horses for herding are employed to some extent in the interior but have yet to be tried along the coast. Sled reindeer and dog teams are used during the winter for hauling camp supplies; in summer, transportation is largely by boat and on foot.

ROUND-UPS

The herds are rounded up for marking or branding and castration early in summer, usually in July. Again, in fall and early in winter—October, November, and December—they are rounded up for butchering. During the middle of the winter another round-up may take place for separating mixed herds or breeding and non-breeding stock. All handling was formerly done by roping on the open range or in a crude brush corral. Now, however, the corral and chute method has come into more general use, and roping is being abandoned (pl. 5).

CORRALS

Two methods of corralling are employed, one using the chute, the other the pen. For efficient work with the chute a large force of men is necessary, whereas the pen has the advantage of requiring only a small crew. When the chute is used, all the animals are driven through and caught at the end (pl. 6). When the pen is used, the animals are handled in a central working pen and those to be marked or otherwise handled are captured by means of sheep hooks.

A diagram of a corral of the pen type successfully in use at Kokrines, Alaska, is shown in Figure 2. With this corral a crew of five men has marked reindeer fawns at the rate of 750 a day. A highly successful type of corral of the chute method, and the type most commonly used, is shown in Figure 3. With a crew of 15 men, reindeer may be handled in a corral of this kind at the rate of 125 to 175 an hour.

In erecting the type of corral shown in Figure 3, it is very important to construct the entrance hook leading to the holding pens and chute on the side of the corral meeting the direction of mill. This may be either to the right or to the left depending upon the individual herd. One herd will not mill both ways, always going either clockwise, or counterclockwise. It is therefore necessary to note the direction of mill in order so to construct the entrance hook as to intercept the milling animals and facilitate their capture. Two

hooks, one on each side of the corral, may, of course, be constructed, but only one is needed if the direction of milling be known. It is easy to drive the reindeer into a hook properly placed, but difficult to drive them into a hook not opening toward direction of the mill. Of 25 herds observed in respect to milling, 3 were found always to mill counterclockwise and the remainder clockwise.

HOLDING PASTURE

A recent improvement for handling reindeer when the corral is used at round-up time is a holding pasture adjoining the corral. As the Alaska herds increase in size the use of a holding pasture will become more and more necessary. It not only insures convenient holding of the herd at the round-up but makes it more possible to handle a large herd at one time without starving the animals. The main herd is confined in the pasture on feed and water, and, from time to time as needed, bunches are cut out and driven into the

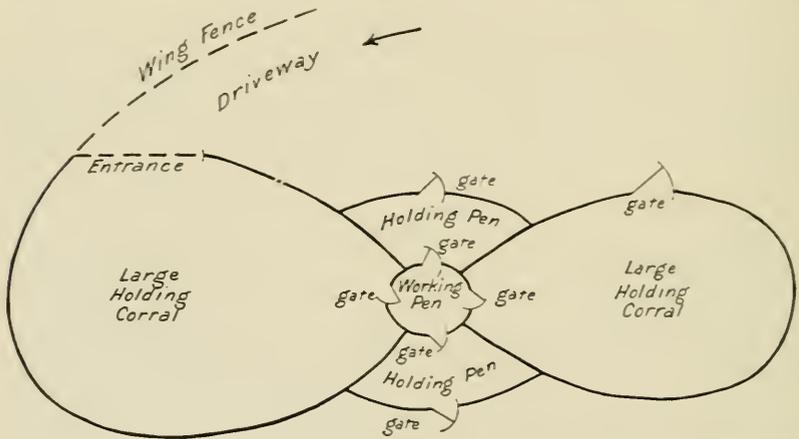


FIG. 2.—Diagram of corral of the pen type successfully used at Kokrines, Alaska. The reindeer are handled in the working pen and the fawns are caught by use of sheep hooks

corral for handling. Thus, except for the relatively brief time when they are being put through the corral, the reindeer are abundantly provided with feed and water in the holding pasture during the round-up period.

BRANDING

Reindeer are mostly marked by cutting off the tip of one ear or notching one or both of them. Some herd owners have used a metal ear tag or button in addition to cutting, but this kind of marking is being abandoned as unsatisfactory. Because of the numerous marks required to distinguish the many small owners, ear marking also has its limitations. Consequently, the organization of cooperative herds under one mark or brand is now being urged, and branding with a hot iron supplemental to ear marking is being considered. Experimental branding has been conducted in several herds and where carefully performed has proved sufficiently satisfactory to

warrant adoption (pl. 7). Branding, usually on the flank, is now being initiated and will undoubtedly become a more general method. A brand law for Alaska recently adopted provides for the marking or branding of reindeer and the registration of the brand or mark.

NATURE OF THE RANGE

RANGE BELTS

There are three distinct range belts of different uses: (1) The immediate coast region, including the islands; (2) the far-interior country; and (3) an intermediate region, which may be termed the inland-coast or coastal-valley belt. In the coast region,

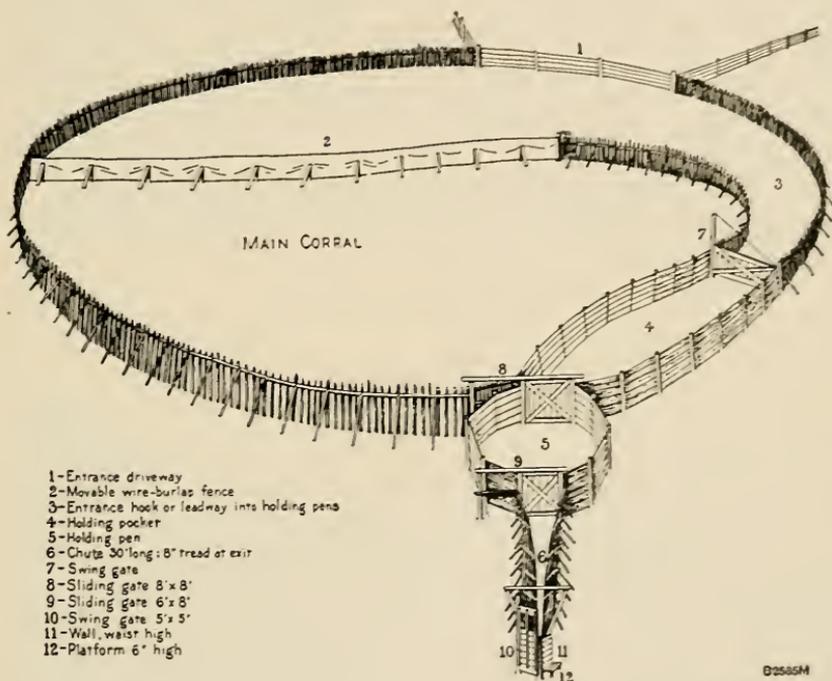


FIG. 3.—Highly successful corral of the chute type. It is important that the leadway into the holding pens be constructed on the side of the corral to meet the direction in which the herd mills. The movable wire-burlap fence is very useful in cutting off bunches of stock from the main herd.

the summer range of mostly tundra flats lies immediately along the coast, and the winter range lies inland on the coast uplands of hills and mountains. In the far interior the grazing lands are in the mountains, and the reindeer usually summer on the mountain tops and winter either on adjoining protected and favorably exposed areas or on lower ground near timber line. In the intermediate, coastal-valley belt, as in the Kuskokwim, Yukon, and Kobuk River Valleys, the reindeer may summer either along the valley flats and bench lands or on the mountain tops, and winter in the middle, usually timbered, zone between the upper and lower elevations.

The chief factors determining the seasonal range areas are (1) forage, (2) exposure, (3) the fly pest, (4) the physical character of

the range, including topography and tree growth, and (5) accessibility. The relation of summer to winter range must also be carefully considered. Availability of lichen forage for winter use is most important, since the successful continuation of reindeer grazing is dependent upon a sufficient winter food supply.

RANGE TYPES

The physical nature of the land and soil varies considerably, producing three main types of range: (1) The dry tundra; (2) the wet tundra; and (3) the rocky areas. In terms of relative carrying capacity, both as to forage content and nature of ground, these type areas vary appreciably. The dry-tundra and the wet-tundra ranges may run about equally high in average forage production, but soft or marshy ground reduces the actual carrying capacity because of the greater harm done to the forage plants when trampled into the wet earth. The rocky type usually has a lower carrying capacity than the other two because of the reduced forage growth (pl. 9; pl. 10, fig. 1).

The coast range bordering Norton Sound and southward, including the lower sections of the Yukon and Kuskokwim, consists largely of the wet-tundra type. Northward the character of range improves and the dry tundra begins to prevail; and north of the Noatak River and up toward Kivalina and Hope the rocky type of range is predominant, intermingled with the dry-tundra areas. Goodnews Bay, in the Kuskokwim region; the interior areas; and Nunivak Island are largely of the dry-tundra type. St. Lawrence Island is mostly the rocky type, with immediate beach areas of wet tundra.

TIMBER RANGE

The general presence or absence of trees furnishes another classification of range (pl. 11, fig 2). About 50 per cent of the Territory is forested to some extent. Excluding southeastern Alaska, the forest areas lie chiefly on the interior ranges over the central portion of the Territory. The importance of the presence or absence of trees on the range lies particularly in offering shelter to the herd and the herder and in providing fuel and ready material for the construction of cabins, corrals, and fences. In many sections of the country it is not difficult to construct necessary range improvements or establish camps; but where there are no trees, as over the major portion of Seward Peninsula and along the Arctic coast, the problem of construction material and fuel for camp use is serious, especially on winter ranges. Thickets of tall willows along rivers and creeks are often a saving factor, and lignite in a number of places provides a convenient fuel. Along the immediate coast, beach driftwood is an important source of fuel and building material, and in the Wainwright and Barrow sections, cakes of ice are sometimes employed in the construction of temporary corrals in winter.

RANGE SITE

Range site or location with reference to transportation facilities, or to mining camps and villages, is also an important consideration both as regards ready access to men, supplies, and equipment and the convenient shipment and marketing of meat. This item accounts



FIG. 1.—WET TUNDRA RANGE

The forage cover consists chiefly of sedges, browse, and lichens



FIG. 2.—ROCKY TYPE OF RANGE

Almost barren and of little or no use for grazing



FIG. 1.—DRY-TUNDRA RANGE

B26501

Forage cover of browse, weeds, sedges, and grasses. Willows heavily grazed by reindeer; foliage stripped



FIG. 2.—TIMBER RANGE

B26462

A luxuriant undergrowth of grasses, weeds, and browse near Kobuk River, above the Arctic Circle

chiefly for the fact that most of the Alaskan herds are at present on or near the coast, with the greatest concentration at the most accessible points. With greater opening of transportation facilities into the interior, more herds will be established away from the coast. Accessibility within the individual range area also affects the problem in that the most conveniently accessible unit or allotment offers the easiest management and promotes greater efficiency later on in putting a range management scheme into effect.

SALTING

In the interior little or no salt is available for the grazing reindeer, and salting the range is highly important both for the best condition of the individual animal and for proper range control. Reindeer are fond of salt, and when held along the coast they get it during the summer by drinking sea water or licking up saline deposits on the beach. This undoubtedly is as important a factor as the fly pest in urging the animals to the coast during the summer months. Under present conditions, salting the range is not a problem on the coast areas, but upon greater stocking and closer utilization it will become an important consideration.

Reindeer take readily to block or rock salt, and the use of this on the range is preferable to that of crushed salt. If crushed salt is used, there is danger that the animal will eat too much and become poisoned. Losses from such poisoning have been reported. The use of rock salt, however, is not dangerous, and for handling on the range, this form is more convenient and economical.

RANGE IMPROVEMENTS

Fencing on the range is yet a minor factor, but in some instances it is now employed for pasture purposes as an adjunct to the summer corral at round-up time. Boundary fences, or short drift fences at strategic places on the range are considered practicable and will undoubtedly be constructed soon on many allotments.

Two or more herding cabins are usually constructed on each grazing allotment. In addition, temporary camps are often made at various places over the range convenient for herding. To facilitate handling the herd, 4 or 5 and in one case even 13 cabin camps have been established over the range. The permanent cabin camps are preferable to the temporary tent camps and they are being more generally constructed (pl. 8).

INFLUENCE OF CLIMATE ON REINDEER GRAZING

A RANGE FACTOR

Climatic conditions have an important effect on reindeer grazing, both as regards the animal and the range and forage. The natural habitat of reindeer is the arctic and subarctic regions, and the animals undoubtedly do best on ranges falling within these climatic zones. Although reindeer are generally adapted to severe climatic conditions, there may be situations that must be considered in which the animals are at a considerable disadvantage. Because of winter

rains certain areas near the coast are subject to periodic crustings of snow, and in such places herds may suffer great losses through starvation, since the animals can not paw through the hard crust to get feed. In case of crusting, the herd must be promptly moved back to protected areas in the interior hills.

Under ordinary conditions the depth of snow on the winter range along the coast does not seriously affect grazing, since part of the area at least is generally exposed to the winds and does not become deeply covered. In the interior, however, particularly on timbered flats and bench-land country, there is less drifting, and the depth of snow then affects the selection of winter range. Where considerable drifting takes place, certain areas may become so deeply covered that the animals can not paw through the snow to reach the vegetation. Ordinarily, to reach the lichen forage reindeer will readily paw through as much as 2 feet of packed snow and 3 feet or more of loose snow.

A FORAGE FACTOR

The effect of climate on plant growth is an important factor in reindeer grazing, especially as regards the lichen vegetation. Lichens attain their maximum development and number in tropical regions. The proportion of cryptogamic to phanerogamic vegetation increases, however, from the Equator to the poles; thus in Alaska the proportion of lichens to other vegetation is relatively high. Furthermore, the numerous species of lichens vary in their climatic requirements, so that the predominating species in Alaska are determined by a preference for the arctic and subarctic habitat; and within the habitat the varied local climatic conditions show a marked effect on the character and development of the growth.

Moisture is a most potent agent in the development of the lichen, but an excess of moisture seems prejudicial to lichen development, in that it produces a sterile state of the thallus and favors the production of pulverulent and dwarfed forms. Season and vicissitudes of climate may variously affect the lichen growth, in some species causing changes in chemical composition and in others altering the form of the thallus, since under abnormal conditions the gonidial element of the thallus may become productive and give rise to various malformations.

LOCAL VARIATIONS

There is often considerable variation in climatic conditions between localities, chiefly on account of topography. One locality may be particularly subject to frequent and severe storms, whereas much more moderate conditions simultaneously exist in immediately adjoining areas. Again, in the general coast region there may be great variation in winter temperature as between the immediate coast and the interior; over a distance of 40 miles the difference may be as much as 20° F., the lower temperature occurring inland. Considerable difference between localities is also shown in the beginning of plant growth in spring. For example, in 1922, the growing season at Unalakleet opened four or five days earlier than at St. Michael, only 40 miles south; two weeks earlier than at Pastolik, 100 miles south; and two to three weeks earlier than at Nome, 150 miles north.

As to general conditions, the climate is considered more moderate in the Kuskokwim River valley to the south, and in the Kobuk River valley above the Arctic Circle, than in the regions lying between. Much lower winter temperatures prevail in the far interior areas than in the coast belt, but the higher winter temperatures of the coast region are offset by the greater humidity and prevalence of wind.

SEASONAL VARIATIONS

Seasonal variations also have an important bearing on reindeer grazing. The summer forage crop may be greatly decreased by a backward season or increased by favorable conditions. Thus there are poor feeding seasons and there are good ones, each in turn being clearly reflected in the condition of the grazing animal. Variation in the advances of the spring season is a problem at fawning time. Under very late conditions greater care must be taken for the protection of the newborn fawns, which often come very early in Alaska. Although reindeer fawns are remarkably hardy and capable of withstanding the ordinary vicissitudes of climate, yet extreme conditions sometimes result in heavy losses unless precautions are taken.

Perhaps most important of all is the effect that the varied seasons have on the fly pest and consequently on the reindeer. During a prevailing cloudy and rainy season, as experienced in 1922, the number of warble flies is greatly reduced and in some sections they may almost disappear. Under such conditions the reindeer are able to graze unmolested.

SOIL CONDITIONS IN ALASKA

Soil conditions are an important consideration in the selection of a range, chiefly as influencing plant growth, especially lichens. Within the three main ground types—dry tundra, wet tundra, and rocky areas—are various kinds of soils, the one predominating on tundra areas varying between a black sandy loam and a sandy clay loam over a blue clay subsoil. The tundra soils are rich in humus or decayed vegetation and often approach a heavy peaty nature. The rocky areas are chiefly of gravelly sandstone soil and quartz to jagged limestone, in some places volcanic. On the coast range permanent frost occurs 1 to 3 feet below the surface, and in some sections, as at Kotzebue Sound, Wainwright, and Barrow, solid ice is frequently found immediately along the coast at a depth of 2 to 3 feet.

A FORAGE FACTOR

Lichens vary considerably in their habitat requirements. Some prefer rocks or stones, some the bark of trees, some the soil, and others the mosses, decayed herbaceous vegetation, decayed wood, or shrubs. Again, some prefer a sandstone rock, others a limestone or quartz. Of lichens which grow on the ground, some prefer moist peaty soil, some a calcareous soil, some silicious, some argillaceous, and some a hardened mud. Thus the soil and ground conditions determine in a measure the lichen cover and control protective management of the forage type. In Alaska the best lichen growth for

forage purposes is usually made up of those species that grow on the soil and on decayed herbaceous vegetation.

FORAGE COVER

The main forage cover on the winter coast range consists of a lichen type with a sedge-browse subtype; that on the winter interior range a lichen type with a browse subtype.

On summer coast range, a sedge-browse type predominates; and in the interior a browse-sedge-lichen type. Table 3 gives a summary of the average types observed on summer and winter ranges in various sections. (See pls. 10 and 11.)

TABLE 3.—*Summary of forage types in the stand on summer and winter ranges showing in percentages the composition density, palatability, and forage value¹*

Section	Composition					Density	Palatability	Forage Value
	Lichen	Browse	Sedge	Weeds	Moss			
Coast summer range:								
St. Lawrence Island.....	0	5	91	3	1	90	65	58.5
Kivalina.....	5	15	47	31	2	79	68	53.7
Kotzebue Sound.....	10	26	51	5	8	93	64	56.5
Seward Peninsula.....	7	15	53	24	1	68	60	40.8
Norton Sound.....	11	22	50	5	12	92	51	46.9
Yukon-Nunivak Island.....	9	15	57	15	4	90	60	54.0
Kuskokwim.....	6	40	34	17	3	70	67	46.9
Average.....	7	20	55	14	4	83	62	51.4
Interior summer range:								
Broad Pass.....	18	28	27	12	15	96	70	67.2
Gulkana-Tangle Lakes.....	16	34	29	10	11	88	68	56.8
Average.....	17	31	28	11	13	92	69	63.5
Coast winter range:								
St. Lawrence Island.....	65	12	2	11	10	40	80	32.0
Kotzebue Sound.....	50	25	15	10	0	60	70	42.0
Seward Peninsula.....	50	15	30	5	0	70	75	52.5
Norton Sound.....	50	10	30	4	6	87	67	58.3
Yukon-Nunivak Island.....	50	10	30	2	8	99	66	65.3
Kuskokwim.....	47	30	10	3	10	70	70	49.0
Average.....	52	17	20	6	6	71	71	50.0
Interior winter range:								
Broad Pass.....	50	20	8	4	18	85	76	64.6
Gulkana-Tangle Lakes.....	53	23	11	6	7	85	83	70.5
Average.....	52	22	10	5	13	85	80	67.5

¹ Forage value derived by multiplying the percentage of density of forage stand by the percentage of palatability.

The forage plants on the summer range consist chiefly of such herbaceous and shrub vegetation as grasses, sedges, weeds, and browse, and are eminently suited to grazing. They are highly organized seed-bearing plants of strong tissue and firmly rooted in the soil. Most of the Alaskan species are perennial plants reproducing both vegetatively and from the seed. They grow rapidly, produce substantial foliage, and are not readily injured under grazing use. Making annual and rapid growth, they produce a successive forage crop from year to year.



B29754

FIG. 1.—TIMBER, GRASS, AND WEED TYPE OF RANGE

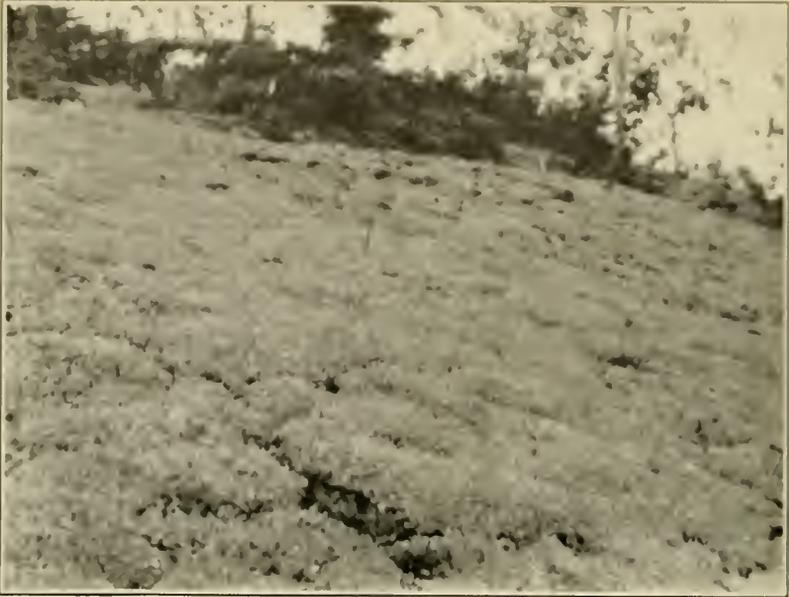
A luxuriant cover of grasses and weeds, usually found along the banks of streams



B26410

FIG. 2.—TUNDRA COVER OF SEDGES AND BROWSE

Most frequent forage type of the coast summer range



B2644

FIG. 1.—TIMBER AND LICHEN TYPE OF FORAGE

Lichen cover often found on the island mountain slopes. The lichens in this case form 85 per cent of the forage stand



B26507

FIG. 2.—TUNDRA AND LICHEN TYPE OF FORAGE

Under favorable conditions a growth of lichens may sometimes occur on the immediate coast. The lichens in this case comprise 50 per cent of the forage stand. The men were gathering and sacking them for use at the former reindeer experiment station at Nome

The most important plants may be grouped, according to abundance, as follows:

MOST ABUNDANT

<i>Eriophorum callitrix</i> (cotton sedge).	<i>Empetrum nigrum</i> (crowberry).
<i>Eriophorum angustifolium</i> (cotton sedge).	<i>Vaccinium uliginosum</i> (blueberry).
<i>Salix</i> spp. (willow).	<i>Vaccinium vitis-idaea</i> (mountain cranberry).
<i>Betula rotundifolia</i> (ground birch).	<i>Rubus chamaemorus</i> (cloudberry).
<i>Ledum</i> spp. (Labrador tea).	<i>Arctous alpina</i> (Alpine bearberry).

FAIRLY ABUNDANT IN PLACES

<i>Arctagrostis latifolia</i> (Alaska bunch grass).	<i>Artemisia arctica</i> (wormwood).
<i>Calamagrostis scabra</i> (coast blue-joint).	<i>Artemisia tilesii</i> (wormwood).
<i>Elymus mollis</i> (dunegrass).	<i>Aconitum delphinifolium</i> (monkshood).
<i>Festuca rubra</i> (fescue).	<i>Coelopleurum gmelini</i> (sea-parsnip).
<i>Poa</i> (bluegrass).	<i>Lupinus arcticus</i> (lupine).
<i>Carex</i> (sedge).	<i>Lathyrus maritimus</i> (beach pea).
<i>Equisetum</i> (horsetail).	<i>Mertensia paniculata</i> (bluebells).
<i>Betula kenaica</i> (birch).	<i>Galium boreale</i> (bedstraw).
<i>Alnus alnobetula</i> (alder).	<i>Pedicularis</i> (fernweed).
<i>Dryas octopetala</i> (dryad).	<i>Epilobium angustifolium</i> (fireweed).

VERY SCATTERING BUT FREQUENT

<i>Spiraea stercis</i> (spirea).	<i>Gentiana</i> (gentian).
<i>Rubus arcticus</i> (raspberry).	<i>Pedicularis</i> (fernweed).
<i>Cornus suecica</i> (bunchberry).	<i>Polygonum</i> (smartweed).
<i>Andromeda polifolia</i> (bog rosemary).	<i>Primula</i> (primrose).
<i>Phleum alpinum</i> (wild timothy).	<i>Heterotrichum</i> (wool aster).
<i>Agrostis</i> (redtop).	<i>Chrysanthemum</i> (daisy).
<i>Astragalus</i> (milk vetch).	<i>Bupleurum americanum</i> (hare's-ear).
<i>Oxytropis</i> (oxytrope).	<i>Anemone</i> .
<i>Petasites frigida</i> (butterbur).	<i>Ranunculus</i> (buttercup).
<i>Senecio</i> (groundsel).	<i>Eritrichum arctioides</i> (forget-me-not).
<i>Saxifraga</i> (saxifrage).	<i>Silene acaulis</i> (moss campion).
<i>Iris setosa</i> (arctic iris).	<i>Viola</i> (violet).
<i>Polemonium acutiflorum</i> .	<i>Cerastium</i> (chickweed).
<i>Capnoides pauciflorum</i> .	<i>Cardamine</i> (bitter cress).
<i>Valeriana capitata</i> (valerian).	<i>Ligusticum scoticum</i> (Scotch lovage).
<i>Campanula</i> (bellflower).	<i>Potentilla</i> (five finger).
<i>Sanguisorba sitchensis</i> (burnet).	<i>Stellaria</i> (starwort).
<i>Arenaria</i> (sandwort).	<i>Rumex acetosa</i> (sorrel).
<i>Arnica</i> (arnica).	<i>Rumex occidentalis</i> (dock).

FORAGE PLANTS GRAZED BY REINDEER

SPRING FORAGE

The first fresh growth in spring usually consists of young shoots or flowering stalks of the cotton sedges and of grasses and weeds. The reindeer are very fond of fresh green growth and in grazing on the hummocks miss very few of the new shoots. They feed also in spring to a small extent upon willow buds, reindeer lichens, and Labrador tea.

SUMMER FORAGE

During the summer the reindeer enjoy a great variety of range plants, but chiefly sedge and browse species. At the beginning of the season, in addition to their main food of sedges and willow

browse they are particularly fond of the succulent young grasses of various kinds and of such herbs as wormwood, fernweed, vetch, fireweed, smartweed, dock, horsetail, sea-parsnip, and groundsel. In the middle and latter part of the summer they feed mainly on sedges, various species of browse, lichens, mushrooms, and the more succulent herbs. Mosses are eaten only incidentally, mixed with the other forage.

In the order of relative forage value, the plants grazed during the summer may be listed as follows:

(1) Most important, because of high palatability and greatest abundance:

<i>Eriophorum callitrix</i> (small cotton sedge).	<i>Cladonia</i> (mostly) (lichens). <i>Betula rotundifolia</i> (ground birch). <i>Ledum decumbens</i> and <i>L. groenlandicum</i> (Alaska tea).
<i>Eriophorum angustifolium</i> (large cotton sedge).	
<i>Salix</i> (willows).	

(2) Of medium importance, because of high palatability and only local abundance or of medium palatability:

<i>Alnus alnobetula</i> (alder).	<i>Lupinus arcticus</i> (lupine). <i>Astragalus alpinus</i> and <i>A. tilloralis</i> (vetch). <i>Polygonum alaskanum</i> (smartweed). <i>Rumex occidentalis</i> (dock). <i>Coclopleurum gmelini</i> (parsnip). <i>Ligusticum scoticum</i> (Scotch lovage). <i>Carex</i> (sedge). <i>Poa</i> (grass). <i>Arctagrostis</i> , <i>Calamagrostis</i> , <i>Festuca</i> , <i>Agrostis</i> , <i>Phleum</i> (grasses).
<i>Vaccinium vitis-idaea</i> (mountain cranberry).	
<i>Empetrum nigrum</i> (crowberry).	
<i>Vaccinium uliginosum</i> (blueberry).	
<i>Dryas octopetala</i> (dryad).	
<i>Ranunculus pallasii</i> (water buttercup).	
<i>Equisetum</i> (horsetail).	
<i>Valeriana capitata</i> (valerian).	
<i>Pedicularis</i> spp. (fernweed).	
<i>Epilobium angustifolium</i> (fireweed).	
<i>Artemisia arctica</i> and <i>A. tilesii</i> (wormwood).	

(3) Of less importance, because of lower palatability:

<i>Rubus chamaemorus</i> (cloudberry).	<i>Conioselinum gmelini</i> (hemlock parsley). <i>Bupleurum americanum</i> (hare's-ear). <i>Merceia physodes</i> (beach starwort). <i>Lathyrus maritimus</i> (beach pea). <i>Mertensia paniculata</i> (bluebells).
<i>Ribes triste</i> (currant).	
<i>Viburnum pauciflorum</i> (cranberry bush).	
<i>Rubus arcticus</i> (raspberry).	
<i>Arctous alpina</i> (alpine bearberry).	
<i>Betula kenaica</i> (birch).	

The palatability of numerous other species of the herbaceous vegetation has not yet been determined, but they are generally of minor importance because of infrequent occurrence.

FALL FORAGE

Toward fall the reindeer graze more and more on lichens, their chief food consisting then of lichens, sedges, willows, ripened tops of grasses, and perhaps some of the other browse species.

WINTER FORAGE

During the winter season, the forage consists almost entirely of the various lichens. The species of *Cladonia* are the most important because of their high palatability and great abundance.

The species of *Cetraria* and *Stereocaulon* are also important but less abundant. Browse and dried herbaceous vegetation are taken to some extent and occasionally some of the mosses.

THE LICHEN PLANT

The plants that furnish the bulk of the forage on winter range are lichens. They are entirely different from herbaceous and shrub vegetation in character and in reaction to grazing use. They do not, like the herbaceous vegetation, furnish a renewed forage crop from year to year, but require a long period of years to recover from one season's cropping. Lichens grow very slowly and are of limited height, but attain a very great age. They are of comparatively delicate structure, infirmly anchored to the soil, and are readily removed either by trampling or picking by hand. Under summer conditions they often become dry and brittle and are then easily destroyed. When moist or wet they are of almost spongy texture and then less easily injured.

The lichen plant is a composite organism—an alga and a fungus living together. The relationship has become so intimate that lichens are often regarded as autonomies or morphological units rather than symbiotic colonies of algae and fungi. The frutification of the lichen is that of the fungus, and reproduction takes place by means of the spore. Many lichens also multiply asexually by means of soredia, produced by the chlorophyll-bearing cells, gonidia, which belong to the algae, the soredia escaping from the lichen thallus usually in the form of a fine powder, and germinating immediately to form new plants. A third mode of reproduction is by the distribution of fragments of the plants by action of wind or animals.

GROWTH HABITS OF LICHENS

Lichens grow under a great variety of conditions of climate and habitat. (Pls. 12 and 13.) Their general distribution both vertically and horizontally is extensive. All are capable of enduring desiccation for long periods without losing their vitality. Their height is limited, but the size to which they may attain varies with individual species and habitat. Along the Alaskan coast, the average growth of the mixed stand is 4 or 5 inches, although in places a 10-inch height has been found (pl. 13, fig. 2). Some species are of diminutive size and consequently of little or no use for grazing; others are of luxuriant growth and highly valuable.

Lichens grow chiefly on soil, on rocks or stones, and on the bark of trees; but they also grow frequently on decayed logs and on mosses, and sometimes on the thalli of other species. According to the base upon which they grow they are classified as terricoline (on soil), corticoline (on bark), saxicoline (on rocks), and muscicoline (on mosses). Those most important for forage in Alaska are largely of terricoline habit. The essentially saxicoline, muscicoline, and corticoline species, with a few exceptions, are mostly of diminutive size or of low form adhering closely to the substratum, and therefore of low grazing value.

Some species of lichens form leaf-like expansions (foliaceous), some are cup shaped, some closely encrust the surface on which they grow (crustaceous), and others are shrublike (fruticose), the branches in this case being either cylindrical or flattened. Their colors vary from almost white to greenish gray, yellow, orange, brown, or a purplish black. Changes in color are greatly influenced by degrees of light and moisture or the nature of the habitat. In Alaska the fruticose lichens form the bulk of the winter forage. (Pls. 14-17.)

For their growth lichens require moisture, light, and heat, and probably derive some inorganic substances from the base upon which they grow, but most lichens probably take a smaller proportion of their food from the substratum and a larger proportion from the air than do the higher vascular plants. They take carbon dioxide from the air in the processes of nutrition, build up lichenin, a substance similar to starch, and return free oxygen to the atmosphere. When wet and in a partially decomposed condition, some lichens are often of a gelatinous consistency. The thallus of some species contains a bitter principle, which in a few instances may make the plant unpalatable to stock.

LICHEN OCCURRENCE AND DISTRIBUTION

On Alaskan coast ranges the best lichen growth is often found on west and north exposures. In thick stands of forest or brush very little of it occurs, but at the edges or in openings in the forest, or in scattering tree growth, a luxuriant lichen cover may usually be found (pl. 12, fig. 1). On moist tundra flats of favorable soil and atmospheric conditions, as on Nunivak Island, lichen growth may be abundant, both in volume and density (pl. 12, fig. 2). On the average summer tundra range of the coast, however, the herbaceous and shrub vegetation competes predominantly with the lichens. On the more rugged inland country the competition is reduced and the lichens often become the predominant vegetation. Here the best lichen cover of value for grazing is on the lower slopes, in coves, and hollows, and at the heads of creeks. The best individual growth occurs particularly in depressions on slopes and in swales and is most luxuriant in hollows between and at the bases and sides of hummocks. Certain valuable species, however, of comparatively short height often occur abundantly on the tops of hummocks in favorable situations and under minimum competition. On rocky upper slopes and tops of ridges the lichen cover becomes scattering and is usually small or dwarfed.

Even among the best of lichen types a pure stand does not occur, either with reference to class of vegetation or to individual species. Generally an admixture of lichens with other vegetation is found, as species of browse, mosses, and sedge. Often in the lichen stand there may occur a considerable portion of such mosses as *Sphagnum* and *Polytrichum*. On most of the winter ranges the lichens average 50 per cent of the cover, although some forage types occur that may contain as much as 90 per cent lichen vegetation.

Within the stand the lichens grow more or less intermingled in a solid mat, with species intermixed generally, but often by indi-



FIG. 1.—OCCURRENCE OF CLADONIA ALPESTRIS

B26356

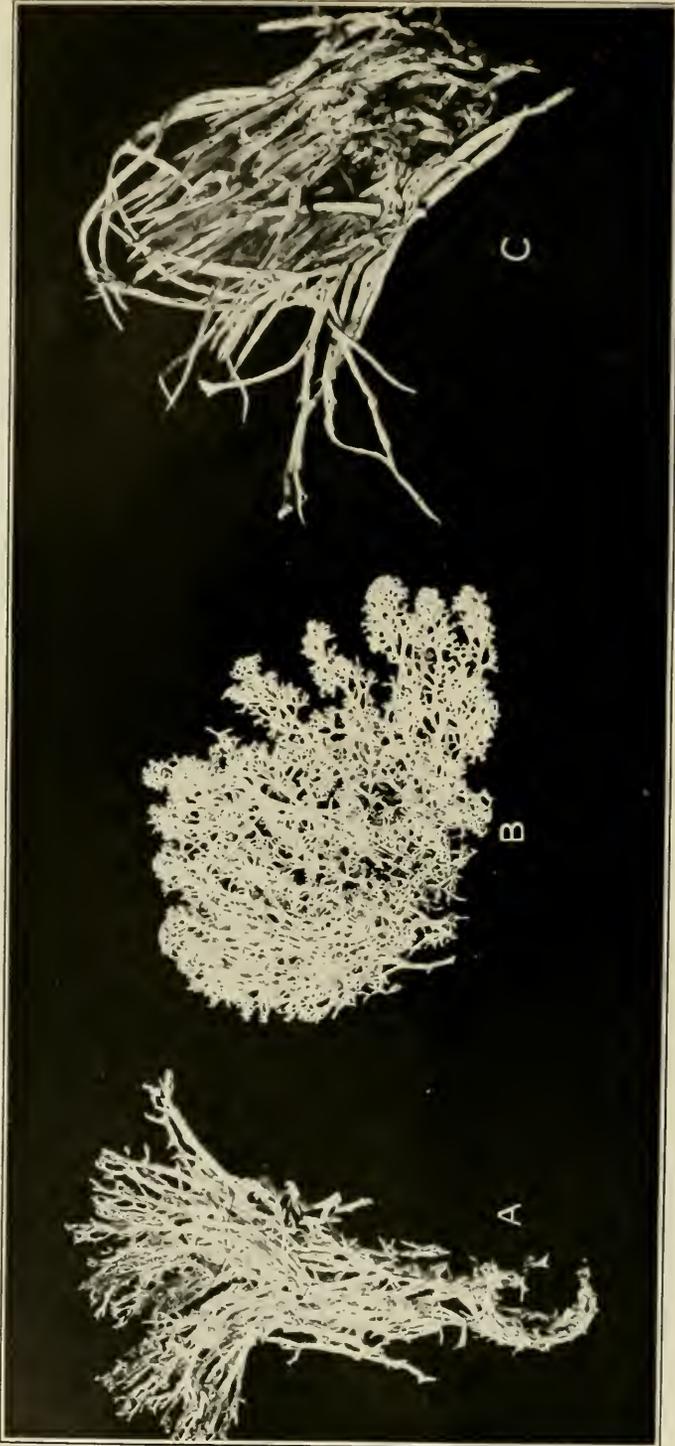
Scattering rounded patches of white. The *alpestris* community is closely surrounded by a mixture of other darker-colored lichens



FIG. 2.—OCCURRENCE OF CLADONIA SYLVATICA SYLVESTRIS

B26348

A thickly matted growth, averaging 4 or 5 inches in height and in places reaching 10 inches



FORAGE LICHENS OF THE CLADONIA GROUP

A, *Cladonia delisei*, B, *Cladonia alpestris*, C, *Cladonia gracilis elongata*



FORAGE LICHENS OF THE CLADONIA GROUP
A, *Cladonia amantrocreta*. B, *Cladonia uncialis turgescens*. C, *Cladonia uncialis*



FORAGE LICHENS OF THE CETRARIA GROUP

A, *Cetraria cucullata*. B, *Cetraria Islandica*. C, *Cetraria islandica platyna*

vidual groups or patches of one or two species (pl. 13, fig. 1). Frequently some one or two species predominates and numerous other species of various kinds are scatteringly intermixed with the base plant. Ordinarily, a handful of lichens picked up off the range will be found upon analysis to contain six or seven or more different species closely intermixed. *Cladonia* is the most abundant of the lichens in Alaska, both in number of species and in quantity; *Cetraria* is second in importance, but of scattering occurrence.

The predominating species on tundra and lower foothills sites are *Cladonia sylvatica sylvestris*, *C. rangiferina*, and *C. sylvatica*, or a combination of these. On a rocky subalpine site of favorable exposure, the predominant plant may often be *C. alpestris*. On higher range, the main plants are often species of *C. amaurocraea* and *C. uncialis*, and sometimes abundantly mixed with them *C. sylvatica sylvestris*. On rocky upper slopes and tops of ridges of inferior cover, the *Cetraria* species often predominate. Some species are cosmopolitan in distribution, occurring scatteringly throughout all types, as *Cetraria cucullata*, *C. islandica*, and *Cladonia gracilis elongata*. On rocky upper areas *Cetraria nivalis*, *C. islandica crispa*, *Cladonia gracilis dilatata*, and *Alectoria nigricans* are commonly found. *Cladonia sylvatica sylvestris* stands out generally as the most abundant and widespread and therefore most important winter forage plant on the coast range.

The more important species of lichens occurring on the coast ranges may be grouped as follows:

(1) Most abundant:

Cladonia sylvatica sylvestris.
Cladonia rangiferina.
Cladonia sylvatica.
Cladonia gracilis elongata.
Cladonia amaurocraea.
Cladonia amaurocraea ozycceras.

Cetraria cucullata.
Cetraria islandica.
Alectoria nigricans.
Alectoria ochroleuca.
Cladonia uncialis.
Cladonia uncialis turgescens.

(2) Fairly abundant in places:

Cladonia uncialis obtusata.
Cladonia alpestris.
Cladonia gracilis cmocyma.
Cladonia amaurocraea celotca.
Stereocaulon alpinum.
Stereocaulon coralloides.

Stereocaulon tomentosum.
Cetraria chrysantha.
Cetraria nivalis.
Cetraria islandica crispa.
Cetraria islandica platyna.
Sphaerophorus coralloides.

(3) Scattering but frequent:

Cladonia (cup cladonias).
Ochrolechia sp.
Parmelia sp.
Cladonia furcata.
Cladonia delessertii.
Cladonia crispata.
Cladonia degenerans.

Thamnochloa vermicularis.
Nephroma arcticum.
Lobaria linita.
Cladonia gracilis dilatata.
Cladonia decorticata.
Cladonia squamosa muricella.

(4) Infrequent:

Cladonia botrytis.
Cladonia subsquamosa.
Cladonia cenotea.
Cladonia cyanipe.
Dactylina arctica.
Dufora ramulosa.

Icmadolophila cricctorum.
Pertusaria bryontha.
Pilophorus cerecolus robustus.
Philophorus cerecolus acicularis.
Cetraria juniperina.
Cetraria hiasecens.

(4) Infrequent—Continued.

Cetraria fahlnuensis,
Letharia thamuodes,
Siphula ceratitidis,
Lecanora sp.

Alectoria divergens,
Psoroma hypnorum,
Ramalina dilacerata,
Gyrophora sp.

In relative forage value, the lichens may be listed as follows:

(1) Most important, because of high palatability and greatest abundance:

Cladonia sylvatica sylvestris,
Cladonia rangiferina,
Cladonia sylvatica,
Cladonia alpestris,
Cladonia amauroceracea subsp.,
Cladonia amauroceracea celotca,
Cladonia amauroceracea oryoceras.

Cladonia uncialis,
Cladonia uncialis obtusata,
Cladonia uncialis turgescens,
Cladonia gracilis elongata,
Cetraria cucullata,
Cetraria islandica.

(2) Of medium importance, because of lower palatability and only local abundance or of medium palatability:

Cladonia delessertii,
Cladonia decorticata,
Cladonia squamosa subsp.,
Cladonia degenerans,
Cladonia amauroceracea celotca,
Cladonia amauroceracea craspedia,
Cladonia uncialis adunca,
Cladonia gracilis dilatata,
Cladonia gracilis cemoecyna,
Cetraria islandica crispa.

Cetraria islandica platyna,
Cetraria nivalis,
Cetraria richardsonii,
Alectoria ochroleuca,
Dactylina arctica,
Nephroma arcticum,
Stereocaulon alpinum,
Stereocaulon coralloides,
Stereocaulon tomentosum.

(3) Of value only as mixed with other species, because of very scattering occurrence:

Cladonia bellidiflora,
Cladonia crispa subsp.,
Cladonia deformis extensa,
Cladonia digitata glabrata,
Cladonia furcata,
Cladonia cyanipes,
Cladonia alpicola,
Cladonia cuneata,
Cladonia fimbriata,
Cladonia alaskana,
Cladonia gracilis chordalis,
Cladonia gracilis,
Cladonia gracilis subtilacerata,
Cladonia subsquamosa.

Cladonia sylvatica laeviuscula,
Cladonia uncialis turgescens,
Cladonia alpestris inturgescens,
Alectoria nigricans,
Cetraria aculeata,
Cetraria chrysantha,
Cetraria hiasecus,
Cetraria islandica crispa,
Cetraria islandica platyna,
Sphaerophorus coralloides,
Dufourea ramulosa,
Letharia thamuodes,
Thamnolia vermicularis,
Parmelia spp.

(4) Of little or no value, because of diminutive size, infrequent occurrence, mode of growth, or unpalatableness:

Cladonia botrylis,
Cladonia coccifera subsp.,
Cladonia degenerans euphorca,
Cladonia pyxidata subsp.,
Cetraria juniperina,
Cetraria juniperina terrestris,
Alectoria jubata,
Imadophila cricetorum,
Lecanora spp.,
Lecidea spp.,
Lobaria spp.

Ochrolechia spp.,
Peltigera spp.,
Physcia pulverulenta muscigena,
Psoroma hypnorum,
Pertusaria bryontha,
Pilophorus cercolus robustus,
Ramalina dilacerata,
Siphula ceratitidis,
Xanthoria lychnea pygmaea,
Gyrophora spp.

REACTION OF LICHENS TO GRAZING USE

To study the reaction of the lichen plant to grazing use, cutting and other quadrats have been established to supplement general

range observations. From results thus far obtained facts have been brought out regarding reproduction and recovery from injury that have an important bearing on the range management problem. The conclusions drawn are here stated, and, though not complete, are indicative of what may be expected in grazing a lichen range.

GROWTH AND REPRODUCTION

The lichens are rapid in rate of reproduction or establishment of new plants. Reproduction and growth take place whenever favorable conditions of high moisture exist, usually in spring and fall. In a wet season growth may continue throughout the summer, but ordinarily the summers are dry and hot, and the lichens then lose their moisture, become brittle, and stop growing. Growth may continue into the winter also in sheltered, rocky situations where the action of the sun on the frozen surface yields water easily.

The average rate of growth of young plants of the species most important as reindeer forage is about an eighth to a quarter of an inch a year, and the initial growth is usually about a sixteenth to an eighth of an inch. In volume—that is, number—of new plants it is indicated that the lichens make rapid progress; in one measured area on overgrazed range they attained about half the normal volume over a period of five years following denudation, or four years following the first appearance of new growth. Or from 1920 to 1923 there is shown on this particular area a progressive annual increase in volume at the rate of approximately 50 per cent. At this rate the normal stand in volume or density of cover, which in this case is 40 per cent of lichen vegetation, should be reached in another two years—that is, seven years following denudation. The plants coming in on this area, in the order of their importance, were *Cladonia sylvatica sylvestris*, *Cetraria cucullata*, *Cladonia bellidiflora*, *C. coccifera*, *Sphaerophorus coralloides*, *Alectoria nigricans*, *Cetraria islandica*, *Cladonia gracilis elongata*, and *C. alpestris*.

On the basis of the foregoing rates of growth and recovery, it would usually require 7 to 10 years of protection for a lichen range to come back to normal volume following initial growth; and 15 to 20 years to attain a normal height of 4 to 5 inches. These estimates, however, are not final, more years of observation being necessary, but the relative rate of recovery is apparently very slow and by reason of this fact, the proper management of winter range presents an exceptionally important problem.

QUADRAT STUDIES

Further results obtained on several observation quadrats 1 meter square (pl. 18) tended to substantiate these estimates and provided additional information on the action of lichen growth under partial cropping, represented artificially by cutting. These quadrats, established within inclosures, were on range containing a high percentage of lichen vegetation (from 70 to 90 per cent). The height of the vegetation was from 3 to 4 to 6 inches, and occasionally 2½ inches at the lowest and 10 inches at the highest. The average height in all cases would be between 4 and 5 inches.

Within each inclosure four plots were laid out: (1) A check quadrat; (2) one on which the cover was entirely removed and the ground trampled; (3) one on which the vegetation was half cut to remove the top portion; and (4) one on which the lichen vegetation was picked by hand or, as in one case, scraped to frost. Scraping to frost under winter conditions removed about the top two-thirds of the vegetation, leaving the plant base intact; and picking under thawed conditions removed most of the plant but left the soil undisturbed.

Examination of quadrats following one and two years of recovery showed that in all cases where the lichen cover had been half cut, about half the vegetation had been killed and the remainder was still in growing condition. There was no evidence of reproduction, the dead and living cover being so matted that no new plants came in. New growth on the living plants, however, was evidenced in the form of numerous small side shoots on the cut tips and branches. Following a two-year period these new shoots were numerous and averaged about an eighth of an inch long; where there had been only one year of recovery the shoots were less numerous, averaging about a sixteenth of an inch long. The effect of cutting lichens in this case closely parallels what takes place in pruning a hedge or trimming off the top of a tree.

The scraped-to-frost quadrat was established on April 19, when the surface of the ground was frozen and covered with a light snow. The snow was lightly brushed away and the lichen vegetation scraped entirely off with a hand rake to the frozen surface, leaving the plant base intact and protected by being frozen into the ground. About 2 or $2\frac{1}{2}$ inches of cover was removed. Later, upon examination following thawing, a cover of half an inch to an inch of lichen plant stubs was found remaining on the area. Examination following recovery after two seasons showed two-thirds of this cover completely killed and the remainder still showing signs of life. New growth in this case as in the area half cut took the form of many small offshoots on the cut tips and branches, a sixteenth to an eighth of an inch long. No new plant or reproduction was observed, the matted cover of dead and living vegetation probably obstructing.

On all the denuded quadrats a scattering reproduction was found following one and two years of recovery, in one case about a hundred new plants showing on the area following the two-year period. The species occurring, in the order of their importance, were *Cladonia* (probably *sylvatica sylvestris*, *rangiferina*, and *sylvatica*), *Cetraria cucullata*, *C. islandica*, and *Stereocaulon tomentosum*. The reproduction seemed to spring mostly from the old remnants of plants left scattered over the quadrat area, appearing also along the sides of the area by spreading from the adjoining cover. The new growth measured about a sixteenth to an eighth of an inch high.

The picked quadrats differed from the denuded quadrats only in degree of denudation. Such nonlichen vegetation as sedges and browse was left standing, with the soil undisturbed, and although the lichen cover was in the main removed, some of the plant base may have been left intact. The beginning of reproduction was evidenced on these areas at about the same rate as on the denuded quadrats. In addition, however, it was found that in a few in-

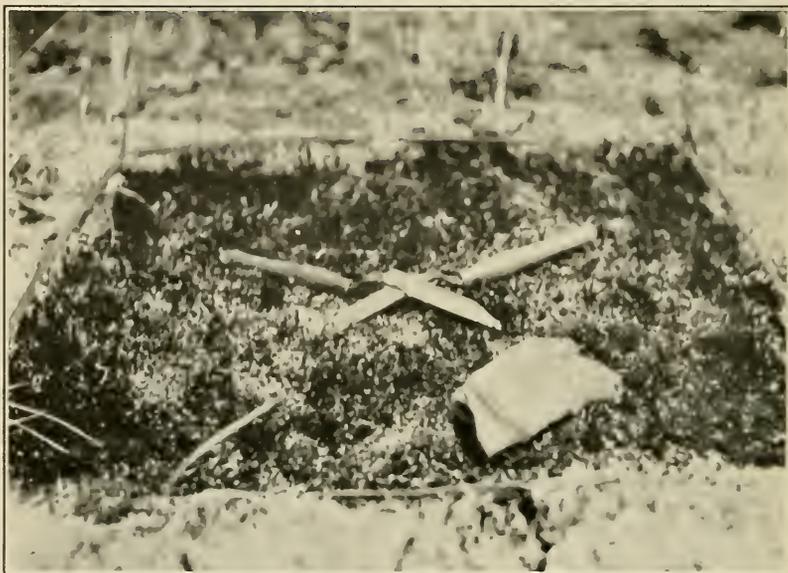


FORAGE LICHENS LESS IMPORTANT BECAUSE LESS ABUNDANT
A, *Dactylina arctica*. B, *Nephroma arcticum*. C, *Alictoria ochroleuca*



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FIG. 1.—LICHEN QUADRAT, UNTOUCHED
Area established for study at Unalakleet, Alaska, April, 1922



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FIG. 2.—LICHEN QUADRAT, COVER REMOVED
Same area as in Figure 1. Photographed after vegetation had been removed by picking, to note the later recovery

stances where an occasional plant base or small plant had been left standing, growth was continuing. The new reproduction measured a sixteenth to an eighth of an inch high, and the few old plants left standing measured 1 or 1½ inches high.

RANGE RECOVERY

The beginning of lichen reproduction takes place one or two years following denudation. Reproduction comes in best where the ground has been cleared of the matted growth, giving the young plants a chance to develop. Where the top of the plant is cropped, a growth of offshoots occurs which will probably result in a bushy, deformed top.

Cutting or cropping the lichen cover results in considerable damage, by killing a large proportion of the growth. The number of plants killed seems to be in direct proportion to the degree of cropping or grazing. Even light cropping or tramping may result in considerable damage. Much trampling in summer when the plants are dry and brittle may entirely kill out the cover. This means that the winter ranges must have complete protection from grazing during late spring, the summer, and early fall, or particularly when the surface is thawed and the lichens are dry and brittle. During winter, on the other hand, the lichens have regained their moist consistency and the ground is frozen with the base of the plant, thus offering considerable protection against ready destruction.

The quadrat observations apply to coast tundras, where it would seem that recovery of the lichen range following full cropping may take possibly 15 or 20 years. On higher ground, where a dry, rocky soil offers less favorable conditions for good growth, undoubtedly recovery will take much longer, perhaps as much as 25 or even 30 years. The rate of recovery of a lichen range depends very much on the site conditions.

RANGE FIRES

One of the greatest sources of injury to range and losses of forage in Alaska is in fires, which in most cases are deliberately set or are due to carelessness. Tundra fires along the coast are common, and burned-over range areas may be frequently found. Fires are often set by prospectors to clear off the vegetation and thus expose the underlying ground and rock or by Eskimos in an effort to be rid of mosquitoes. They are also caused by carelessly leaving a camp fire burning or tossing away a lighted match or cigarette.

Possibly on account of the immensity of the country and the sparse population the injury by fire does not appear very impressive nor a need of its suppression important. It has not, perhaps, been called sufficiently to people's attention in the past, although a Territorial law is in effect providing penalty for the deliberate setting of range fires. What is needed for Alaska is a general fire-prevention program, and in that connection a wide, educational propaganda against forest and range fires, particularly in the northern and western sections of the Territory, reaching the Eskimos through the schools.

Damage to range by fire involves not only loss of forage and trees but also of game and fur animals, since the small ground animals as well as the cover of vegetation are destroyed by the fire.

The damage to lichen range is particularly serious. It may take a burned-over lichen area as much as 25 years to come back; or where so badly burned that the cover of humus is destroyed, the changed site conditions may result in a recovered stand of inferior species, or virtually in a permanent removal of the lichens, so far as practical grazing use is concerned. In view of the importance of the lichen areas for winter grazing, it is vital to all reindeer men to guard against fires; and because of the damage to game and fur animals and to tree growth, it is the concern of everyone that fires be prevented and fire protection sought.

CARRYING CAPACITY OF RANGE

WINTER REQUIREMENTS

Brief studies of carrying capacity conducted on a range in the Norton Sound section indicate a requirement of 30 acres for each reindeer for the yearlong period. This, however, does not allow for a recovery period for the lichen areas under full cropping; consequently, a higher yearlong acreage must be allowed. For the six months of summer grazing, 10 to 15 acres a head are required, and in some cases 8 acres, but for winter grazing on lichen forage the requirement is much higher for proper range use and protection. As regards carrying capacity generally, winter grazing requires a larger acreage than summer for a number of reasons:

First, the lichens which constitute the principal winter food are, as mentioned, wholly different from the herbaceous vegetation making up the summer forage, in nature, habits of growth, and reaction to injury. By reason of these differences greater care must be taken in grazing lichen areas to avoid total destruction of the individual plants or checking their continued healthy growth and reproduction.

In the second place, the inland winter areas and top country generally are not so well covered with vegetation as the summer areas adjacent to the coast or lying along the lower foothills. Much of this top country may be almost barren in places, or the lichen growth of patchy occurrence. In some cases only a third or a half of the total winter range may be available for grazing use. The average summer range, on the other hand, is usually of full cover and the total acreage is available for grazing. Thus an increased acreage is required for winter grazing to provide sufficient forage.

Further, reindeer graze more quietly over a smaller area in winter than in summer, and remain for the most part in one general locality. This means closer utilization and greater danger of overgrazing. To offset this and to guard against overuse, a larger acreage must be provided to put into effect a scheme of deferred and rotation grazing.

All three factors, then, point to the necessity of a larger acreage requirement under winter grazing, although the second factor may result in considerable variation in the final estimate given as between different localities.

CARRYING CAPACITY ESTIMATES

For the reindeer ranges, as now known, a carrying capacity of 10 or 15 acres a head is indicated for summer grazing plus 30 to 45

acres for winter. Yearlong, this requirement would become 40 to 60 acres. The extensive reconnaissance thus far conducted indicates that 40 to 45 acres a head will probably apply generally to the Norton Sound section and south, and 50 or 60 acres for the Seward Peninsula and north. The Seward Peninsula, for example, now carries about 83,000 reindeer, and from computations of acreage and on a basis of a 60-acre requirement, it has a future carrying capacity of 200,000 head. A 60-acre requirement is fixed for the peninsula section at this time to insure a safe basis for stocking. Later, if it should be found that the range is not being fully utilized, following careful inspection of the individual allotments, a gradual increase may be made until full capacity is reached.

If, as indicated by the present studies, it may take a depleted lichen range from 15 to 30 years to recover, the importance of carefully protecting the winter ranges becomes readily apparent. Some system of deferred and rotation grazing must be devised, and sufficient acreage provided to make it practicable. Under a permit system, based on an estimated carrying capacity for each allotment, it would be advisable first to proceed on the basis of 60 acres a head, and then later, should underutilization be found, gradually to increase the stocking to full capacity, as determined by careful and continuous inspection.

On the basis of a 40 to 60 acre requirement, the total available range in Alaska suitable for grazing should support 3,000,000 reindeer. The coast section now occupied by herds should when fully stocked carry 1,000,000 reindeer.

MANAGEMENT

The reindeer herds in Alaska are rapidly increasing in size, so that better and proper methods of management are more important. Former methods of handling applicable to small herds are no longer sufficient; better and modern methods to conform to the larger herds must now be adopted. Under proper management and organization the reindeer industry has a promising future, but a decided change toward better methods must now take place if full progress is to be maintained.

RANGE CONTROL AND REGULATION

As a natural development of the growing use of the open range, some system of range control and grazing regulation is certain sooner or later to be established. Such a system, which is necessary if a permanent industry is to be built up, would contemplate the division of range into allotments, as determined by natural units, each owner being given a permit to graze a certain number of head upon a certain unit. In the presence of numerous small owners, this will require that reindeer be held in cooperative herds and that the owners organize into cooperative reindeer associations or livestock companies.

To avoid future difficulty it is undoubtedly best that Eskimo-owned and white-owned herds be kept separate as far as practicable. In instances of mixed ownership, where controversies arise, every effort should be made toward readjustment, and the herds should be separated and combined with others to obtain uniform ownership.

In some cases, where such a move may not be feasible at this time in full justice to all concerned, a cooperative herd by white and Eskimo owners must continue. But the attempted splitting up of a natural grazing unit, by dividing the herd and allowing the two or more parts to remain on the same unit, is impracticable.

With an allotment system in operation, definite assignment of range among owners may be made and a protective management adopted for each grazing unit. Such management would involve stocking the range on the basis of actual carrying capacity and proper control and distribution of stock in order to insure a uniform utilization based on the forage requirement. Careful herding, construction of range improvements, and eventually the adoption of range salting are important aids to proper control.

SUMMER RANGE MANAGEMENT

Protective management on summer ranges is a comparatively simple problem, and a ready solution is to be found since it involves a known quantity, namely, herbaceous and shrub vegetation, as grasses, sedges, herbs, and browse. Valuable information that applies directly is available in the publications on forage and range studies that have been conducted for many years on the grazing areas of the western United States. The principles determined by these studies apply to Alaska as well and may be followed in working out the management scheme. Proper seasonal grazing, deferred and rotation grazing, open grazing, and proper distribution of stock over the range must all be put into practice.

WINTER RANGE MANAGEMENT

The problem on winter range is more difficult. From the nature of the lichen forage it is evident that the treatment in range management will have to be much different from that applicable to such rapid-growing forage crops as grasses, sedges, herbs, and browse. Although one or two croppings of herbs and grasses may be safely permitted each season under a rotation grazing scheme of three years, without seriously injuring the growth or lowering a continued maximum forage yield, this could not be permitted with the slow-growing lichen vegetation. Recovery from cropping in this case requires not one season or part of a season, but several years. Instead of a three-year deferred and rotation grazing scheme, a more extended system will have to be worked out and applied.

Management of the winter reindeer ranges calls for a deferred and rotation scheme of grazing, but to what degree each area should be grazed before deferring is still uncertain. Observations suggest that probably one of two things must be done: (1) Either close utilization must be followed or (2) there must be a very light cropping. Close utilization to remove all cover down to the frozen ground will get the greatest value out of each crop and will open up the cover for readier reproduction. It will also be the easier method for the grazier.

Light cropping, on the other hand, would require greater movement of the herd, constant changing from one area to another, and

consequently more effort on the part of the grazier. In addition, much forage would be killed instead of being eaten upon a second grazing. Furthermore, the cover would not be opened up for ready reproduction, and it remains to be seen what sort of a second or renewed crop might be expected from an offshoot type of growth.

At present the writer favors the close utilization method, perhaps by alternate strips of range, and then by deferring the area over a period of several years, the period to be determined later as studies progress. In any case, complete removal of the cover would not take place on the winter range because of the protection afforded by the frozen ground.

The general management scheme, however, will vary with the nature of the cover and the character of the site. Closer utilization can probably be applied more readily on a tundra site of favorable moisture, a luxuriant cover, and a *Cladonia* vegetation. On a drier, rocky site with less-abundant plant growth, lighter utilization probably must be practiced. Again, heavier grazing may be withstood on an area of gentle topography than on one of steep slopes, and on the more sheltered areas than on those that are exposed. In any event, open grazing rather than massed grazing by the herd should be practiced on winter as well as on summer range, not so much to avoid close utilization as to prevent overutilization.

HERD MANAGEMENT

Not only is improvement in range management necessary, but better herd management also must be effected along the lines advocated in Department Bulletin No. 1089. The more important points to be considered in attaining a better herd management may be briefly summarized as follows: (1) Open herding; (2) proper castration by use of knife and emasculator; (3) reduction of herd bulls to the ratio of 5 to 10 for each 100 does; (4) selection of the largest and best bulls of dark color for breeding purposes; (5) elimination of white-colored and light-spotted animals from the breeding herd; (6) removal of scrub stock, both male and female, from the breeding herd—scrub stock and old barren females should be slaughtered; (7) injection of new blood into the herd by an interchange of bulls between herds, and by use of caribou bulls; (8) employment of the corral and chute method of handling the herd at round-up time for branding, castration, and separating, and abandonment of roping as much as possible; (9) use of a holding pasture for a large herd in connection with the corral; (10) marking fawns on a basis of percentage ownership; (11) organizing small owners by communities into livestock associations or companies, with one mark or brand adopted for each community herd, and in the case of the Eskimo, placing the best reindeer men in charge of the herd; (12) training and keeping in the herd at least 10 sled reindeer for each 1,000 head of stock.

The necessary reorganization of the round-up and herding operations in the majority of Alaska herds may be obtained by employing pack and sled reindeer in hauling supplies and getting over the range, and by constructing cabins on all parts of the range to facilitate efficient patrol. Where temporary tent camps must be relied

upon instead of cabins, and where the herder must carry his supplies and equipment on his back in hiking over the range, there can be no efficient herding or rounding-up of stock. When the herder must carry his own pack, the time he can spend out on the range is limited, and consequently on a large range he may fail to bring in all the stock at a round-up. Furthermore, hiking with a pack over Alaska tundra is grueling work and consequently not conducive to the best results. By using pack reindeer to carry his supplies, therefore, the herder's task is made easier; he is able to stay out on the range a long time; and by being able to cover his range thoroughly he is assured of a complete rounding-up of all stock. The use of permanent cabin camps, well situated to cover all parts of the range, is also an important aid in this respect. With supplies stored at these camps, the herder can conveniently work his range by patrolling between cabins and by working out from them during the round-up. The cabins also provide a comfortable abode and make reindeer herding a more attractive occupation.

SUMMARY

The stock of 1,280 reindeer imported from Siberia into Alaska between the years 1892 and 1902 has increased to approximately 350,000, not including about 125,000 utilized for food and clothing. The annual gross increase in herds is between 33 and 45 per cent. About a third of the Alaskan reindeer are now under white and two-thirds under Eskimo ownership in individual and company herds. One incorporated company owns about 50,000 reindeer in six herds.

In the two years 1924 and 1925 reindeer meat weighing more than 1,000,000 pounds was exported from Alaska, and a steady increase in the output and in the demand for it is indicated. The meat is fine-grained, compares favorably with beef, and when fresh is exceptionally juicy and tender.

A rapidly growing industry requires that scientific studies be made for its best development, and under congressional authorization such studies were begun by the department in 1920 through the Biological Survey. Improved methods have been recommended to herd owners for handling reindeer and utilizing the range, and investigations on these lines are being continued, with the reindeer experiment station of the Biological Survey at Fairbanks as a center. A study of range units is being made with the view to inaugurating a permit system of grazing allotments. Careful and continuous inspection will be required to determine whether an area is being under or over grazed.

Of the two types of reindeer in Alaskan herds, the long, rangy type is usually heavier and better for meat production. The dressed weight of a carcass averages 150 pounds, with 300 pounds as the maximum. Experiments in the development of a heavier type are being conducted on Nunivak Island through crossbreeding with caribou bulls captured in the interior of Alaska and transported to the island for the purpose.

The use of sled reindeer is recommended for herd management and other transportation uses, and studies have been made in breaking and training the animals and in feeding them on other than a lichen diet.

Reindeer have been successfully fed grain and hay with other cultivated crops, and lichens are found not to be essential to their maintenance. As a ready source of food, lichens will continue to be the chief sustenance of the herds, however, and are what make reindeer grazing possible in Alaska. Studies will be continued to determine the effect of a varied diet on meat quality.

Grazing in Alaska is tending toward permanent ranches with natural boundaries, each grazing unit having its own summer and winter ranges. Under a fixed-allotment system open herding is found more practicable than the close herding introduced by the Lapps.

Coastal, interior, and intermediate range belts have been studied with a view to establishing for each unit definite summer and winter grazing areas. As forage is likely to be trampled in wet tundras, and growth reduced on rocky areas, the carrying capacity is greater on the dry-tundra type of range.

Timbered ranges have an advantage over the treeless in that they afford shelter to herds and herders and supply fuel and materials for cabin, corral, and fence construction. On many allotments two or more herders' cabins are needed, and boundary and drift fences are considered practicable.

As regards range belts and types, the main forage cover on winter ranges consists of lichens—on the coast range with a sedge-browse subtype, and on the interior ranges a browse subtype; on summer coast ranges a sedge-browse forage predominates, and in the interior a browse-sedge-lichen type.

Lichens are seldom present in pure stand, their average proportion in the total cover on winter ranges being about 50 per cent, the remainder consisting of a varying admixture of browse, sedges, and mosses. The most abundant of the lichens are those of the genus *Cladonia*, with *Cetraria* second in importance.

To determine the reaction of lichens to grazing, quadrat studies have been begun on the range, and the results reached indicate a rapid rate of establishment of new plants after denudation, depending upon moisture, but a slow recovery to normal stand. One denuded area regained 50 per cent of its former stand in four years, and it is indicated that the normal vegetative stand, including other growth, should be reached in 7 to 10 years after denudation, but 15 to 20 years seem required to attain a normal lichen height of 4 or 5 inches, except in rocky areas, where recovery might take as long as 25 or 30 years. Such slow recovery makes evident the necessity of extinguishing and preventing range fires, of limiting the stocking of an area to its carrying capacity, and of carefully protecting winter ranges.

Winter grazing requires a greater acreage per head than summer. Yearlong, from 40 to 60 acres for one reindeer is indicated—10 or 15 for summer and 30 to 45 for winter grazing. About Norton Sound the acreage per animal is 40 to 45, and farther north 50 to 60. These figures furnish a basis for determining the future carrying capacity of definitely marked areas. The areas available to grazing in Alaska should ultimately support 3,000,000 reindeer, a third of this number on the coast section now occupied.

Full progress in the reindeer industry can come only from the adoption of better management methods, not only in range control and regulation but in herd management and provisions for transporting and marketing the meat. This involves open herding, reduction of the proportion of bulls in the herds, selection of the best stock for breeding, infusion of new blood by transferring bulls and cross breeding with native caribou, adoption of improved methods of corralling, branding, and castration, keeping sled reindeer in each herd, and providing for herd ownership on the percentage basis for increases, with one registered brand for a community herd, and for cold-storage facilities to assist in marketing.

ORGANIZATION OF THE UNITED STATES DEPARTMENT OF AGRICULTURE

September 13, 1926

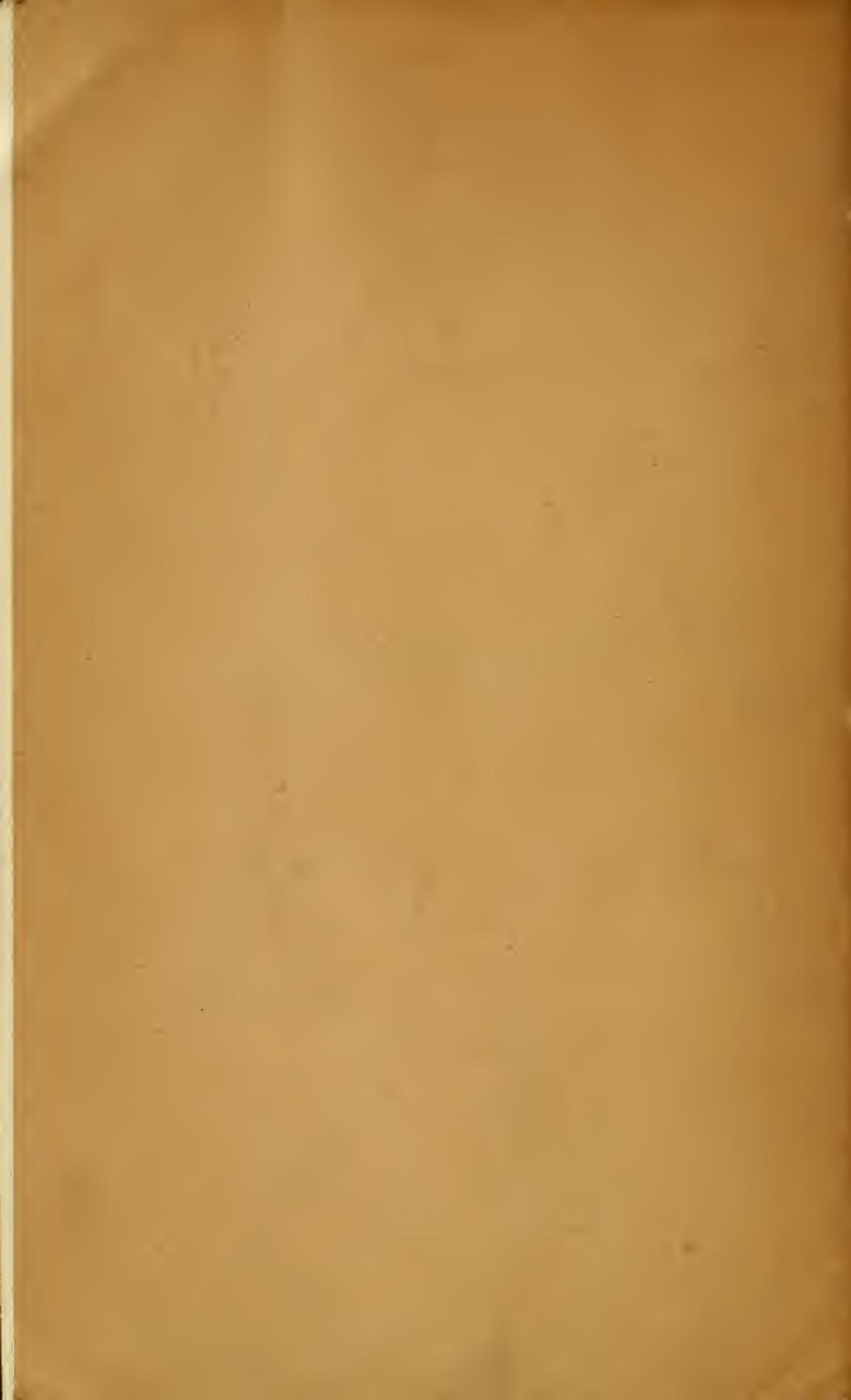
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UNITED STATES DEPARTMENT OF AGRICULTURE



DEPARTMENT BULLETIN No. 1426



Washington, D. C.

August, 1926

THE CLOVER ROOT BORER

By

L. P. ROCKWOOD, Associate Entomologist
Cereal and Forage Insect Investigations
Bureau of Entomology

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WASHINGTON
GOVERNMENT PRINTING OFFICE

1926

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INTRODUCTION

The clover root borer, *Hylastinus obscurus* Marsham, an insect of European origin, is now present in almost all agricultural regions of the United States where red clover is an important crop. This insect is one of the principal factors limiting the life of a red clover stand after the first crop year² and has frequently caused large losses by

¹ *Hylastinus obscurus* Marsham; subfamily Hylesiniinae, family Ipidae, superfamily Scolytoidea, order Coleoptera.

² The term "first crop year" as used throughout this bulletin refers to the first calendar year following the year in which a given field of clover was seeded. Though a late crop of hay or seed is sometimes, under favorable conditions, obtained from a clover field seeded in the spring of the same year (49, p. 20¹), this is usually not the case throughout most regions where red clover is grown.

³ Numbers (*italic*) in parentheses refer to "Literature cited," p. 46.

severe infestation of clover, even in the first crop year. It has been under observation for the last several years at the field station of the Cereal and Forage Insect Division of the Bureau of Entomology at Forest Grove, Oreg.⁴ In the course of this investigation many new data on the bionomics of the insect have been accumulated. These observations are contained in this bulletin and an attempt has been made to correlate them with previously published records and with unpublished notes from the bureau files. The results of these studies are presented as a possible aid in the problem of successful clover culture. It should, however, be emphasized that insect injury is but one phase of a complex of factors affecting red clover as a crop.

SYNONYMY

The species was first described by Marsham (31, p. 57) as *obscurus* in the genus *Ips* De Geer, in 1802. The first description to be accompanied by biological notes was that of Müller (32), in 1807, who described it as *trifolii* in the genus *Bostrichus* of Fabricius, according to the title of his paper. Schmitt (39), in 1844, published descriptive and biological notes on Müller's species as *Hylesinus trifolii* Müller. Chapuis (7, p. 231) in 1873 placed Müller's species in the genus *Hylastes* (Erichson), and was followed in this classification by Eichhoff (10, p. 97) in 1881. Bedel (3, p. 390) in 1888 erected a new genus, *Hylastinus*, for Marsham's species (*obscurus*) and considered it synonymous with *trifolii* Müller. Hagedorn (17, p. 7; 18, p. 43) in 1910 made *Hylastinus* a subgenus of *Hylastes* and did not recognize Marsham's species, but retained the name *trifolii* Müller. Reitter (36, p. 280) in 1916 retained the genus *Hylastinus* and recognized the synonymy of *trifolii* with *obscurus* and also listed *Hyl. crenulatus* Duft. as a synonym. The species was listed with descriptive notes by Swaine (41, p. 9) in 1918 under the name *Hylastinus obscurus* Marsham. The more important synonymy is as follows:

Ips obscurus Marsham, 1802 (31, p. 57).

Bostrichus trifolii Müller, 1807 (32).

Hylesinus trifolii Müller (Schmitt), 1844 (39).

Hylastes trifolii Müller (Chapuis), 1873 (7, p. 231).

Hylesinus trifolii Müller (Riley), 1879 (37).

Hylastes trifolii Müller (Eichhoff), 1881 (10, p. 97).

Hylastinus obscurus Marsham (Bedel), 1888 (3, p. 390).

Hylastes obscurus Marsham (Davis), 1894 (9).

Hylastes (sub. g. *Hylastinus*) *trifolii* Müller (Hagedorn), 1910 (17, p. 7; 18, p. 43).

Hylastinus trifolii Müller (del Guercio), 1915 (16, p. 263).

Hylastinus obscurus Marsham (Reitter), 1916 (36, p. 280).

Hylastinus obscurus Marsham (Swaine), 1918 (41, p. 9).

⁴ Valuable aid has been rendered by C. W. Creel, in charge of the Forest Grove station during much of the investigation, Max M. Reeher, James M. Langston, and Merton C. Lane, all of whom are, or at various times have been, attached to the station, and have aided in field observations and control experiments. The writer's thanks are also due to A. J. Pieters and H. A. Schoth, of the Bureau of Plant Industry, for cordial cooperation and interest; also to G. R. Hyslop, of the Oregon Agricultural College. E. A. Schwarz, of the Bureau of Entomology, with his usual kindness, assisted in the study of the synonymy of the species. E. E. Cowin, of Wapato, Wash., and William A. Hermens, of Verboort, B. H. Reeher, of Gales Creek, Menold Bros., of Cornelius, and Morris M. Goodrich, of Yamhill, all in Oregon, have aided materially in the work by their cooperation. Credit is given hereafter for the use of unpublished notes which have been of material assistance. Sadie E. Keen, of the Bureau of Entomology, has assisted in the preparation of the manuscript and tabular matter, and the writer is indebted to W. R. Walton, Entomologist, Cereal and Forage Insect Investigations, for suggestions regarding the matter included and for preliminary editorial work on the manuscript.

HABITS OF RELATED SPECIES

Hylastinus obscurus Marsham is the only representative of its genus known in America and is quite distinct in several ways from its near relatives in the subfamily Hylesiniinae of the family Ipidae of the superfamily Scolytoidea. Other members of its subfamily in America and Europe form characteristic egg galleries in the trunks or branches of trees or woody shrubs. Many of them prefer injured or dying plants to healthy ones, but several species have the reputation of attacking healthy trees on occasion. *Alniphagus aspericollis* Lec., which of western species is anatomically the nearest to *H. obscurus*, tunnels under the dying bark of western alder; *Hylurgopinus rufipes* Eichh. (*Hylesinus opaculus* Lec.), which also resembles *H. obscurus*, tunnels in the dying bark of elm and basswood in the eastern part of the United States. Reitter (36, p. 280) has described another species of *Hylastinus*, *H. fankhauseri*, which mines under the bark on the stems of the leguminous shrubs *Laburnum anagyroides* and *L. alpinum* in the mountainous regions of south-central Europe.

As the great majority of the Nearctic species of the Ipidae breed normally in the bark or wood of trees, the habit of *Hylastinus obscurus* of mining and breeding in the roots of herbaceous leguminous plants may be considered decidedly aberrant. It would seem from several apparently authentic European records that the species may occasionally have the habit, more normal to the subfamily, of mining under the bark on the stems of woody leguminous shrubs (*Cytisus*, *Ulex*, and *Spartium*), especially on plants which have been injured by frost or other agency. Some of these records may refer to *Hylastinus fankhauseri* Reitter, but the observers in a few cases, notably Bedel (2), were systematists with an extensive knowledge of the Ipidae, and their records can hardly be questioned without further study of the species collected on these host plants in Europe, especially as Reitter (36) retains *Spartium junceum* and *Ulex europaeus* in his list of hosts of *H. obscurus* and records *H. fankhauseri* only from south-central Europe.

ECONOMIC HISTORY

EUROPE

Apparently *Hylastinus obscurus* has rarely attracted attention in Europe. Damage to clover serious enough to be noted in entomological literature has occurred in Germany and more recently in France and Italy. Müller (32) reported a very serious infestation of red clover near Mainz in the year 1803, which afforded an opportunity for studying the species. His report of conditions leading up to the outbreak, as given by Schmitt (39), is very interesting and informing. According to this account, the year 1802 was so dry and hot that much of that year's clover seeding was lost and the farmers, contrary to their custom, had left a large acreage of second-year clover for another crop. After an unfavorable spring in 1803, which probably thinned the clover stands, almost all of the remaining clover was destroyed by the root borer. Müller arrived at the opinion that the root borer was principally responsible for the dying out of clover the third year from seeding. Later (1844) Schmitt (39) studied the species in the same region and contributed further to our

knowledge of its life history. He disagreed with Müller as to the damage caused by the species and expressed the opinion that red clover under the system of culture in that region died out from natural causes in the third year, and that the root borer attacked only dying plants, as was the habit of its near relatives which attacked injured or dying trees. Bach (1) in 1849 confirmed the earlier observations of the two other writers as to the true host plant of the species.

In spite of these observations some controversy arose as to the true host of the species.⁵ In 1869 T. Algernon Chapman (6) gave an interesting account of the occurrence, habits, and partial life history of what he determined as Marsham's species on furze (*Ulex europæus*) and Scotch broom (*Cytisus scoparius*). He noted that usually only large stems of furze or Scotch broom were attacked; sticks which had been cut down were rarely attacked, but living stumps and stems of plants dying of age were often infested. He recorded the species as associated with *Phloeophthorus rhodactylus*. According to Løvendal (29, p. 118), Nördlinger, in September, 1850, found larvæ, pupæ, and adults of *Hylesinus trifolii* inside the thickest roots of 2 or 3 year-old red clover; but the plants, though apparently infested during the previous year, showed no sign of unhealthiness. In the clover the egg galleries were not regular, but Nördlinger also found the species breeding in arm-thick stems of *Cytisus (Spartium) scoparius* in September, 1855, at la Teste, near Bordeaux. In these shrubs the egg galleries were two-armed and horizontal, and had furrowed both the bark and the outer part of the wood. In 1876 Perris (34, p. 175), stated that *trifolii* was undoubtedly a misnomer and that he had never found the species on clover. Bedel (2) corrected this statement in the same year and named three hosts of the species (*H. trifolii*) belonging to three different genera of papilionaceous plants. Of these, *Trifolium pratense* was the preferred host near Paris, as in Germany. It was also found on (*Sarothamnus*) *Cytisus scoparius* in living stems of unusual size in Brittany, in company with a *Phloeophthorus*. Bedel also stated that he had found the insect on *Ononis natrix*, in an old woody root exposed on the side of a bank at Belmont. Ceconi (5, p. 164) in 1899 described galleries of what were determined as *H. trifolii* Müller in stems of *Cytisus alpinus* weakened by frost. Del Guercio (16, p. 268) reported in 1915 that red clover was damaged in Tuscany, and also noted the occurrence of the species (*H. trifolii* Müller) on *Cytisus laburnum*, but stated that he considered the individuals on *C. laburnum* to be a different biological race. Marchal (30, p. 9) reported injury to clover in the Gironde in 1913, and Wahl and Müller (44, p. 35) reported injury to red clover, probably by this species, in Baden in the same year.

AMERICA

The clover root borer is believed by all American authors to have been introduced from Europe. It was not noticed by American entomologists as a pest until 1878, when Riley's (37) a count of the insect in western New York was prepared. In all probability the insect had been present for many years. Henry (19) reported

⁵ Some of this confusion may have been caused by failure to recognize the species afterwards described as *H. fankhauseri* Reitter, but for reasons already stated the writer hesitates to disregard all of these records.

that, on July 6, 1880, the clover root borer had taken all the clover in portions of Genesee County, N. Y. Lintner (27, 28) published notes on the species in 1880 and 1881. White (50) reported "incalculable damage" to clover fields near Edmonton, Ontario, June 9, 1888. Fletcher (11) reported damage to clover in Harwich Township, Ontario, in August, 1891. The clover root borer was first observed in Michigan in 1889, near the west end of Lake Erie, and became destructive in southern Michigan in 1893. Davis (9) made a study of the species in Michigan in 1893-94, and published original observations on its life history and control experiments. The insect was injurious in Ohio by 1890 and was recognized as a serious pest in the northwestern part of that State in 1893. Webster (46) made original observations on the species in Ohio, which were published in 1899, together with a report on control experiments. His account is probably the best that has been published on the species. Cordley (8) reported the occurrence of the clover root borer in Oregon in 1896. Folsom (12) made some original observations on the species in Illinois, which were published in 1909.

Unpublished records of the destructive work of the species, taken from the files of the Bureau of Entomology, are here noted. A. J. Porter, of Bern, Ind., reported September 24, 1905, that a whole field of clover had been destroyed since the last of June. W. J. Phillips, of the Bureau of Entomology, reported root borers in destructive numbers at Wellsburg, W. Va., in November, 1905, stating that the farmers complained of short clover crops for several preceding years. The same observer noted such severe injury at Defiance, Ohio, on August 22, 1908, as to lead a number of farmers to plow up their fields. The late E. J. Vosler, formerly of the Bureau of Entomology, reported serious injury to red clover near Murray, Utah, in August, 1911. A. F. Satterthwait, of the Bureau of Entomology, reported serious injury by root borers near Van Wert, Ohio, on June 17, 1915, but in this case a fungous disease and possibly other factors were also involved in the failure of the clover crop. Virgin Browning, of McClure, Ohio, June 25, 1915, reported the clover-hay crop ruined by clover root borers. The description of the injury in this case also indicates that fungous disease may have been an important factor in the damage. H. L. Parker and W. E. Pennington, of the Bureau of Entomology, reported serious damage to clover in western Maryland in 1915 and 1916.

THE PACIFIC NORTHWEST

Red clover was not generally grown in the Willamette Valley of Oregon until the eighties and early nineties (24, p. 3), when decreasing yields of cereal crops under continuous cropping or occasional summer-fallowing led many farmers to rotation of crops with red clover included in the rotation as the best-paying legume. The red-clover crop became very profitable to western Oregon farmers as, besides its other advantages, excellent seed yields were obtained (23, p. 4). Until recent years clover stands remained productive for several seasons, but at present it is not usually profitable to maintain a clover stand for more than one crop year. The clover root borer is largely responsible for this failure of clover to withstand more than one cropping in western Oregon and Washington. There have also

been many instances of very severe damage to clover in the Willamette Valley, even during the first crop year. This pest first attracted attention in Oregon about 1895, as Cordley (5) noted its occurrence under date of March 24, 1896. It therefore was present even in the early days of red-clover culture in Oregon.

Clover culture for hay and seed was introduced on the Yakima Indian reservation of Washington within recent years. All the clover pests of the Willamette Valley soon became prevalent there, particularly the clover root borer. It is thought that the pest was introduced into this section with Willamette Valley hay used at the construction camps of the irrigation project.

The only section of the Pacific Northwest where clover is largely grown and where the clover root borer has not yet been found is the clover-seed section in the Twin Falls region of Idaho. This region was settled before the advent of the railroad and has always raised



FIG. 1.—Distribution of clover root borer in the United States, as recorded in the literature. The insect is probably more generally distributed in the northern part of the United States than is here indicated

a surplus of hay, so that probably no hay has ever been imported into the region. In this section clover stands have often remained productive for several years, although recently injury by nematode worms is leading to the adoption of a shorter rotation.

DISTRIBUTION

According to information compiled from various sources, the clover root borer is now found in Russia (Kief); Germany; Austria; Czechoslovakia; France; England; Canary Islands; Denmark; Italy (Tuscany); Canada (southern Quebec and Ontario); in the northern portion of the eastern United States, from western Maryland, West Virginia, Pennsylvania, Ohio, Indiana, Illinois, and Iowa, to the Great Lakes, and covering a portion of New England; in Utah (Salt Lake Valley); in Idaho (Boise, Moscow); in Washington (Pullman, Yak-

inia Valley, western Washington from Oregon to the Canadian boundary); and in western Oregon, at least as far south as Medford. Figure 1 presents the known distribution in the United States.

The wide distribution of this species over regions of the world where red clover is a common crop and its early appearance in most new clover regions would indicate that the species is readily transported by commercial intercourse. Root borers may be transported in hay shipments, because the beetles are sometimes found mining in the stems of clover, and, in cases of severe infestation, the clover tops and even portions of the root crown may be pulled out by the mower and become part of the hay. Adult root borers may also be transported in soil taken from the vicinity of clover plants, and in other ways during the period of flight, when they are often found in unexpected places.

DESCRIPTION

EGG

The egg (fig. 2) is short-oval in shape, with one side somewhat less rounded than the other, pearly white in color, smooth and glistening. Eggs in which development has begun are transparent at one end, because of retraction of the egg contents; whereas the fresh eggs are altogether opaque. The egg measures 0.67 mm. long by 0.43 mm. wide at the widest part. Eggs are found in niches, which are plugged with wads of frass, in the walls of the egg galleries.

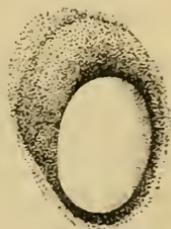


FIG. 2.—Egg of clover root borer, $\times 28$ diameters

LARVA

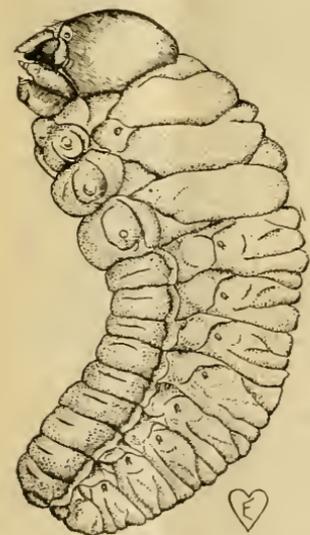


FIG. 3.—Larva of clover root borer, lateral view, $\times 16$ diameters

The mature larva (fig. 3) is of the usual scolytid type, short subcylindrical, wrinkled, and legless. The thoracic region is distinctly larger than the abdominal region, which tapers gradually posteriorly. The body setae are short, fine and sparse, very obscure. The color is creamy white, with straw-yellow to light-brown head capsule and red-brown, triangular, dark-tipped mandibles, which have two broadly blunt teeth at the apices. The immature and still feeding larvæ appear dirty white or gray, because of the contents of the intestinal tract. The setae of the head are light colored, fine, somewhat longer than the body setae. The head capsule (fig. 4) has the epicranial suture⁶ strongly

impressed; front with a convexity anterior to the middle, with oblique ridges extending above to the sutures of the front on either side and below to the angles of the epistoma, forming concavities between the ridges. Front with posterior apex subacute. Labrum with raised

⁶ The anatomical nomenclature here used is for the most part that of A. D. Hopkins, in his treatise on the Genus *Dendroctonus* (20).

median triangular area, truncate, or faintly emarginate. Clypeus with raised W-like rugosity with corresponding lateral and anterior mesial concavities; anterior margin truncate or obscurely broadly emarginate. Mature head capsules in pupation chambers vary greatly in dimensions, the minimum being 0.55 mm. long without mandibles, front 0.31 mm. by 0.29 mm., epistoma 0.23 mm., pleurostoma 0.12 mm.; the maximum 0.70 mm. long without mandibles, front 0.36 mm. by 0.34 mm., epistoma 0.28 mm., pleurostoma 0.15 mm.

The larva differs from the larva of *Sitona* sp., also found on clover roots, in being relatively smaller and stouter, without long hairs, and with more evident distinction between the thoracic and abdominal regions. *Sitona* larvæ are always external feeders, *H. obscurus* larvæ always internal feeders.

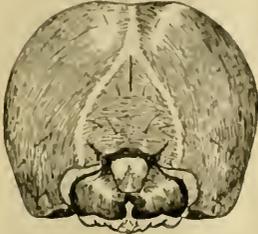


FIG. 4.—Head of larva of the clover root borer. Front view, greatly enlarged

The pupa (figs. 5 and 6) is truncate fusiform in shape, with the apex of the abdomen squarely truncated on a line between the caudal spines on the ninth abdominal segment. The wing pads extend to near the hind margin of the sixth, and the elytral pads to near the hind margin of the fifth abdominal segment. The color of the fresh pupa is pearly white to white and shining. Setæ on all parts of pupa are short, fine, inconspicuous. Setal spines are also short and inconspicuous, except the two anterior dorsal spines on the prothorax, which are considerably more prominent than other thoracic spines and setæ, and the two very prominent conical, slenderly pointed, and slightly recurved caudal spines on the ninth abdominal segment. The two frontal setal spines opposite the upper inside margin of the eye mark the vertical limits of carinæ which form the outside margins of crescent-shaped concave areas. There is also a median inverted V-shaped concavity just above the pseudolabrum on fresh pupæ. The sculpture of the head varies with the age of the pupa. Anterior and middle femora with two setæ of unequal size on small papillæ. Elytral pads rugose.

The pupa becomes pigmented as it matures; the eyes and mandibles become red-brown; wing pads dusky; the area around the mouth parts shows faint chitization; later the face, legs, prothorax, and elytral pads assume a faint brownish tinge. The size varies considerably, typically 2.5 mm. to 2.7 mm. long by 1.1 mm. wide. The pupa is found in a pupal chamber at the end of the larval mine inside of the clover root.

PUPA



FIG. 5.—Pupa of clover root borer. Ventral view, $\times 16$ diameters

ADULT

The body of the adult (fig. 7) is oblong oval; pronotum slightly wider than long, a little narrower than elytra, sides rounded, unarmed, strongly arcuate, narrowed roundly anteriorly, without anterior constriction dorsally; head visible from above; elytra deeply striate but unarmed except for shagreening posteriorly and laterally, roundly con-

vex posteriorly. The face, prothorax, elytra, legs, antennæ, and venter are distinctly clothed with short golden-brown hairs, hairs longer on venter than on dorsum; side pieces of mesothorax and metathorax; that is, the metathoracic episternum of Hopkins and mesothoracic episternum and epimeron, clothed with oval, gray or silvery, fringed scales. The convex head is finely and shallowly punctured with a faint transverse median impression at the base of the short beak. The antennæ, whose scrobes are distinctly separated from the front of the elliptical eyes, have a 7-segmented funicle, about as long as the distally inflated scape, and a short oval-connate, slightly compressed club, of which only the first suture is strongly chitinized and distinct, the first and second segments about equal and each longer than the third and fourth together. Swaine (41, p. 43) stated that the proventriculus has— a short diagonal band of small costal teeth backwards from base of bristles, almost obsolete on disc which is not finely granulate; ligula widened distally and truncate at tip.

The prothorax is closely and deeply punctured, punctures irregular in size and shape, with a tendency to rugosity, vestiture of hairs short, fine, obscure. Median line absent, or present and more or less interrupted and obscure, usually vestigial, scarcely elevated if at all when present, marked by dividing line between prothoracic hairs even when not otherwise evident. Elytra clothed with three types of vestiture, punctures of striæ large, deeply indented, and tending to rectangular, each with a very fine, appressed, obscure, pale hair; interspaces more finely and obscurely punctured, punctures well separated, each accompanied by a single, coarse, brown, backward-directed scalelike hair. The interspaces are roughened between and around punctures, becoming shagreened or granulate posteriorly and laterally, and sparsely clothed with shorter golden-brown appressed scalelike bristles. Interspaces and striæ almost straight. Ventrally, the anterior coxæ are widely separated and clothed with long golden hairs, the second visible ventral abdominal segment, or sternite 4 of Hopkins, about as long as the fifth, or sternite 7 of Hopkins, and nearly double the third, or sternite 5 of Hopkins. Venter and legs shallowly and evenly punctured and clothed with hair. The tibiæ are toothed and dilated, the anterior pair with exterior angle of anterior margin nearly rectangular, with four

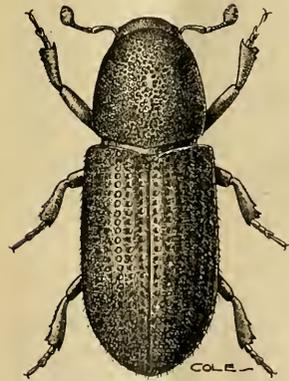


FIG. 7.—Adult of clover root borer, $\times 30$ diameters



FIG. 6.—Pupa of clover root borer. Dorsal view, $\times 16$ diameters

short, blunt, recurved teeth close together on anterior margin and a stronger lateral tooth usually posterior to others on outer margin; the median pair have three strong teeth along anterior half of outer margin; the posterior pair have two well-separated strong teeth along outer margin. The third joint of the tarsus is deeply bilobed.

The color of the adult varies with age and hardness. The fresh callow adult is almost cream-colored and requires several days to become chitinized. As the insect hardens the color ranges through dull yellow and various shades of red-brown. The old, fully matured adult is a very dark pitch-brown, sometimes almost black; the head, prothorax, sides of body, and venter always a shade darker than the elytra, which almost always have a distinct red-brown tinge, even when very dark. The legs and antennae are light red-brown, the antennae paler on club. Eyes and mandibles black in the mature form. The smallest specimen seen measured 1.82 mm. long by 0.82 mm. wide; the largest measured 2.5 mm. by 1.18 mm. The average is about 2.2 mm. by 0.92 mm.

Secondary sexual characters are very obscure; the male head tends to be narrower than the head of the female. There are apparently no reliable characters for distinguishing between living males and females.

SEASONAL HISTORY

EARLY SPRING ACTIVITY

Clover root borers usually pass the winter well down in the roots of the clover plants on which they were nourished during their larval life of the preceding season. The great majority at this time are fully matured adults and remain more or less dormant, either singly or in small groups, in enlargements of the larval mines. Adults which for any reason have become separated from clover roots may pass the winter in the soil or, rarely, under trash on the surface of the ground. Occasional larvæ, usually well grown, are found during the winter in larval feeding burrows. Apparently these are larvæ which hatched from eggs laid in the late summer of the preceding year.

When the soil warms up to a temperature of about 45° F.⁷ in the early spring, the activity and feeding of the adults and the few overwintered larvæ are gradually resumed in the roots. More or less activity probably occurs also during the winter when temperatures are high enough to permit of metabolism. The adults work their way from the lower parts of the roots towards the crown, where they are often found congregated in March and April. They feed on the root tissues and their so-called fat bodies begin to develop. As the soil temperatures rise above 50° F. this activity becomes more pronounced, and when the temperature of the air at the surface of the ground is between 55° and 60° F. the borers often leave the roots and walk about. This form of activity may rarely take place on warm days in February, from plowed-up clover and dead clover roots, but usually occurs in late March or early April and on days later in the spring when air temperatures range below 65° F. In case of a cool, backward spring, this movement of the beetles on foot is the only method of migration to new host plants until late in the season.

In clover fields plowed up during the preceding summer and fall, soil conditions, and the disturbed, abnormal state of the residues of the clover root borer's host plant, induce premature activity of the

⁷ Temperatures for field observations were recorded from portable air temperature thermometers and portable soil thermometers. Observations made on the laboratory grounds were correlated with standard Weather Bureau maximum and minimum thermometers, a Friez hygrothermograph, and a Friez soil thermograph, the bulb being buried 3 inches under growing winter wheat.

adult borers, which attempt migration in response to the stimulus of the first warm days of late March. In 1919, root borers were swept as early as March 29 from winter wheat which had been seeded on clover sod the previous fall. This was three weeks earlier than the emergence of beetles from undisturbed clover. On February 25, 1921, six weeks earlier than the first flight from undisturbed clover, Max M. Reeber noted a root borer crawling on the ground in a wheat field seeded on clover sod. That this unseasonable activity is detrimental to survival is indicated by the writer's unsuccessful attempts to start outdoor colonies in cages much earlier than the normal period of flight.

MATING

The first mating is believed to take place in the spring during the time just previous to flight. Copulation at this time probably occurs in the hibernation chambers in the roots of the host plants, on the clover crowns, and on the surface of the ground. Whenever in the writer's experiments males and females were brought together at room temperatures during this season, or even in the fall, mating or attempted mating was observed. Mating in the field has been observed very rarely, although Schmitt (*39, p. 394*) stated that near Mainz the beetles are often found in copula and resting on clover plants at the end of April and beginning of May. The writer observed one case of mating in an enlarged larval burrow of the previous year in an old clover root dug up in the field on May 13, 1915. An attempted mating (unsuccessful) was observed on the surface of the ground on April 24, 1918, when the temperature at the surface was 62° F. A case of mating in a cage in the laboratory was more closely observed. In this instance the male appeared to choose a female whose head and part of the prothorax were concealed in a superficial burrow. The male established connection after about 10 minutes' endeavor. Copulation lasted 25 minutes, with very slight movement on the part of either, the female discontinuing feeding during the process. All other cases of mating observed in cages occurred either remote from the roots or on the exterior of the roots. The observed facts that females predominated in the first flights, and that all but a very small percentage of them had been fertilized before capture in flight, are also indicative of a general mating previous to the first spring flight.

MATURITY OF OVERWINTERED LARVÆ

The overwintered larvæ resume feeding in their burrows as the temperature permits and, according to records of observations made in various parts of the country, usually reach maturity, pupate, and become adults in May, sometimes as early as April or as late as June. Webster (*46, p. 144*) reported overwintered larvæ in Ohio as late as May 27, and a pupa of an overwintered larva on May 31, 1898. E. J. Vosler noted, at Murray, Utah, a large percentage of overwintered larvæ in April, and pupæ, apparently from overwintered larvæ, on June 6 and June 20, 1912. Overwintered larvæ have been found as late as May 17, 1915, at Forest Grove, Oreg.

FLIGHT

When the temperature of the air rises above approximately 65° F. migration of the adult borers may take place by flight. At such a temperature borers have been seen to climb grass stems and clover tops and prepare for flight. Few beetles fly, however, until an air temperature of 70° F. or more is attained. The time of the first spring flight is variable, depending on whether the soil temperature has been high enough to induce activity within the roots for some time previous to the rise of temperature above the critical point for flight. In the Pacific Northwest the times of occurrence of soil and air temperatures sufficient to induce flight are exceedingly variable from year to year, and these conditions have an important bearing on the early infestation of new clover fields, and the resultant damage.

The earliest recorded first flights of beetles from undisturbed clover in the Pacific Northwest were observed April 7, 1916, and April 8, 1921, at Forest Grove, Oreg. Late records for earliest spring flight were, in the case of backward seasons, May 8, 1917, and April 26, 1920, also at Forest Grove, and May 5, 1917, at Wapato, Wash. According to records of the Hagerstown, Md., field station, made by H. L. Parker, the first spring flight probably occurred about the second week of April in 1915 and in 1916. Webster and Mally recorded April 26 as the date of first flight for the season of 1899 at Wooster, Ohio. Davis (9) reported the first capture in flight on May 3, 1893, probably near Lansing, Mich. E. J. Vosler reported the first borers in flight on May 18, 1912, at Murray, Utah. Schmitt (39, p. 394), of Mainz, Germany, reported adult root borers in greatest abundance above ground at the end of April and the beginning of May. Del Guercio (16, p. 265) stated that in Tuscan movement of borers begins about the middle of April in a mild year, or, in the contrary case, towards the end of that month. Eichhoff (10, p. 97) reported swarming of this species before and about the middle of June at Mülhausen, Alsace.

In Oregon favorable temperatures usually occur in the afternoon between 1 and 6 p. m. during May and June, and similarly at Murray, Utah, according to Vosler's notes. Eichhoff (10, p. 4) noted that at Mülhausen, Alsace, bark beetles, including clover root borers, were in flight in summer and fall only during the afternoon hours. The optimum temperature for flight appears to be 70° to 80° F. In the Pacific Northwest, because of unfavorable weather conditions, the normal flight period is often interrupted for several days at a time. The time of maximum flight, therefore, is usually several weeks later than the first flight of the earliest adults, and, in the Pacific Northwest, often occurs in May. The maximum flight at Forest Grove, Oreg., in 1916, occurred about May 2; in 1917, a backward season, about May 28. The maximum flight is of comparatively short duration, and there is a rapid dropping off in flight records after the maximum is passed. Scattering adults are rarely taken in flight as late as July. The latest recorded date for the Willamette Valley is July 14, 1915 (M. M. Reeher sweeping), and for the Yakima Valley in 1917 it was June 18 (one observed by E. E. Cowin, on screen).

The period of flight appears to be a time of great restlessness among the adults. The beetles do not settle upon the first plant on which

they alight but usually maneuver to the highest point on the plant and again essay to fly, not always successfully, as they are clumsy in taking off. Negative geotropism is very pronounced at this time, so much so that if two root borers happen to climb the same grass blade, the second will climb upon the back of the first as the highest available point. This tendency is closely related to the temperature; and even the obscuration of the sun by a cloud will often cause borers which have climbed plants to turn and descend to the ground. Observations indicate that borers commonly fly from 6 to 10 feet above clover fields, usually against the wind. Their flight is fairly straight and not rapid.

Females predominate in the early days of flight, being frequently 85 to 95 per cent of those collected. Of these, more than 90 per cent were found to have been fertilized before capture. In 1921, when a careful count by sexes of those collected was made, males



FIG. 8.—Small bannerlike screen covered with sticky tree-banding material and used in flight experiments

became more numerous (68.6 per cent of the total catch) than females on May 13, near the time of maximum flight.

FLIGHT EXPERIMENTS

As flight is the principal means of interfield dissemination of root borers, and as the time and extent of infestation of clover fields in the first crop year are therefore almost entirely dependent on habits of flight, this phase of root-borer activity was given special attention. Experiments with flight screens coated with sticky tree-banding material were conducted near Forest Grove, Oreg., in the humid Willamette Valley, and near Wapato, Wash., in the irrigated Yakima Valley. Screens of two types were used, the first being small and bannerlike (fig. 8), 18 or 24 inches wide by 3 feet long, placed on poles stuck in the ground and anchored by guy wires or nailed to

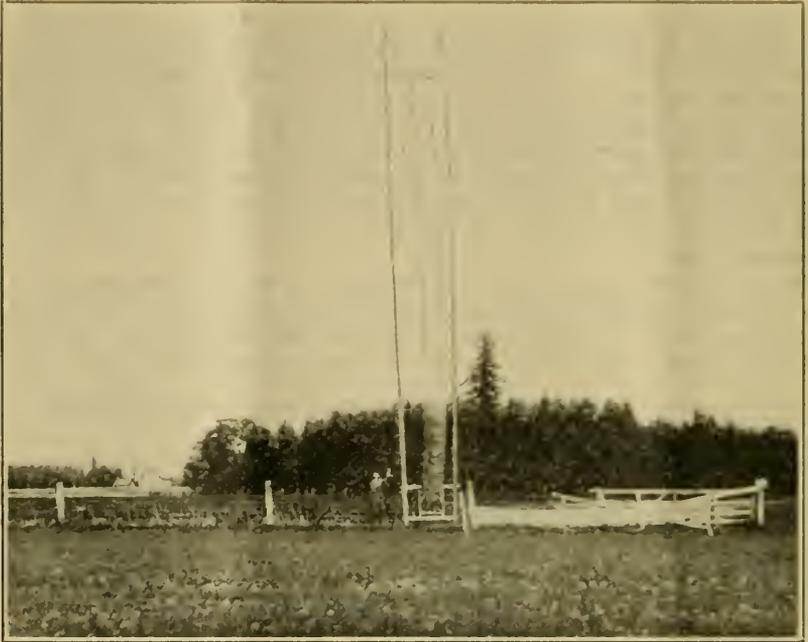


FIG. 9.--Full-length view of 50-foot screen used in flight experiments



FIG. 10.—Windlass used to reel in 50-foot screen

fence posts; the second of similar width but 50 feet long (fig. 9), raised between two wooden poles and reeled in on a windlass (fig. 10) for examination. As a rule counts were taken during the morning hours, when root borers were not flying. These experiments afforded some of the data on flight which have already been given. Tables 1 to 3^s summarize the more important experiments with these two types of screens.

TABLE 1.—Counts of clover root borers caught on screens 24 by 36 inches, erected on the four sides of an infested field at Wapato, Wash., on April 2, 1917

Date	Time of observation	Temperature at time of observation °F	North screen			East screen			South screen			West screen			Total for field
			North side	South side	Total	East side	West side	Total	North side	South side	Total	East side	West side	Total	
1917															
May 3	2 p. m.	58	0	0	0	0	0	0	0	1	1	0	0	0	1
5	3 p. m.	68	1	2	3	1	0	1	1	2	3	2	0	2	9
7	5 p. m.	74	3	5	8	4	1	5	23	8	31	3	0	3	47
8	10 a. m.	86	1	2	3	1	2	3	8	8	16	2	0	2	24
10	3.30 p. m.	78	4	5	9	2	4	6	19	14	33	3	0	3	51
12	2 p. m.	70	4	2	6	0	0	0	7	2	9	0	0	0	15
14	4.30 p. m.	64	0	1	1	0	0	0	5	2	7	0	0	0	8
16	12.30 p. m.	56	0	0	0	0	1	1	2	1	3	0	0	0	4
18	9.30 a. m.	63	1	0	1	0	1	1	2	1	3	0	0	0	5
20	9.30 a. m.	1	0	1	0	0	0	0	1	1	2	0	0	0	3
22		0	1	1	0	0	0	0	0	2	2	1	0	1	4
26	4 p. m.	72	1	2	3	0	0	0	0	0	2	1	0	1	6
28	4 p. m.	80	0	0	0	0	0	0	2	0	2	0	0	0	2
30	4 p. m.	70	1	1	2	0	1	1	3	1	4	0	0	0	7
June 1	4 p. m.	56	1	0	1	0	0	0	2	1	3	0	0	0	4
3	4 p. m.	76	0	0	0	0	0	0	1	0	1	0	0	0	1
16	3 p. m.	86	0	0	0	0	0	0	1	0	1	1	0	1	2
18	2.30 p. m.	91	0	0	0	0	1	1	0	0	0	0	0	0	1
Total			18	21	39	8	11	19	77	46	123	13	0	13	194

Table 1 presents the counts of clover root borers caught on screens measuring 24 by 36 inches, at Wapato, Wash., in the season of 1917. The screens were erected one each on the north, east, south, and west sides of an infested field, and were examined (usually) every second day from April 2 to June 18, except on May 24. From April 2 to May 1 and from June 4 to June 15 no borers were found on the screens. The temperatures at the time of examination are recorded for the days on which borers were found. During April the temperatures on the dates of examination ranged from 38° to 64° F.

From an examination of the table it may be seen that in the case of each screen the side turned toward the field collected in the aggregate more borers than the opposite side, as was to have been expected; and that the screen erected at the south side of the field caught more than the other three combined. The borers counted on May 7, 8, 10, and 12 total nearly 71 per cent of the entire catch.

^s The screens at Wapato were examined by E. E. Cowin; those at Forest Grove by C. W. Creel, M. C. Lane, M. M. Reeher, J. M. Langston, E. J. Taylor, and the writer. The screens were designed by C. W. Creel.

TABLE 2.—Counts of clover root borers caught on a screen 24 inches wide and 50 feet high, erected April 22, 1916, at the eastern edge of a field of spring-plowed clover near Forest Grove, Oreg.

Date of count	Height (in feet) of section of screen										Total
	0 to 10		10 to 20		20 to 30		30 to 40		40 to 50		
	East side	West side	East side	West side	East side	West side	East side	West side	East side	West side	
1916											
Apr. 25.....	0	2	0	0	0	2	0	0	0	0	4
May 2.....	7	5	8	13	3	3	0	4	2	3	48
13.....	9	35	18	36	13	4	7	2	5	11	140
24.....	4	3	2	5	1	0	0	0	3	3	21
July 24.....	0	1	0	0	0	0	0	0	0	0	1
Total.....	20	46	28	54	17	9	7	6	10	17	214

TABLE 3.—Counts of clover root borers caught on a screen 18 inches wide and 50 feet high, erected May 1, 1917, at the western edge of a field of spring-plowed clover near Forest Grove, Oreg.

Date of counts	Height (in feet) of section of screen										Total
	0 to 10		10 to 20		20 to 30		30 to 40		40 to 50		
	East side	West side	East side	West side	East side	West side	East side	West side	East side	West side	
1917											
May 2.....	0	0	0	0	0	0	0	0	0	0	0
7.....	1	0	0	0	0	0	0	0	0	0	1
10.....	5	0	4	1	7	0	6	0	3	0	26
15.....	0	0	0	0	0	0	0	0	0	0	0
22.....	11	1	4	0	4	0	2	1	1	0	24
24.....	70	1	27	1	24	1	9	0	7	0	140
29.....	237	23	147	15	102	23	63	7	37	4	658
31.....	7	1	1	0	2	3	0	0	3	4	21
June 12.....	7	1	28	3	14	2	7	0	11	0	73
27.....	1	0	0	0	0	0	0	0	2	0	3
Total.....	339	27	211	20	153	29	87	8	64	8	946

A long screen 24 inches wide and 50 feet high was erected April 22, 1916, at the eastern edge of a recently plowed clover field near Forest Grove, Oreg. To facilitate the counts of borers caught at different heights above the ground the screen was divided into sections of 1 foot each, beginning at 3 feet (the height of the windlass from the ground). A count was made on April 25, only 4 borers being found, all on the west side of the screen. When next visited, April 29, it was found to have been torn down by a windstorm, and was replaced. On May 2, 13, and 24, counts were made, the total numbers found on the respective dates being 48, 140, and 21. On July 24, two months after the last of these dates, another inspection was made; only a single borer was found on the screen. The counts made on this screen, for the season of 1916, are given in greater detail in Table 2. The maximum temperatures, read at Forest Grove, approximately 2½ miles southwest of the screen, on April 24, May 1,

May 2, and May 16, respectively, were 68°, 79°, 82°, and 77° F., each being the maximum attained since the preceding examination.

The same screen, except for a reduction in width to 18 inches, was again erected on May 1, 1917, at the western edge of a recently plowed clover field in the same location as in the previous season. Counts of borers were made from May 2, when none were found, to June 12, this date included, at intervals of from 2 to 12 days; and, finally, after a further interval of 15 days, on June 27. Table 3 presents these counts in detail, in the same manner as the counts are presented in Table 2. Maximum temperatures and their dates of reading at Forest Grove were as follows, each being the maximum attained since the last previous reading: May 1, 61°; May 2, 67°; May 8, 74°; May 10, 65°; May 18, 64°; May 23, 65°; May 28, 75°; May 31, 72°; June 6 and 7, 76° F.

Of the 214 borers caught on the screens in 1916, 140, or about 65 per cent, were counted on May 13, 11 days after the last previous count. A majority of the separate counts of that date, for the opposite sides and the several sections of the screen, were more than half the corresponding totals for the season. These were probably caught on the afternoon of May 2, after the examination of the screen in the morning of that date, and on May 3, 4, and 12, when the maximum temperatures were 82°, 74°, 76°, and 67° F., respectively. The temperature did not rise above 60° F. on the other days.

Similarly, as shown in Table 3, on May 29, 1917, a date 16 days later than that of the maximum count for 1916, the total count of borers on the screen was 658, or approximately 70 per cent of the total for the season. The borers counted at that time were caught in the five days from May 24 to May 29, the maximum temperatures for each date being 60°, 57°, 64°, 71°, 75°, and 75° F., including the maxima of May 24 and May 29. Nearly every one of the separate counts for that date was a large majority, two-thirds or more, of the corresponding totals. It will be observed that the screen caught in 1917 more than four times the number of borers caught by it in 1916, and in a shorter interval of time. This may be accounted for on the theory that the borers left the plowed clover east of this screen in great numbers on the warm days of May 27, 28, and 29, 1917, after a preceding interval of cool weather. In flying most of them flew against the prevailing westerly winds. The fact that the screen in 1916 was east of plowed clover and the prevailing winds are westerly at this time may account for the fact that fewer borers were caught in that year.

As to the height to which borers fly, it is plain that numbers of them fly 40 or 50 feet above the surface of the ground. Of those caught on the 50-foot screen in 1916, approximately 13 per cent flew more than 40 feet, 19 per cent more than 30 feet, 31 per cent more than 20 feet, and 69 per cent more than 10 feet above the ground. The corresponding percentages for 1917 were 8, 18, 37, and 61; and for both seasons combined, 9, 18, 36, and 63.

Near Forest Grove, in the season of 1917, an experiment with the small bannerlike screens, 18 by 36 inches, placed one each on the north and west sides of a field of spring-plowed clover gave interesting data as to the numbers of root borers flying from this field on

certain days. As many as 497 beetles were counted on the east side of the west screen on May 31. These were caught in the period from May 24 to the date of examination. The maximum temperatures, at Forest Grove, 2 miles west, were 60°, 57°, 64°, 71°, 75°, 75°, and 68° F., on the days preceding the count. In the same season the screen illustrated in Figure 8 was erected in the sagebrush near Wapato, Wash. This screen was located at least 1¼ miles west of land under irrigation and 2 miles from the nearest clover field. On May 22 one root borer was found on this screen, indicating that this beetle had flown as far as 2 miles from the nearest clover, which was probably the only possible source from which it could have come.

The experiments with flight screens therefore indicate that root borers may fly as high as 50 feet and possibly as far as 2 miles. The large numbers caught on small screens indicate the tremendous numbers of beetles flying simultaneously on favorable days, especially from clover fields which have been plowed in the spring. A study of these flight data leads to the conclusion that the grower can, single-handed, do little to control this pest. Only by community action can control be attained.

EGG BURROWS

Shortly after the first spring flight, root borer adults are found in short new burrows in the roots of clover of the preceding year's seeding or in new mines on older roots. Burrows containing early eggs and females are found in the latter part of April and commonly in the month of May. Often two adults, male and female, are found in one egg gallery, so that it is evident that the males have lost no time in following the females to new host plants. Rarely two females are found together in one egg gallery, and in such cases the usual number of eggs in this common burrow is doubled. Unattached males are found feeding in superficial grooves and burrows on the clover crowns.

Toward the end of May or the beginning of June egg galleries, containing usually four to six eggs, are found abandoned by the adult borers. The earliest laid eggs at this time are found hatching minute, first-stage larvæ. New and apparently recently started mines are then found in considerable numbers on clover roots, and it seems safe to assume that in some cases the parent borers have changed roots or at least burrows. This assumption is strengthened by the observation that a single female in a cage placed over several clover plants formed egg mines in and infested more than one root. Sometimes four out of five roots in the cage were thus infested. Indications have been noted that possibly one or two other changes are made by some borers in the field. New burrows have been found in the last week of June and about the middle of July. Some of these, however, may be attributed to belated adults which overwintered as larvæ.

Egg galleries made in June and July are shorter than those of May, and the eggs are usually more numerous and closer together than in the earlier egg burrows. True pairs of adults are often found in these mines—in 1916 even as late as July 22. Adults, however, become fewer and fewer as the season progresses, so that by July old beetles are rarely found. Dead adults seldom are found in egg gal-

leries, but more commonly in superficial burrows in the crowns. It seems probable that many die outside the host plants when their reproductive life is ended, as the dead parent adults are rarely recovered in cages over growing plants.

The maximum number of eggs are found toward the end of May or the first week of June. Eggs become less common by June 30, uncommon in July, rare in August, and very rare in September. Davis (*9*, p. 45) reported that L. Whitney Watkins found an egg in a clover root at Manchester, Mich., on September 18, 1893. The writer found one egg (which hatched the next day) on September 27, 1918, at Forest Grove, Oreg.

LARVAL AND PUPAL DEVELOPMENT

The first newly hatched larvæ are recorded in the field in late May or early June. By the first of July many well-grown larvæ are present but they occur in greatest number after July 15.

The earliest recorded observations of pupæ were made in the field at Wooster, Ohio, on July 6, 1896 (46), and at Forest Grove, Oreg., on July 10, 1918. Pupæ do not usually occur in western Oregon until after July 15. As observed there they have not been numerous until about the middle of August, and never so numerous as other stages occurring at the same time, probably because of the brief period of this stage and the great diversity in the age and development of the larvæ. Larvæ remain in the majority until after August 15, when new adults rapidly become more numerous than the other stages. The first callow adults occur about a week after the first pupæ are observed. Occasional pupæ and newly transformed adults are observed as late as October, and more rarely in November. Soil temperatures usually are too low for development after November 15, and only larvæ and adults are observed then. A condensed summary of the seasonal history of the insect is given in Table 4, in which are listed the places and dates of observations of various life phenomena.

TABLE 4.—*Tabular summary of seasonal history of the clover root borer*

First flight of beetles	Maximum flight	Last beetles in flight	First eggs
Forest Grove, Oreg.: Apr. 16, 1915. Apr. 7, 1916. May 8, 1917. Apr. 19, 1918. Apr. 22, 1919. Apr. 26, 1920. Apr. 8, 1921.	Forest Grove, Oreg.: May 2, 1916. May 28, 1917. Wapato, Wash.: May 10, 1917.	Yamhill, Oreg.: July 14, 1915. Forest Grove, Oreg.: July 11, 1916. Silverton, Oreg.: July 13, 1917. Wapato, Wash.: June 18, 1917.	Forest Grove, Oreg.: Apr. 21, 1915. Apr. 22, 1916. Apr. 29, 1918. Apr. 27, 1921. Hagerstown, Md.: May 18, 1916. Wooster, Ohio: May 17, 1898. May 17, 1899. Michigan: June 4, 1893. May 20, 1894.
Wapato, Wash.: May 5, 1917.			
Hagerstown, Md.: Apr. 27, 1915 (?) Apr. 19, 1916 (?)			
Wooster, Ohio: Apr. 26, 1899.			
Lansing, Mich.: May 3, 1893.			
Murray, Utah: May 18, 1912.			

TABLE 4.—*Tabular summary of seasonal history of the clover root borer—Contd.*

Last eggs	First larvæ	Maximum larvæ	Larvæ less than 50 per cent
Albany, Oreg. Aug. 9, 1915.	Forest Grove, Oreg.: May 15, 1915.	Forest Grove, Oreg.: July 19, 1915.	Forest Grove, Oreg.: Aug. 26, 1915.
Forest Grove, Oreg.: July 22, 1916.	May 17, 1916 (cage). June 8, 1917 (cage).	July 18, 1916. July 25, 1917.	Aug. 28, 1916. Aug. 22, 1917.
Sept. 12, 1917.	June 3, 1919.	Hagerstown, Md.	Aug. 24, 1918.
Sept. 27, 1918.	Hagerstown, Md.: May 21, 1916 (cage).	July 22, 1916 (?). July 27, 1916 (?).	Hagerstown, Md. Aug. 25, 1916.
Hagerstown, Md.: Aug. 23, 1916.	June 8, 1916.	Murray, Utah: Aug. 12, 1911 (?).	
Manchester, Mich.: Sept. 18, 1893.	Murray, Utah: June 20, 1912.	Wooster, Ohio: July 12, 1898 (?). July 17, 1899 (?).	
	Wooster, Ohio: June 8, 1898.		
First pupæ	Maximum pupæ	First adults	
Forest Grove, Oreg.: July 19, 1915.	Forest Grove, Oreg.: Aug. 27, 1915.	Forest Grove, Oreg.: July 27, 1915.	
July 29, 1916.	Aug. 23, 1916.	Aug. 15, 1917.	
July 25, 1917.	Aug. 22, 1917.	Aug. 2, 1918.	
July 10, 1918.	Wapato, Wash.: Aug. 12, 1915.	Yamhill, Oreg.: July 24, 1916.	
Hagerstown, Md. July 22, 1915.	Hagerstown, Md.: Aug. 15, 1916.	Hagerstown, Md.: July 26, 1915.	
July 21, 1916.		July 21, 1916.	
Wooster, Ohio: July 6, 1896.		Wooster, Ohio: July 6, 1896.	
July 12, 1898.		July 17, 1899.	
July 7, 1899.			

FALL ACTIVITY

In about four days from the time of emergence from the pupal stage, the new adults become sufficiently matured to begin feeding, and they continue to feed, by enlarging the larval burrows in the roots in which they matured, until low soil temperatures limit their activity. The adults, with few exceptions, pass the winter in the roots in which they have undergone complete development. In the event of the death and desiccation of the root in summer or early fall, the adults gnaw their way out and seek living roots in which to feed and hibernate. Such forced migration may be by flight, as two root borers were taken on flight screens at Forest Grove between September 18 and October 7, 1918. Larvæ and adults may survive until spring on dead roots, provided these do not become too dry. In fact, dead, punky clover roots containing many old larval galleries are the most successful wintering quarters for the adults. Larvæ probably hibernate most successfully on roots in which there is some life.

LIFE HISTORY

OVIPOSITION

After the first mating the fertilized female burrows into a clover root of the preceding year's seeding, or a still older root. These burrows usually start on the clover crown but occasionally begin on the side of the root an inch or two below the crown. The egg galleries vary considerably in character of construction and in length. Some are simply grooves, some pass from grooves to completely inclosed galleries, some are completely inclosed galleries from the

first. They may run parallel with the longitudinal axis of the root or at right angles to it or occasionally there is a combination of both. Maternal galleries are sometimes spiral grooves almost girdling small roots. Occasionally, especially in the case of a root crowded with borers, the egg gallery runs into the center of the stem above ground and eggs are laid in the pith.

A root borer was observed starting its burrow on an exposed root in the laboratory. When first noticed it had dug in up to its mesothoracic legs, these being used to maintain a grip on the rim of the hole, while the hind legs were often waving in the air. The body was occasionally rotated in a complete circle, the head not being withdrawn from the hole.⁹ Evacuation of feces took place during the observation, and as there was only a small quantity of whitish sawdust outside the entrance, the indications were that the borer ate most of the material taken from the burrow. In about 24 hours this borer was completely within the gallery, having progressed approximately 3 mm. since the observation of the previous day. In another instance the borer advanced at about the same rate, or approximately 6 mm. in two days.

The females burrow to a depth of at least 6 mm. before starting oviposition. Oviposition was not observed, but probably proceeds as described for other scolytids; the female backs out of the gallery and then backs in to deposit her egg in a niche in the wall of the gallery which she had previously prepared for its reception (4, p. 34; 15, p. 17). After the egg is laid in its niche, the opening into the egg gallery is securely plugged with frass cemented together with a sticky material, probably secreted by the female beetle (4, p. 34). These egg pockets usually are 2 to 6 mm. apart, but sometimes are almost contiguous. Those in longitudinal mines are in the side toward the core of the root; those in a horizontal mine are usually on the upper and lower sides alternately. Those in completely inclosed galleries are often on alternate sides of the gallery. The egg galleries formed in May measure from 20 to 30 mm. in length, have four to six well-separated egg pockets, and are usually longer than those found later, in June and July. These later galleries, probably the second or later effort of the females, measure from 15 to 20 mm. long and usually their egg pockets are very close together and more numerous than in the May galleries. Sometimes as many as nine eggs are found in one short gallery. Rarely two females are found together in one egg gallery, which is longer and contains more eggs than in the case of a single female; in one such case the gallery contained two females and 12 eggs.

The construction of the egg gallery and oviposition in it are together a rather slow process. In the laboratory, under conditions of higher temperature than would prevail in the soil in the field, one female extended her mine 13 mm. and laid four eggs in 14 days. It is therefore probable that the construction of the first egg gallery occupies the female for nearly a month. This assumption is corroborated by field observations, which indicate that the second egg galleries are started about the end of May and during the first part of June.

⁹ See Blackman (4) for a good description, with figures, of a scolytid starting an egg gallery.

Males accompanying females in the egg galleries are common during the whole period of reproduction, and it is believed that the female is fertilized more than once during her reproductive period.

Only one case has been observed where eggs were laid in the walls of what appeared to be a hibernation chamber or last year's larval mine. This, a case of three eggs (two in one pocket), in pockets leading from an old central boring, was recorded at Yamhill, Oreg., May 13, 1915.

INCUBATION PERIOD

The incubation period of the eggs is apparently dependent on the temperature to which they are exposed. In determining the length of this period under northwestern conditions the writer found that his records varied to an unusual extent from those of workers in other parts of the country, as well as from those of earlier authors, both American and European. Schmitt (39, p. 394) stated "Schon nach 8 Tagen findet man die kleinen Lärchen." The American authors, Riley (37), Webster (45, 46, 47, 48), and Davis (9) apparently accepted Schmitt's egg period, as their papers on this insect contain no intimation that they attempted to ascertain the incubation period. H. L. Parker made several incubation experiments at Hagerstown, Md., placing root-borer eggs on moist blotting paper in tin salve boxes, the location of which during the incubation is not stated. The egg period under these conditions was 10 or 11 days; "eggs from burrow," May 18 to May 29; "deposited since yesterday," May 19 to May 29; and "eggs of June 8," June 8 to June 18, 1916. He recorded a large percentage of eggs as dead in from 12 to 17 days.

Incubation chambers identical, or nearly so, with those used by Parker were used in the writer's experiments, carried on at Forest Grove. Most of the salve boxes contained plaster of Paris cells, which were moistened as needed. In a few cases the eggs were left in position on a piece of clover root which was then placed on a moist blotter or in a plaster cell in a tin salve box. All of the writer's records given here refer to these types of incubation apparatus, which were placed outdoors, in the shade on the north side of a building, beside a thermograph, or on a bench in a screened insectary. The eggs used were of unknown age, dissected from roots collected in the field. With a little experience in observing such eggs, it was easy to distinguish between a fresh or recently laid egg and one laid several days previously. The records secured for eggs collected in the field soon after oviposition began may be considered approximately correct for the egg period at that season. Later records, when the freshness of eggs could not be assumed *a priori* but was necessarily estimated from their appearance, would be less reliable. On the other hand, of the same lot, the eggs taking longest to hatch under exactly identical conditions as compared with others hatching earlier are assumed to have been the freshest of the lot when the experiment was started. These records are given in Table 5, together with the mean temperatures during the period and a summation of the effective temperatures as estimated according to Pierce (35) and Sanderson and Peairs (38). The estimated zero of effective temperature is 45° F., and the approximate temperature constant is 300.

TABLE 5.—Results of experiments on incubation of eggs of the clover root borer, conducted at Forest Grove, Oreg., in 1916, 1918, and 1919

Number of eggs	Date of beginning of incubation	Date of hatching	Mean temperature	Time of incubation	Number of days above 45° F.	Effective temperature	Accumulated temperature
	1916	1916	° F.	Days		° F.	° F.
2	May 3	June 6	53.8	35	32	8.8	281.6
2	1	2	53.9	33	30	8.9	267.0
[12]	12	10	54.5	30	30	9.5	285.0
[12]	12	11	54.8	31	31	9.8	303.8
[5]	19	13(2)	55.6	26	26	10.6	275.6
[5]	19	14	56.1	27	27	11.1	299.7
15	25	14(1)	57.4	21	21	12.4	260.4
24	29	15(4)	59.2	18	18	14.2	255.6
18	June 20	July 8(3)	59.3	19	19	11.3	271.7
26	15	2	60.7	18	18	15.7	282.6
2	26	11	60.9	16	16	15.9	251.4
1	23	11	61.0	19	19	16.0	304.0
[51]	2	19	61.9	18	18	16.9	304.2
[51]	2	18	62.3	17	17	17.3	294.1
25	9	24(2)	62.3	16	16	17.3	276.8
Uncounted	1918 May 21	1918 June 10	59.4	21	21	11.4	302.4
Do	1919 June 3	1919 June 24	58.8	22	22	13.8	303.6
Do	3	25	58.9	23	23	13.9	319.7

¹ Bracketed items in the first column refer to the same lot of eggs.

² Figures in parentheses in third column indicate the number of eggs found hatched on the date named.

It appears from these records that the incubation period in the Pacific Northwest is very much longer than Schmitt (39, p. 394) noted for Germany, or than Parker recorded for Hagerstown. The records also show that this period is longest in May and considerably shorter in June. As incubation occurred in what may be assumed to have been an atmosphere of uniformly high humidity, temperature is probably the determining factor causing the difference in incubation period. It is possible that there are sufficient differences in the mean daily temperatures at this season in different localities to account for some of the recorded differences in the incubation period.

The incubation period of about 30 days in April and May as determined by laboratory methods is shown by field observations to be approximately correct for the Willamette Valley, and seems more nearly to correspond with the seasonal history as recorded in the field at other places. It is concluded from experimental evidence that the incubation period in clover roots at effective temperatures varies from 32 days in May and early in June to 16 days in June in western Oregon, and, judging provisionally from observations made elsewhere, is perhaps as short as 10 days in some localities where soil temperatures average considerably higher.

LARVÆ AND LARVAL MINES

Newly hatched clover root borer larvæ were found to be helpless, inactive creatures incapable of locomotion on a smooth surface. The leverage made possible by the small egg cell, with its opening into the egg gallery securely plugged, seemed absolutely necessary for the successful attack of the larvæ on the clover roots. The young larva

excavates a fine threadlike mine, usually at right angles to the egg gallery, for from 3 to 5 mm. At this point the larva molts for the first time and starts off again at right angles to the first part of the burrow, but usually parallel to the longitudinal axis of the root. The first several millimeters of the young larva's burrow are eaten out very cleanly, leaving as a residue only a blackish excrementitious material. As the larva increases in size its burrow often becomes sinuous, but conforms in a general way to the longitudinal axis of the root. Frequently its later extensions are nearly straight, and at this stage the tunnel often runs down the center of the root. This latter part of the burrow is closely packed with a bright brown frass in which the broken remains of the molted head capsules are found at intervals. An extensive study of such burrows indicated that these head capsules occurred approximately as follows: The first at 3 to 5 mm. from the egg niche; the second at 5 to 8 mm. from the first; the third at 7 to 10 mm. from the second; the fourth at 10 mm. from the third, or, in case of apparently only four molts, at 15 to 16 mm. from the third; the fifth at 6 to 8 mm. from the fourth.

Larval mines vary much in length, the shortest being nearly 20 mm., the longest 35 to 40 mm. long. The clean, smooth-sided pupal chamber occurs at the end of the mine, usually well down in the root, but sometimes on or near the crown. The pupa usually lies with its head toward the surface of the soil; this was believed to be invariable and is so stated by Schmitt (39, p. 395). However, a few pupæ lying head downward were found September 24, 1921, on clover roots. It is possible that the position of the pupa is reversed soon after pupation.

The actual number of larval molts is very difficult to determine, because of the difficulties met in rearing the larvæ under observation and because of the fragile nature of the lightly chitinized molted head capsules left in the larval burrows. Another difficulty encountered was that of tracing individual burrows in heavily infested clover roots, as burrows often crossed and frequently ran together, so that two larvæ were sometimes found at different parts of one burrow. Evidence secured from the examination of many larval burrows indicates that there may occur a variable number of molts, four or five, or perhaps occasionally only three. There was also so great a variation in the size of the larvæ at all stages, except perhaps the first, that it was not possible from larval measurements to assign a given larva to any instar. The measurements of the larval head capsules, as the most chitinized parts, were used for comparison. In some cases measurements immediately following the molt showed very little increase in the size of the head capsule. This fact was occasionally noted by H. L. Parker, at Hagerstown. Head capsules varied in the relative proportions of their length to their width, and it seems possible that this variation may be partly sexual, as the male adult head is relatively narrower than the head of the adult female.

The larval head capsules cast at the first molt measured as follows: Length (without mandibles), 0.30 to 0.35 mm.; pleurostoma, 0.07 mm.; width of front, 0.13 mm.; epistoma, 0.13 mm. The last molted heads taken from the pupal chambers measured as follows: In length (without mandibles), 0.55 to 0.70 mm.; pleurostoma, 0.13 to 0.14 mm.; width of front, 0.32 to 0.36 mm.; epistoma, 0.23 to 0.26 mm.

LARVAL PERIOD

The larval period varies with the conditions under which the larvæ develop, both temperature and the condition of the host root being factors of importance. The shortest larval period, contained in a tin salve box on an insectary bench, was estimated at 32 days, that is, 42 days hatching to callow adult, less 10 days pupal period, June 13 to July 25, 1917. Other individuals under similar conditions had larval periods of 39 to 65 days. When the newly hatched larvæ were placed in artificial pockets formed with a needle in young living clover roots, the openings plugged, and the plants grown in the insectary, the following larval periods were recorded in June, July, and August, 1919: 55 days minus (fresh pupa), 52 days plus (prepupal larva), 46 days plus (well-grown larva), 62 days minus (fresh pupa). These results indicate a larval period of at least 50 days under nearly natural conditions for development. Seasonal field records indicate a minimum larval period of about this length, or nearer 60 days for the Willamette Valley, more than 40 days for Hagerstown Md., in 1916, according to notes made by H. L. Parker and W. E. Pennington, and about 40 days for Wooster, Ohio, in 1898, according to notes made by Webster and C. W. Mally. Later in the season, when temperatures are lower, in cold or shaded soil, on large, healthy roots little affected by borer attack, field records show that the larval period is prolonged. Such records indicate that borers develop more rapidly on dying roots than on healthy roots. Observations in a field containing many dying and dead plants indicated that most of the root borers attained the adult stage by the middle of September, at the same time that roots in neighboring fields where most of the plants were still living contained many larvæ and pupæ.

PUPAL PERIOD

The pupal period was determined by placing naked pupæ, whose date of entering pupation was known, on a piece of moist blotter or moistened plaster of Paris in a tin salve box kept on a bench in a screened insectary. The pupal period was determined as 10 days, from August 17 to August 27, 1917. In September and early October the pupal period was often 12 to 13 days. Webster and Mally recorded a pupal period of 7 to 11 days on moist sand at Wooster, July 6 to July 13, 15, and 17, 1896, observing pupæ of unknown date taken from roots. H. L. Parker noted a pupal period of 7 or 8 days in the early part of August, 1916, at Hagerstown, Md.

Adults fresh from the pupal stage are of a pale creamy white color, and several days elapse before they become sufficiently chitinized to feed on the clover roots.

By reviewing the life history of this species, it may be observed that its development is a very extended process. Field and laboratory records indicate a total period from fresh-laid egg to adult of 60 or more days at Hagerstown, Md., and Wooster, Ohio, and at least 70 days, or even as much as 90 days or more, in the Willamette Valley in Oregon. The life history and seasonal occurrence of the clover root borer are illustrated graphically in Figure 11.

SEXUAL DEVELOPMENT

In order to obtain information as to the time of sexual maturity, rate of reproduction, and number of generations annually, studies of the genital organs (fig. 12) of the root borers were undertaken at different seasons.

Examinations of females in the fall seem to prove conclusively that there is but one generation in a season. Records of fall examinations are as follows: September 7, 1915, 10 females showed no egg development; 6 males had testes well developed. October 7, 1915, 2 males and 1 female were collected from new burrows in clover crowns in a field, a strip of which had been plowed in the summer; no eggs were found developing in the ovaries of the female. On the same date 38 males and 27 females were taken, mainly from dead roots; 4 of the females had first traces of egg formation (in one case estimated to be one-eighth grown); no others had any indication of incipient egg formation. October 7, 1918 (a warm, dry season), 3 female adults were taken from a plant collected and transplanted August 26. All of these were contained in burrows in live root tissue; only 1 female had any egg development; in this case 3 very immature eggs were contained in the ovarian tubes. October 2, 1918, of 6 females

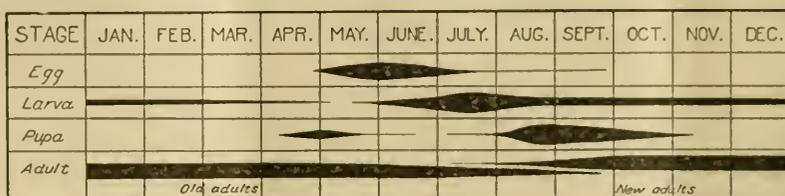


FIG. 11.—Diagram illustrating life history and seasonal occurrence of the clover root borer

taken from living roots, 3 contained no eggs, 1 contained two incipient eggs appearing as dusky spots, and 2 contained eggs barely visible in the ovaries. Of 31 male and 30 female borers collected October 7, 1918, in dead roots, and examined October 10, only 1 female had any trace of egg development, there being two very small developing eggs in the ovarian tubes. Three females were taken October 14, 1916, from roots in a cage, all of which were reared from a female introduced into the cage March 9 (almost a month before the first spring flight); none of these daughters were found to have any eggs developing in the ovarian tubes. Another female reared under the same conditions was found with an incipient egg.

Males evidently are mature in the fall, as they have been observed to mate or attempt mating when brought with females into the laboratory by the writer and by H. L. Parker, at Hagerstown, October 16, 1916, and October 6, 1915, respectively. Folsom (12) reported a pair, taken from roots in the field, in copulation in a cage in the laboratory on September 9. On October 3 he found on this plant larvæ, but no eggs, and one of the adults (sex not stated) died before November 21. The female in this case may have been a belated adult of the previous generation.

Examinations of the sexual organs of borers during the latter part of February, 1916, revealed but 2 females showing egg formation; of

these one contained an egg about one-fourth grown; the other, two immature eggs about one-eighth grown. Fifteen females, taken from roots in the field March 23, 1920, were almost without signs of egg development in the ovarian tubes. The single exception showed traces of first egg formation. Both sexes of the latter date had been feeding and evinced some development of the fat bodies. On March 28, 1916, of 6 females from roots collected in the field March 15 and stored in a root cellar, none contained eggs, but 3 had been recently fertilized, as they contained balls of sperm in the accessory sacs. In one case, May 6, 1915, a female from a hibernation chamber in an old root had no egg development.

Incipient egg formation, with rarely an egg as much as one-half grown, more frequently with eggs one-fourth grown, was usually found in females collected in flight. This state of the ovaries was the same in females swept late in the season of flight, according to records for June 3, 1916, and June 4, 1915.

A careful examination of 14 females collected in flight April 26, 1920, corroborates the former statement and, in addition, shows that only one of the 14 females was unmated. All the others had mated previous to capture in flight, most of them so recently that the accessory sac was distended with sperm and in at least one case so recently that no spermatozoa had yet reached the spermatheca, although the accessory sac was much swollen with sperm.

Examinations of the female genital organs during the oviposition period brought out the fact that eggs mature and are laid very slowly. Such examinations indicate that the ratio of developing eggs is approximately $1: \frac{1}{2}: \frac{1}{4}: \frac{1}{8}$, etc. Examinations of females in egg galleries indicate a considerable interval of time between the maturation of the eggs, except in the rare case of simultaneous development in two ovarian tubes. The interval is apparently occupied by the female in feeding, prolonging the egg gallery, and forming the cell for the reception of the egg. Observations and dissections of females in egg galleries have also indicated that there is a considerably longer interval between maturation of individual eggs at the time an egg gallery is completed. In one case a female, which was in a mine with five eggs, had no other eggs in her ovarian tubes more than one-eighth grown. It seems likely that such interruptions

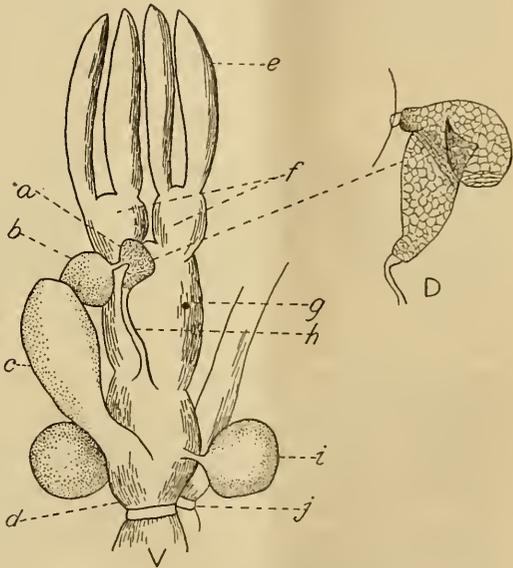


FIG. 12.—Diagrammatic drawing of sexual organs of the female. *V*, ventral side; *a*, spermatheca; *b*, spermathecal gland; *c*, accessory sac; *d*, vagina; *e*, ovarian tubes; *f*, paired oviducts; *g*, unpaired oviduct; *h*, seminal duct; *i*, cement glands; *j*, anus. *D*, Spermatheca further enlarged. Redrawn from Rockwood. Greatly enlarged

of development may occur periodically, perhaps between matings, and thus afford the female the few days necessary for preparing a new egg gallery. Such females swept late in the season in flight would have a sexual development similar to that of those on their first flight. It is a doubtful point, therefore, whether the individual makes more than one flight.

Examinations of individuals of both sexes of the parent generation indicate that some were reproducing as late as July 18, 1916, and August 13, 1920. On the latter date one male had testes still functioning and one female had been recently mated. Two females had living spermatozoa in the spermatheca, but no sperm in the accessory sac. In a cage experiment started with a male and a female March 20, 1918, the female was still alive July 25 and her ovaries were developing eggs, although visibly near depletion. It was found from a record made at Forest Grove that a male introduced into a cage April 24, 1917, still survived September 27, neither the female of the pair nor any offspring being recovered.

NUMBER OF GENERATIONS

There has been considerable difference of opinion as to the number of generations produced annually by this species. American authors are unanimous in their conclusion that there is but one generation a year. Most European authors, with the exception of Schmitt (39), have maintained that this species has two or more generations. Del Guercio (16, p. 271), the latest European writer to treat of the species, seems to conclude that there are three generations per year on *Trifolium pratense* in Tuscany, although his seasonal notes agree closely with those recorded above for Oregon, western Maryland, and Ohio.

American workers, notably Riley (37), Webster (46), and Davis (9), who have studied the species carefully, have noted that there are no well-defined periods in the seasonal development. The studies of the writer, the results of which are here given under the heads of sexual development, seasonal history, and life history, seem to afford the explanation of this fact. Records of other workers have afforded confirmatory evidence.

All the evidence based on the facts observed in the development of the clover root borer tends to show that there is but one generation in a year, or even that a single generation overlaps the year. The female already noted, which had in all probability matured the previous August or September, was alive in a breeding cage and reproducing on July 25 following. There is also the case of the male previously mentioned which survived in a cage from April 24 to September 27. It is safe to assume that one of these individuals passed an adult life of almost a year. The male may have been produced in April from an overwintered larva, but even in that case it must have belonged to the parent generation, the offspring of the previous season. Adults of the parent generation have also been recorded as alive and reproducing as late as August 13.

Eggs of the clover root borer have been found in clover roots in the field as late as August, and once on September 27. In the latter case the egg hatched the next day and must have been at least

20 days old. It is possible that oviposition in this case may have been done by a precocious individual of the new generation, but no evidence appears to indicate that such early sexual development takes place; whereas there is evidence that an adult, the mature form of an overwintered larva, might lay an egg on that date. As adults produced at the normal time (August or September) are known to have an active reproductive period of at least three months, in addition to the active feeding period of several months in fall and early spring (making an adult life of about 10 months, of which perhaps 5 are active), adults produced in May from overwintered larvæ would almost certainly, barring accidents, be alive and reproducing about the beginning of September. As the period of development from newly-laid egg to adult is about two and a half months in spring and summer, larvæ hatched from eggs laid in the late summer and fall are not able to complete their development before winter causes a cessation of activity. Some of the offspring of these belated individuals tend to be belated also. This is a plausible explanation of the frequent occurrence of hibernating larvæ, and rather conclusive evidence that there is but one generation a year on red clover in America. Evidence in support of this theory is afforded by Parker's notes at Hagerstown, Md. Parker took adults from clover roots on August 25, 1916, and placed them on clover roots in tin boxes. These individuals had laid no eggs by September 29. In another case he confined early adults of the new generation on clover all summer, but obtained no eggs in the fall.

RATE OF REPRODUCTION

As already noted, the female beetles mature eggs slowly, and but few eggs are laid in the first egg galleries during a period of three to four weeks in May, when the soil temperatures range low. There is evidence that the female changes her egg gallery two or three times during the reproductive period, thus occasioning delay or diminution of egg production.

Experiments to determine the total progeny of one pair of borers were conducted at Forest Grove, Oreg., using cages of three types: (1) Flower-pot cages containing one or two clover plants and covered with a lantern globe; (2) cylindrical wire-mesh cages buried in the ground, planted with one, two, or three clover plants, and covered with a lantern globe; and (3) wire-screen cages 3 by 3 by 3 feet in size, lined with cheesecloth and placed directly over five young transplanted clover plants growing in the soil. Clover plants were collected from fields sown the previous spring, gathered before March 15, and apparently free from infestation. Cages were started before the first flight of borers, except in 1920, when the experiments began coincident with the first flight. Each cage contained a single pair of borers.

The flower-pot cages dried out very rapidly in midsummer, undoubtedly thereby shortening the life of the adults. The borers were also too closely restricted, a pair having but one or two roots to work on. The total progeny of one pair recovered from each of six cages of this type in one season was 6, 6, 3, 8, 8, and 26, respectively.

The wire-mesh cages sunk in the ground more nearly approached natural conditions, but the borers were again in some cases restricted

to too few roots. The total progeny of one pair in each case recovered from 12 cages of this type was, in cages containing one root, 13, 14, 9, 16, and 9, in the season of 1917; in those containing two roots, 13, 16, and 15 in the same season; in those containing three roots, 4, 21, 14, and 21, in the season of 1918. For all cages of this type the average progeny of a single pair is 13.75.

The square screen cages placed on the ground over five clover plants furnished practically optimum conditions for reproduction. Unfortunately, however, these cages allowed access to other borers from below, in case any had wintered over on the spot of ground selected for a cage. As it was discovered that a control cage supposedly kept free from root borers contained infested roots, some of the records for this type of cage were disregarded. However, one cage of this type was examined early enough (July 25, 1918), to be certain that only the one female had had access to the roots. In this case a pair of borers in copulation had been introduced into a cage on March 20; when the cage was examined July 25, 19 larvæ in all stages, 2 pupæ, and the living female parent were recovered on four of the five roots. The beetle, when dissected, contained 1 half-grown and 3 immature eggs in shrunken, depleted ovaries. She therefore showed an actual progeny of 21, or an estimated possible progeny of 25. In 1920 particular care was taken to bar out of the cages all root borers other than those intentionally introduced. In one of these experiments a cage which contained a verified pair of borers, placed in it May 3, contained, when examined August 11, 4 pupæ and 4 larvæ on one root, or a total progeny of 8. Another true pair, placed in another cage May 6, yielded 4 pupæ and 5 larvæ on August 11, or a total progeny of 9. Three similar attempts with single females swept in flight failed to produce young.

From a survey of the conditions attending these experiments, it is believed that the most reliable information as to the rate of reproduction results from the use of the cylindrical wire-mesh cages containing three clover plants, in soil known to be free from infestation. In each of two cases in 1918 the maximum progeny thus obtained was 21. A reliable result is also thought to have been reached with the cubical wire-screen cage examined before the death of the parent female, in which were found actual progeny numbering 21, or estimated possible progeny of 25. In all experiments the borers were protected from natural enemies and were on clover plants in partially shaded ground, the cages being covered with cheesecloth. These conditions were believed to be more favorable to root borer activities than would be the case in plants in soil under natural conditions. It is therefore deduced that the total progeny of one female in nature rarely exceeds 25 in number, and probably averages considerably fewer than that.

It may therefore be concluded from the foregoing data on the reproductive activities, life history, and seasonal history of this insect that it is a slow and by no means prolific breeder, and that if some of the existing agronomic practices, together with its protected mode of life, were not favorable to its undisturbed increase, it would not be a widespread, destructive pest.

ECOLOGY

TEMPERATURE

Many of the data that have been given indicate that the activities of this insect are greatly influenced by temperature. This factor controls the activities and migration of the borers in the spring. At this time migration from old to new clover fields is determined by the temperatures of the soil and air. The dates on which these migrations occur vary not only from one season to another but also from field to field, as borers leave clover roots in cold, wet, poorly drained spots several days or even weeks later than flights of borers from clover on warmer soil. Soil temperatures during the period of development determine the time consumed in the completion of that development. Field observations indicate that on clover in shaded places, such as orchards, where the soil temperatures doubtless are lower than in the open fields, the development of root borers is so much delayed that an unusual number of overwintered larvæ are found in such places in the spring. Unpublished notes made by E. J. Vosler at Murray, Utah, in 1912, record an unusually large number of overwintered larvæ, and indicate that the period of development is affected by low soil temperatures, owing to the short season at high altitudes, or perhaps to the cooling effects of soil moistened by irrigation. The comparatively low temperatures of the heavy clay-loam soils near Forest Grove, Oreg., in the spring and early summer appear to prolong the development of the insect to an appreciable extent as compared with the conditions in the spring and early summer in Ohio and western Maryland.

MOISTURE

Moisture is also an important factor in the life of the species, both directly and in its secondary effects on soil temperature (26, p. 220) and the condition of the host plant. Clover root borers in any stage are very susceptible to injury by dryness; even the well-matured adults survive but two or three days in a dry vial. All stages, even adults, if they are unable to escape, are killed by the rapid drying of the host roots. If the roots dry slowly, as in the case of undisturbed roots dying in early summer, adults that are sufficiently hardened to gnaw their way out hasten to escape and find moist living roots. A lack of moisture in the soil affects the root borers indirectly through its effect on the host plant and the soil temperature. In spite of the unfavorable effect of dryness on the species, however, it has often been noted by workers that in a dry summer the root borers are more injurious to clover. As will be shown, the borers thrive best on weakened plants, such as result from droughts; not only is the moisture insufficient for the natural growth of the plants, but the accelerated development of the borers enables them to inflict all the more damage.

CONDITION OF HOST PLANT

The condition of the host plant is of course of great importance in the life history of the insect. Although there is little evidence to support the theory advanced by Schmitt (39) and others that weak-

ened or dying plants are the preferred food of the clover root borer, there is evidence that development is most rapid and secure on the roots of clover plants which have received a check to their vegetative activity. This fact was also noted by Riley (37), who stated that the root borer "flourishes most in the roots of plants that have been injured and that have already begun to decay." Such a vegetative check usually occurs naturally in most clover regions in July and August, when the second crop of clover has matured its foliage and is producing seed. Summer droughts also check the vegetative growth and thereby accelerate the development of the root borers. An artificial or mechanical check to vegetative growth is produced by the simultaneous attack of several root borers, whose combined burrows seriously interfere with the functions of the root. Checks to vegetative growth may also be occasioned by disease or by the attacks of other insects and may sometimes be due to a failure of the soil to produce the elements required for continuous growth of the plant.

Hibernation has frequently been noted to be more successful on very much weakened roots or roots which have died late in the season and are more or less decayed than on roots still in a healthy condition. An indication of the disadvantage to the root borers of a healthy growing root as a place of hibernation was observed on October 4, 1917. In this case three root borers were found dead in their pupal cells and crushed out of shape. This fatality apparently was due to the partial closing up of the cells caused by the growth of the root before the adults were sufficiently hardened to enlarge the chambers.

Data showing the effect of a continuous vegetative period on the clover root borer were obtained in observations made on the bottom lands along the sloughs of Coos River and in the Coquille Valley, Oreg. Under conditions occurring there, clover grows very rapidly and probably almost continuously, because the winter temperatures are mild (42°), the climate humid, and the soil rich and well supplied with moisture by a natural subirrigation as well as by considerable precipitation (42°). Root borers are very scarce in this clover on the bottom lands, even in the second and third years. Yet, on the poorer hill soils in the same region, which are not naturally subirrigated, the borers are as bad on first- and second- crop-year clover as anywhere in the Willamette Valley.

TOPOGRAPHY

The distribution of the clover root borers and the damage done by them are often influenced by the topography of the region in which they occur. Low, wet, poorly drained soils, which remain cold late into the spring, retard the development of the root borers and encourage fungous diseases; but higher, warmer land may accelerate their development over much of the surrounding country.

It has been observed that small farming communities isolated from the surrounding cultivated country by woods or wooded hills are often very severely infested. Often the portion of a field along the windward side of a grove is more severely infested than the rest of the field. A case was observed where a field about one-fourth of a mile from an old field that had been plowed in spring, with open country between the two, was very severely damaged by July. On the contrary, a second field, about as near the source of infestation as the

first and in approximately the same direction from it, but with a small wooded area between, showed at the same time no serious damage. These observations may be explained by the fact that the greater number of root borers appear to fly below a height of 30 feet, and thus the wooded country encountered acts as a barrier and causes them to gather in indentations on the edges of the woods, or turns them back into the clover fields on the windward side. This assumption is borne out by accumulated flight records and records of collections of beetles taken in flight along the windward margin of woodland areas. Advantage might be taken of this barrier effect to ward off root borer injury in farming communities that are isolated by surrounding woodlands from other farming communities.

OTHER HOST PLANTS

Common red clover, *Trifolium pratense*, and mammoth clover, *T. medium*, are the preferred host plants of the clover root borer. Alsike clover is attacked and may be severely injured, especially in sections where recent changes have been made from red clover to alsike in the general cropping practice. The roots of alsike do not appear so well adapted as a nidus for the root borer as are those of red clover, probably because of their more sappy, tender texture. That alsike is not an altogether suitable host is indicated by the fact that adults which had been killed by a fungus before penetrating very far in alsike roots were commonly observed at Forest Grove in 1921.

Clover root borer adults have been observed attacking alfalfa and sweet clover plants in the Yakima Valley, Wash. They were found, two or three to a root, in superficial burrows in the crowns of these plants, which were growing in an orchard where the clover had been practically all killed by the root borers. Adults were found dead of fungous disease in such superficial burrows on sweet clover crowns. These observations were made on May 22; on a later visit, C. W. Creel was unable to find living root borers in any stage on these plants. The indications in this case were that the root borers had been forced by hunger to attack alfalfa and sweet clover roots, finding no other food in the immediate vicinity, and had not been successful in reproducing on these plants. The roots in this case were of large size. It is possible that the borers might have been more successful on younger, smaller plants, as Gibson (13) stated that in Ontario "In some fields of alfalfa this borer was working freely, causing noticeable loss. In one field examined 31st July, two adult beetles were found in a root which had been tunneled by the larvæ." Folsom (12, p. 114) also stated that the root borer feeds on alfalfa, "but not enough to have done any damage up to the present time."

Schmitt (39, p. 392-393) stated that he did not observe clover root borers on *Medicago sativa* and *Hedysarum onobrychis* (*Onobrychis visiaefolia*) near Mainz. Kaltenbach (25, p. 121) included *Medicago sativa* among the plants whose roots are attacked by this species, and Vassiliev (43) listed this insect as a pest of lucerne in Russia. Del Guercio (16, p. 264) stated that alfalfa is not known to have been attacked by it in Tuscany.

There is a large acreage of alfalfa in the Yakima Valley, Wash., in the vicinity of clover fields severely infested by root borers, but no evidence of infestation by root borers has yet been found in these

alfalfa fields. Fields of alfalfa in the Willamette Valley have frequently been examined, but no root borers have been found there on alfalfa roots, even when they were close to badly infested clover roots. At Murray, Utah, repeated examination of large numbers of alfalfa roots, even in badly infested clover fields, by T. H. Parks, E. J. Vosler, and P. H. Hertzog, resulted in the discovery August 23, 1911, by Hertzog, of but one pupa of a clover root borer on an alfalfa root. H. L. Parker tried unsuccessfully to transfer the larvae from clover to alfalfa roots at Hagerstown, Md. It seems improbable that the clover root borer will become a serious pest of alfalfa, as the rapidly growing, tough roots of alfalfa do not appear well adapted to the successful propagation of the species.

Adult root borers were found by C. W. Creel attacking a field of common vetch near Junction City, Oreg., May 24, 1918. Two out of ten roots examined were infested and some roots were almost girdled by the burrows of the adults. There were no signs of immature stages, and the vetch roots probably would not be sufficiently large to serve as a breeding place for root borers.

Root borer adults were found in burrows in the crowns of *Lupinus* sp. near Albany, Oreg., on May 29, 1919. The burrows were superficial and more in the stems than in the roots.

F. M. Webster noted an attack by clover root borers in pea vines at Wooster, Ohio, June 30, 1892. In this case the burrows were in the stems, near the ground. A. L. Lovett, of the Oregon Agricultural College, reported¹⁰ that commercial plantings of garden peas over a limited area in Marion County, Oreg., were damaged by clover root borers to the extent of 60 per cent of the crop on June 2, 1922. Professor Lovett noted that these plantings were adjacent to fields of old, abandoned clover heavily infested by root borers.

On April 4, 1922, at Forest Grove, Max M. Reeher found a plant of Scotch broom, *Cytisus scoparius*, with a stem about one inch in diameter and turning yellowish on the terminal twigs, which contained a typical bark-beetle burrow in the soft wood under the green bark. This mine was some distance up the stem, but below any branches. The gallery was two-armed, the branches extending in opposite directions from the entrance. This burrow was much discolored and must have been formed some time in the previous season, and perhaps represented a true hibernation burrow (22, p. 203), as there were no signs of reproductive activity. The bark beetle was accidentally mutilated with a knife, only a part of the thorax, the legs, and the head being recovered. These parts had all the characters of *Hylastinus*, and after careful comparison of legs and antennæ mounted in balsam, the specimen was determined by the writer as *Hylastinus obscurus*. Scotch broom from the same locality and elsewhere has been examined several times since this discovery, but without finding any other borers or signs of their work. Furze, *Ulex europæus*, has also been examined near Portland, Oreg., and Seattle, Wash., but no *Hylastinus* has been found upon this plant.

Swaine (41, p. 73) recorded the occurrence of this species on "White Dutch clover, and sainfoin (cutting tunnels but not breeding) in Canada." Bedel (2), Nördlinger (33, p. 234) and Chapman (6) recorded *Hylastinus obscurus* as a stem miner on (*Spartium*) *Cytisus scoparius*;

¹⁰ In correspondence, published by Professor Lovett's permission.

Chapman (6) on *Ulex europaeus*; Cecconi (5, p. 160) on *Cytisus alpinus*; and del Guercio (16, p. 264) on *Cytisus laburnam*. Bedel (2) found it also on an old, woody root of *Ononis natrix*, exposed on the side of a bank. Some of the records on *Cytisus* may refer to *Hylastinus fankhauseri* Reitter (36, p. 280) rather than *H. obscurus*, but are retained here for reasons stated on page 3.

DAMAGE

FIRST CROP YEAR

The earliest injury to new clover (first crop, seeded the previous year) is observed in the spring a week or two after the time of the first migratory flight. The females at this time are busily engaged in making the first egg galleries, and the males are feeding, usually in grooves on the crowns. The simultaneous attack of five or six root borers on one small root often girdles it, causing wilting and early death of the plant. This injury first appears late in April or in May.

A fungous disease, caused by *Sclerotinia trifoliorum* Erik. (14), is prevalent at this season, and in the Pacific Northwest for several months preceding, and may easily be mistaken for this injury. Injury caused by this fungus differs from root-borer injury in that the several stems of the diseased clover plant usually wilt at different times. Often a few stalks of the plant remain normal, while infected stalks are stunted and killed back to the crown. In the case of injury by root borers all the stems of the plant usually wilt at the same time. An examination of plants affected by the fungus will also show discoloration of the stems and often, on dead stalks, a thin whitish fungous growth.

In new clover no further injury is usually noted until haying time, when, in case of severely attacked fields, many plants are broken off at the crowns by the mower. This is often the first injury observed. Toward the end of July, when the new second growth is well up, a severely infested field shows many sickly and dead plants and the seed of ripe heads is often withered and light. In one case observed a 5-acre field of clover in its first crop year had been destroyed by the end of July, 1914. Early the next spring the ground was bare except for weeds and the dried dead stems of the second hay crop, which had not been worth cutting. At this time the clover roots in this field had been almost completely consumed by the borers; the dried stems had fallen or were sticking out of the ground, attached to small pieces of clover crowns which the hordes of borers were rapidly consuming. This severe and unusual damage was attributed to the fact that a 40-acre field of old clover about one-quarter of a mile away had been plowed in April, 1914, and borers leaving this field in large numbers had migrated and concentrated on this small field with fatal results. A similar case was noted by Davis (9, p. 47) in July, 1893, the clover being of the mammoth variety. Cases of complete destruction of a clover stand have also been reported from the States of Indiana, Ohio, and New York. Severe injury to red clover in the first crop year is likely to occur whenever near-by fields of old clover are plowed in the spring.

Usually, however, the injury to young clover consists of a gradual dying of the plants during July, August, and September. The plants that are most severely infested and die first (in July) set light and

withered seed, but plants killed later in the summer may have set good seed. This injury late in summer and in the fall is due to the feeding of the rapidly maturing larvæ and the young adults (fig. 13). Injury is greatly enhanced by drought, and the extent and severity of the injury often seem directly related to the fertility, or at least the physical state, of the soil.



FIG. 13.—Red clover roots, showing root borers and injury caused by them

All the plants on four separate areas taken at random in a field at each of several places in Washington County, Oreg., the four areas in each field amounting in all to one ten-thousandth of an acre, were dug up, taken to the laboratory, and carefully examined to determine the extent of the damage done to them by clover root borers. The results are presented in Table 6. The record indicates considerable diversity in thickness of stand and brings out the more severe injury to clover on the poorer soil of the first field noted. Where clover fields are left for a second crop, the table indicates that the stand is, under the most favorable conditions, reduced approximately 50 per cent by the second season. When there is a good stand originally, a fair crop of hay may be obtained in the second season, and in a favorable season some seed may be harvested.

TABLE 6.—Extent of damage done by clover root borers in selected areas in Washington County, Oreg.

COUNTS ON CLOVER OF FIRST CROP YEAR, ONE TEN-THOUSANDTH OF AN ACRE

Date collected	Number of plants	Condition of plants						Soil type ¹
		Uninfested	Infested	Alive and strong	Weak	Dead	Place	
1921								
Sept. 27----	36	0	36	6	17	13	Verboort----	Amity silt loam, undrained.
Sept. 26----	62	17	45	16	16	13	Hillsboro ...	Amity silt loam, tiledrained.
Sept. 29----	45	11	34	11	10	13	Forest Grove	Chehalis silt loam.

COUNTS ON CLOVER OF SECOND CROP YEAR, ONE TEN-THOUSANDTH OF AN ACRE

Sept. 24----	53	0	53	5	25	23	Forest Grove	Melbourne loam.
Sept. 27----	37	0	37	7	15	15	----do-----	Chehalis silt loam.

¹ Soil Survey of Washington County, Oreg., by E. B. Watson, in charge, and E. C. Eckman, of the United States Department of Agriculture, and A. L. Fluharty and C. V. Ruzek, of the Oregon Agricultural Experiment Station. Bureau of Soils, Washington, 1923.

SECOND CROP YEAR

The count indicates that, under severe infestation, unless the field is self-seeded there will be practically no clover left at the end of the second crop year. In the second crop year the clover is sometimes killed out after the hay crop is harvested, no further cutting for hay or seed being possible.

It has been the general practice in the Pacific Northwest, and is still so to some extent, to maintain clover fields for two crop years, and often for three (23), occasionally even for four, without plowing or reseeding. This probably was practicable in the early days, because of the scarcity of destructive clover insects and the continued self-seeding which replaced plants killed by animals, insects, and disease. However, land costs at present are so high as to lead progressive growers to keep their land as nearly as possible at maximum production. In the Willamette Valley the clover root borer is largely responsible for the fact that as a general rule more than one crop year of clover is no longer profitable.

The number of borers necessary to kill a root is not easy to determine, as many other factors are involved, such as the age of the clover, soil conditions, rainfall at critical periods, and attacks of other insects and fungous diseases. As many as 45 borers in various stages have been found on a single root, and 25 to 30 on a root are commonly observed in the severely infested field. Sixty-three borers of the new generation, 56 of them mature, in a cage where they had developed from eggs on the roots, killed 3 out of 5 roots by August 23; the 2 other roots were alive, 1 being uninfested. In another case 47 borers infested 3 out of 5 roots, and all roots were alive on August 23; only 1 root showed serious injury. In still another case 57 borers infested 2 out of 5 roots, and on August 26 1 of the 2 roots was still alive and looked fairly healthy with 26 young adults on it; but the root was so severely injured that it would probably have died before winter.

INJURY TO SEEDLING CLOVER

It has been commonly stated by entomologists and others that clover roots of less than a year's growth are not attacked by root borers. A field near Lebanon, Oreg., was seeded in April, 1915, to red clover, with a thin stand of oats as a nurse crop. When observed August 10, following, the clover had been noticeably damaged by clover root borers. The clover plants at that time were 12 to 14 inches high, and blossoming. The roots were less than one-fourth of an inch in diameter at the crowns. One larva, almost mature, was seen, indicating that development would be successful on some of these roots. An old clover field located across the road had been plowed in March. These two fields were in a long, narrow valley, bounded by wooded hills and crossed at intervals by small groves of trees, and the nearest other clover field was distant a mile up the valley. Root borers apparently had been forced to attack the young clover when the old roots of the plowed field dried out and the roadside clover in the vicinity had been killed. In another case 1 root in 20 was found infested by root borers June 10, 1918, in a field seeded in November, 1917. Young seedlings in old fields are not uncommonly attacked by adult root borers.

NATURAL ENEMIES

Very few natural enemies of the clover root borer are recorded in literature. Riley (37) recorded a soldier beetle larva, probably (*Telephorus*) (*Cantharis bilineatus* Say, as predacious on the clover root borer. H. L. Parker has reared the soldier beetle, *Chauiognathus pennsylvanicus* DeG.¹¹ from "black velvety" larvæ which ate root borer larvæ. Adults were reared from "white slender naked pupæ slightly over one-half inch long" on November 18, 1914, and April 27, 1915.

In the Pacific Northwest the only natural enemy observed to attack the borers in the roots and on the ground was a fungous disease caused by the well-known entomogenous fungus (*Sporotrichum*) *Beauveria globulifera* Speg., as determined by the writer. This fungus attacks many ground-frequenting insects, whose spore-covered bodies are commonly found in clover fields. Root-borer adults are exposed to infection while above ground, moving from root to root, mating, and starting burrows. They are less likely to become infected while in mines in the root. This disease is most prevalent in the fall and spring, and any reduction in the number of root borers at this time, prior to the breeding period, is of economic importance. Larvæ and pupæ in mines in the roots are occasionally attacked by the same fungous disease. It appears to be very prevalent on low, wet, poorly drained land, and there are also indications that root borers on less-favored host plants are especially susceptible to the infection. The disease is certainly parasitic, as the cylindrical conidia and short sections of hyphæ have been found in the blood of living borers.

An attempt was made in April and May, 1920, to find bird enemies of the clover root borer at Forest Grove. Only those birds were killed, 53 in all and of 22 species, which were found near clover fields on days when it was known that the root borers were migrating by flight. On examination of their stomachs, 39 root borers were found

¹¹ Determined by J. A. Hyslop.

in the contents of 12 of them, representing 8 species of birds.¹² The 8 species, the number of each sex, if determined, and the number of root borers, if any, found in each stomach, are set forth in Table 7.

TABLE 7.—Species and sex of birds in the stomachs of which root borers were found, with the number of borers in each stomach

Species	Number of each sex			Root borers in each stomach
	Male	Female	Doubtful	
Streaked horned lark, <i>Otocoris alpestris strigata</i> Hensh.	1	—	—	1
Brewer blackbird, <i>Scalcocephalus cyanocephalus</i> Wagl.	3	1	—	0, 0, 0, 0, 1, 0, 0
Oregon vesper sparrow, <i>Pooecetes gramineus affinis</i> Miller.	5	1	—	0, 0, 0, 3, 0, 0
Townsend sparrow, <i>Passerella iliaca unalaschcensis</i> Gmel.	—	2	—	1, 0
Golden-crowned sparrow, <i>Zonotrichia coronata</i> Pall.	—	—	2	0, 1
Cliff swallow, <i>Petrochelidon lunifrons</i> Say.	3	1	1	13, 4, 0, 0, 1
Northern violet-green swallow, <i>Tachycineta thalassina lepida</i> Mearns.	2	1	—	1, 2, 0
Pacific house wren, <i>Troglodytes aedon parkmanni</i> Aud.	1	—	—	2

CONTROL

The mode of life of the clover root borers, which for most of their comparatively long lives are confined to the interior of the host roots, spending but a short time above ground, renders extremely difficult the application of any immediately effective control measures. The statement of Hopkins (21, p. 31) referring to the futility and needlessness of efforts at complete extermination of the bark beetles of the genus *Dendroctonus* seems applicable also to the clover root borer. Repressive measures tending to reduce the numbers of this insect pest seem to be sufficient to reduce its injury to a negligible minimum. The ability of the adult borers to migrate considerable distances at the time of the spring flight indicates that, to be appreciably effective, any effort at control must be initiated on a community or regional basis and may involve a change in customary farm practice. The one hopeful fact brought out by the investigation is that the species is a comparatively slow breeder, and this indicates that continued repressive measures should have a cumulative effect and eventually should result in freeing a severely infested clover section from serious root-borer injury. Field observations, in various regions differing widely in farm practice, bear out this conclusion. Data bearing on possible control measures have been collected from experiments performed, and from field observations on the results of different methods of farm practice in various parts of the Willamette Valley.

CONTROL EXPERIMENTS

1. To test the effect of heat and drying on clover root borers, roots were dug from a field on August 22, 1916, and some of them placed on the surface of the ground and some lightly buried (to a depth of about one-half inch) in a spaded plot. Eighty per cent of the borers were in the pupal and prepupal stages. The temperature rose as high as 98° F. in the shade. Two days later the roots were very dry and hard, and all stages of the borers were dead, except that one fully hardened adult escaped to the outside of a root.

¹² Skins determined by W. A. Shaw, of Washington State College, Pullman.

2. A strip in a badly infested clover field in its second crop year was plowed 8 inches deep and disked six times on August 28, 1917. Borers in all stages were present, approximately 20 per cent of them being new, soft adults; only one fully hardened adult was seen. The ground was very dry and hard, and plowed in large clods very difficult to work up. Flight screens were erected to determine if the borers flew from the plot. On September 5 all the borers, even adults near the outside of the roots, were dead in the dry, hard roots lying on the surface of the ground, or covered by an inch or less of dry soil; some exit holes, however, indicated the escape of a few root borers. Deeply buried roots were still moist, and contained living root borers in larval, pupal, and adult stages. On September 15 a count on several roots collected from the surface and beneath it to a depth of 2 inches showed 70 per cent dead. Living larvæ, pupæ, and adults were usually on roots which were partly rotten, soft, and punky. On November 8, living adults were found on two roots buried 4 to 5 inches deep. Some time between September 15 and November 8 screens caught two borers flying from this plot. The maximum temperature during the first 10 days following the plowing of this plot was 86° F. Precipitation began on September 6.

3. A small field seeded in May, 1916, was plowed and harrowed with a spring-tooth harrow on August 2, 1918. The ground was very dry and hard and worked up many hard clods. The spring-tooth harrow worked fairly well in raking the roots to the surface, with the exception of those deeply buried. The cultivation was as good as the average farmer could accomplish at this season. Ten roots were found to contain 70.5 per cent of larvæ, 20.8 per cent of pupæ, and 8.7 per cent of adults, there being in all 149 borers.

On August 10, 50 per cent of the borers in 10 roots gathered from the surface were still alive. The roots were dry and hard on the outside, but the interiors usually were not yet hard. The weather had been cloudy, with light precipitation since the plowing.

On August 20, 10 roots collected from the surface contained 47 dead larvæ, 12 dead adults, and 1 living larva, or 98.3 per cent of all were dead. Since the last examination the temperature had reached 90° F. on one day.

On October 7 several buried roots were examined, most of them being dried up, with no living borers. Live adults were found on two roots which were badly decayed, and therefore soft.

On March 29, 1919, a few adults were swept from this plot, more than three weeks before the time of their normal flight; many were coated with mud from the hard treatment they had received. On July 23, a dead adult was found in a groove eaten into a wheat stem. Evidently the insect had been driven to abnormal activity by the plowing of the clover.

Webster (46) performed a similar experiment at Wooster, Ohio, in 1899. In this case the plot was plowed on July 8, about nine days before the first occurrence of pupæ in the field. On August 10, living larvæ and pupæ were found on roots buried from 3 to 5 inches below the surface. On October 19, a rather thorough examination of the plot resulted in the finding of only four living beetles on buried clover roots.

FIELD OBSERVATIONS

Observations were made on clover fields plowed in December, January, February, and March in various parts of the Willamette Valley. In all these cases root borers were found alive on buried roots up to the time of the spring flight, and in some cases there was only a small percentage of mortality among the beetles in roots not buried by the plow. In April and May great numbers of beetles were observed migrating from some of these fields.

A field of old clover on creek-bottom land was plowed August 31, 1920. Rainy weather began September 1, and there was an unusual amount of precipitation throughout the late summer, fall, and winter. On February 26, 1921, a few living root borers were found on roots fully exposed on the surface of the ground. Many dead borers were also found, a large proportion of them showing a fungous growth.

A field which had been seeded in June, 1914, was turned under for green manure, without harrowing, about June 4, 1915. Most of the roots were completely upended and buried, except for their tips. On June 26 the roots were still infested by borers, there being present adults, larvæ, and eggs. Several adults were found which had been killed by fungus. Ten months after plowing, on April 4, 1916, living adults, which must have matured from eggs laid on the turned-under clover roots, were found on the moist, rotting crowns of buried roots, although many of the clover roots had completely rotted away.

Part of a field was plowed and harrowed in late June or early July, 1915. On August 13, the roots on the surface of the ground were hard and dry and on them were many dead borers, but none living. On October 7 no living borers in any form were found on the roots. Remains of larvæ and pupæ were found dried up in their mines, and new adults were found dead and imprisoned in groups in the centers of the dried roots, which were so hard as to turn the edge of a knife. Now and then a beetle had died after forming an opening to the exterior, but one not large enough to permit emergence. The roots had dried so rapidly that the beetles were unable to gnaw their way out before death overtook them.

A study of these data indicates that where clover sod is plowed and the roots harrowed out in the period between June 15 and August 1, a large percentage of the borers are killed, provided the weather is hot and dry after the plowing. Borers on roots that are deeply buried by this treatment often survive, so that complete extermination in a field is rarely if ever possible. No experiments were performed in an irrigated region, but the writer is convinced that summer plowing of clover and subsequent withholding of irrigation water would be very effective under irrigation conditions.

The data presented also show that the percentage of mortality among the borers is increased by plowing in late summer and early fall, because of the exposure of the borers to an unfavorable environment on the plowed-up roots. A disturbance of the normal activities of the clover root borers in the fall and early spring also results from this treatment, and undoubtedly interferes with the propagation of the pest in the following season. Unsuccessful attempts to secure offspring in cages started too early in 1919 (three weeks before the

first flight) showed that root borers, even when partially protected in a cheesecloth cage, are adversely affected above ground by rigorous weather in early spring. Considering the normally low rate of reproduction in this species, it is probable that a regular practice of early fall plowing in badly infested localities would progressively diminish the amount of infestation and eventually reduce the numbers of the pest to such an extent that little damage would occur to clover in the first crop year. Fall plowing would probably be especially effective in an irrigated region where the winter rainfall is light.

The data show that late fall or winter plowing has little effect as a control measure for the clover root borer. They also show and field observations very strongly emphasize, as Webster (46) and Davis (9, p. 46) have noted, that spring plowing of clover is absolutely ineffective in the control of the species, and may be a most harmful practice in the case of heavily infested fields. Such spring plowing causes the mature adults to leave the field almost simultaneously,



FIG. 14.—View of second-year clover field, showing weedy places where clover has been killed out by the root borer.

and they may afterwards settle on any new clover in the vicinity in such numbers that the simultaneous attack of many borers will very seriously injure or utterly destroy it early in the season.

The practice of green manuring, at least under conditions prevailing in western Oregon, is shown to have little restraining effect on the clover root borer. Some of the insects are able to mature, even from eggs on clover roots which have been turned under. The only practicable way of killing root borers is by the drying and hardening of the roots; and in western Oregon this is possible only by harrowing out the roots in the summer or early in the fall of a dry season.

In some localities in western Oregon where the ranchers still attempt to follow the practice of maintaining clover fields for three or more years, root borers have for some time been extremely destructive. In other localities, where a one-crop system of clover culture is practiced, the insect has been appreciably reduced in numbers and no

longer occasions serious loss. The writer, after studying this problem in all its phases, is convinced that the early practice of allowing clover to stand over a considerable period is responsible for the tremendous increase of the insects in recent years in western Oregon (fig. 14). This opinion seems to gain some support from the apparent reduction in numbers of these insects since the reduction in the acreage of clover and the adoption of a short clover rotation, both brought about in many localities by war-time conditions.

A farm practice (23, p. 5) that has proved very successful in parts of Yamhill County, Oreg., especially on the lighter soils, is the seeding of clover either alone or with rape, in May or June, on well-prepared ground, and the subsequent pasturing of the clover during the late summer and fall of the same year and until about June 1 of the following year. The stock are then taken off and a seed crop obtained. Usually the clover is subsequently plowed up and seeded to grain, although occasionally it is maintained for another year. This practice, where generally followed, has reduced damage by the root borer and has also practically eliminated damage to the seed crop by the clover flower midge and the clover seed chalcid. The practice could be improved upon by less close pasturing during the year of seeding. It may happen that the clover is pastured so closely that the roots are kept small (40, p. 91) and therefore are injured severely by a few root borers and clover root curculios (*Sitona hispidulus* Fab.) than if they had made a larger, more vigorous growth.

The practice of cutting the first crop of clover early for hay, as recommended for the control of the clover flower midge, would also tend to reduce injury to the seed crop by the clover root borers, as, except in case of an unusually heavy infestation, the clover seed would mature before any large number of clover plants would be killed by their work.

There are many good reasons why clover should not be left undisturbed for a number of years. Not only does such treatment permit the increase of root borers, but all kinds of clover insects multiply rapidly in old fields, especially root curculios, clover leaf weevils, cutworms, grasshoppers, leafhoppers, plant bugs, and aphids. Young clover, seeded into the following year's wheat crop, is often severely injured by some of these insects when it has been preceded by clover sod of some years' standing. Vetch sown on old clover sod is often more or less severely injured by clover root borers and curculios. Old clover fields in western Oregon also become breeding places for rodents, which are often destructive to clover and other crops. Figure 15 illustrates the damage in a clover field in its second crop year by root borers, grasshoppers, and rodents.

FERTILIZER

Davis (9, p. 46) experimented with large quantities of commercial fertilizer as a possible repellent for the clover root borer, finding that such heavy applications had no apparent effect on the root borers but often severely injured the clover.

The writer tried applications of phosphatic fertilizers to clover, hoping to induce more rapid root growth. The plots of experiments at Corvallis, Oreg., conducted by the Bureau of Plant Industry in cooperation with the Oregon Agricultural Experiment Station, were also available for study. From these sources no definite conclusions

could be drawn regarding any difference in infestation of the various plots by clover root borers. These experiments, however, indicated that the growth of the clover, both in roots and tops, was considerably stimulated by applications of acid phosphate, even on fertile bottom lands. The plots at Corvallis manifested a similar stimulation by both acid phosphate and gypsum.

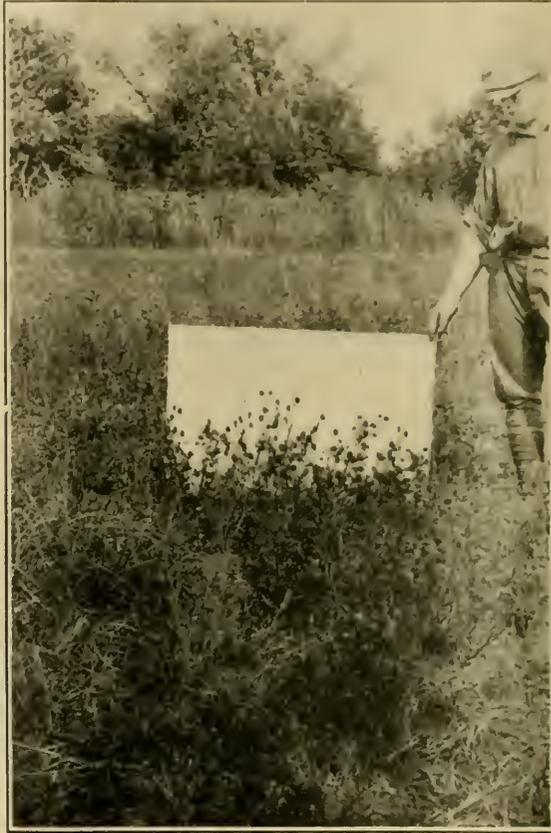


FIG. 15.—Damage to clover, in its second crop year, by clover root borers, grasshoppers, and rodents

REPRESSIVE MEASURES RECOMMENDED

Adopt a one-crop system of clover culture throughout the community.

Plow clover sod as soon as possible after seed harvest or second hay crop.

Plow and harrow badly infested clover sod after the hay crop in late June or July; a plow making a flat furrow and a spring-tooth harrow serve best for harrowing out as many roots as possible.

Never plow badly infested clover sod in early spring; early and severe damage may be caused to neighboring young clover.

Cut clover early for hay, in case of an early infestation by the root borer, in order that as many plants as possible of the second crop may mature seed before being killed by root borers.

Adopt any agricultural practice that makes for a healthy, rapidly growing root system, such as good seed from a locality known to produce a good strain of red clover; provide a good seed bed and good drainage; maintain in the soil the elements required for optimum growth of the plant. Root borers do not thrive as well on rapidly growing, sappy roots as on those the growth of which has been checked.

SUMMARY

The clover root borer is an insect of wide distribution throughout the world, wherever red clover is an important crop.

It belongs to a group of beetles which are commonly found attacking injured or weakened woody plants.

The clover root borer feeds most commonly upon the roots of red clover. It is one of the principal factors limiting the life of a clover stand after the first crop year, and even in the first crop year has frequently caused large losses of hay or seed.

The beetles migrate from old clover to new clover fields on favorable days in April, May, and June, the maximum flight usually occurring in May.

The eggs of this insect are laid in niches in the walls of burrows in clover roots, beginning late in April or in May, and hatch in 17 to 30 days. Comparatively few eggs, probably seldom more than 20, are laid by each female.

The larvæ develop slowly, and the first pupæ are not found until about the middle of July. The pupal period lasts from 8 to 13 days.

As the egg-laying period of each female extends over a considerable length of time, there is at all times a great diversity in the stage of development of the root borers.

New adults are not numerous before the middle of August, although the first new adults are found about the middle of July.

Some larvæ are still immature when winter arrives, and do not pupate and transform into adults until April or May of the following year.

The total developmental period from egg to adult is not less than 60 days and may be 90 days or more. The total life span of the individual borer may be a year or even longer. There is but one generation a year.

The borers pass the winter in the roots where they mature.

The development of the clover root borer and the damage caused by it are influenced by climatic and soil factors, by the condition of the host plant, and by topography.

The most noticeable damage to red clover by the clover root borer is observed in the second crop year, when the stand may be so badly thinned as materially to reduce the crop. Often by late summer the stand is practically killed out unless there has been abundant self-seeding.

In regions where root borers are very abundant serious injury may be done to the crop in the first crop year. Young clover fields may be entirely killed out soon after the first hay crop, when such fields are situated near badly infested clover sod which has been spring plowed.

Red clover is occasionally attacked even in the year of seeding.

Alsike clover is not usually seriously injured by clover root borers.

Injury to peas and vetch may occur when these crops are grown near badly infested old clover fields.

Clover root borers have been found on alfalfa plants, but there is probably little danger that alfalfa will be generally or seriously attacked.

The clover root borer has but few natural enemies; an entomogenous fungus, eight species of birds, and the larvæ of predacious beetles have been recorded as preying on the species.

Clover root borers can be killed in large numbers by plowing up badly infested clover roots and harrowing them to the surface of the soil, at any time between the middle of June and the beginning of August.

Many root borers may be killed by plowing and harrowing clover soon after the seed crop or second cutting of hay. This practice also induces an abnormal activity of the surviving root borers in the fall and early spring, which is detrimental to their successful propagation.

Late fall and winter plowing and the practice of green manuring have little restraining effect on the clover root borers.

Spring plowing of heavily infested clover sod has no remedial value and may cause severe damage to new clover in the vicinity.

Serious injury to clover in the first crop year may be avoided by cooperation of the community in farm practices which will reduce the numbers of the root borers to a point where they can not aggressively attack the clover. A one-crop system of clover culture, together with a general practice of early fall plowing of clover sod, and, in exceptionally severe cases, summer plowing and harrowing, should free a community from appreciable damage by the clover root borer in the first crop year.

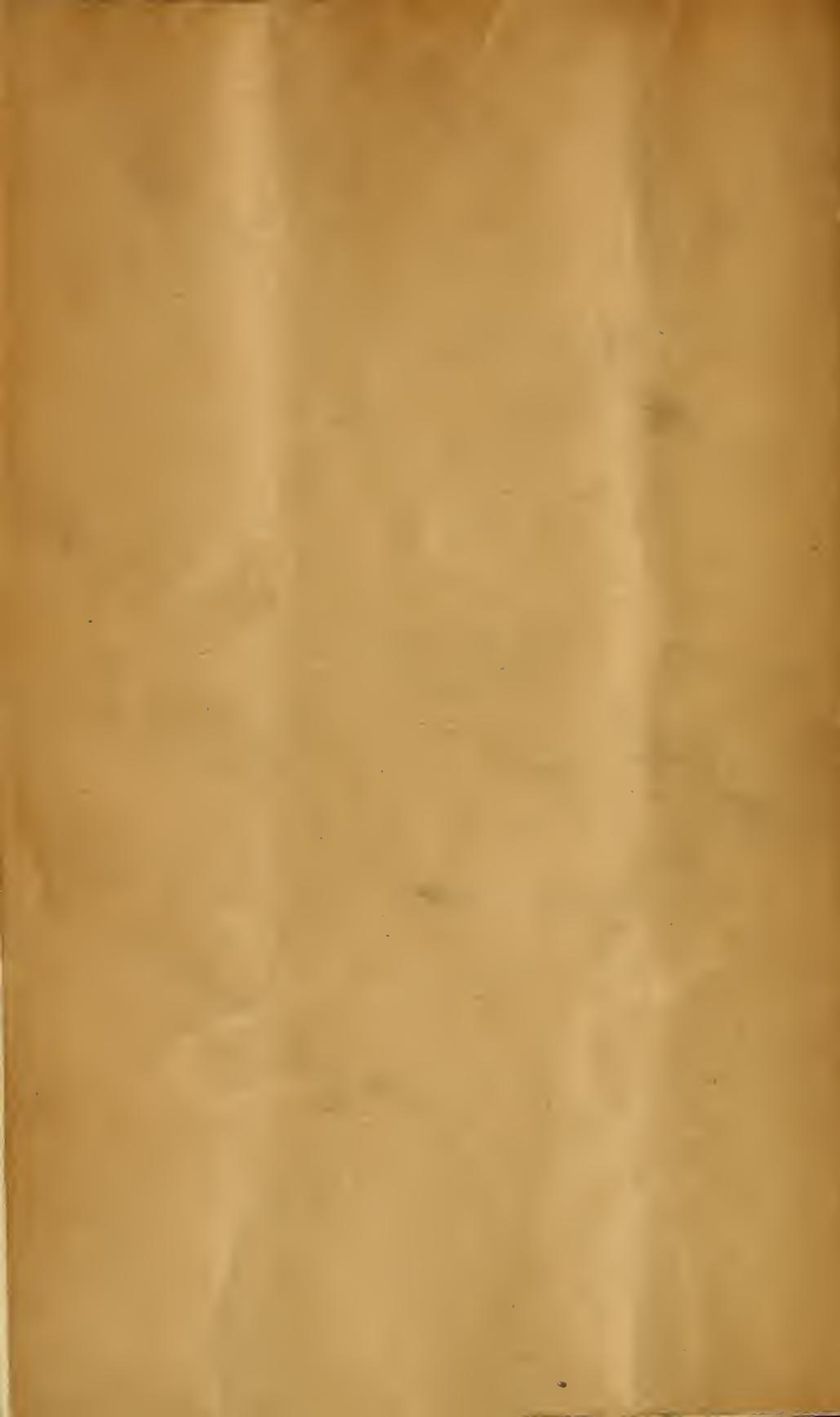
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UNITED STATES DEPARTMENT OF AGRICULTURE



DEPARTMENT BULLETIN No. 1428



Washington, D. C.

October, 1926

THE CADELLE

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ORIGIN AND SYNONYMY

The cadelle (*Tenebroides mauritanicus* Linné) is an important pest of grains and of grain products such as flours and milled breakfast foods. It belongs to an extensive family of beetles, nearly all of which are inhabitants of the New World. For this reason it has been thought by some to be native to America. The fact, however, that it alone of the genus *Tenebroides* has the habit of feeding upon grain or grain products—a habit that must have been acquired centuries ago—leads one to suspect that it may possibly be a native of the Old World, where the custom of storing grain for food was first established. Early English writers thought it had been introduced to England from Africa. At the time of its description in 1758 it had undoubtedly been carried by commerce to nearly all parts of the civilized world.

In 1758 it was first described by Linné (20, p. 417),¹ who gave it the name of *Tenebrio mauritanicus* and classified it with the meal worm, *Tenebrio molitor*, which he described at the same time. Thirty-two years later, in 1790, Olivier (23, p. 242) published a short account of this insect and proposed for it the generic name of *Trogossite* (from the Greek words τρογωσ, to eat, and σίρος, grain). For many years thereafter it was known as *Trogossita mauritanica* and until recently the family of beetles to which it belongs was known as the Trogositidae.²

¹ Numbers in italic in parentheses refer to "Literature cited," p. 39.

² The family was later known under the name of Temnochilidae and is now called the Ostomidae.

In 1783, however, a few years previous to the publication by Olivier, Piller and Mitterpacher (26, p. 87) described a beetle under the name *Tenebroides complanatus* and characterized their genus *Tenebroides* on this species. A rather poor illustration accompanied the description, but it has been generally recognized by scientists as the *mauritanicus* of Linné. Hence the name *Trogosita* gave place to that of *Tenebroides*, under which the insect is now known.

The conspicuous size and habits of this insect attracted the attention of many scientists, and during the eighteenth century it was described several times under different names. The synonymy of *Tenebroides mauritanicus* (Linné) as given by Lèveillé (19, p. 438-439) is as follows:

mauritanicus LIN. Syst. Nat. ed. X. l. p. 417 (1758).—J. Dev. Gen. II. t. 42. f. 208.—[<i>Larva</i>] Cf. RUFFERSBERGER, Biol. Käf. Eur. p. 130	cosmopolit.
<i>bucephalus</i> HERBST, Arch. p. 141. t. 29. f. 16 (1784).	
<i>caraboides</i> FABR. Syst. Ent. p. 256 (1775).—STURM. IBS. II. p. 242. t. 48	Europa.
<i>complanatus</i> PILLER, II. Poseg. p. 87. t. 9. f. 9 (1783).	
<i>dubius</i> SCRIBA, Journ. p. 42. G (1790)	Germany.
<i>fuscus</i> GOEZE, Ent. Beytr. I. p. 125 (1777).—GEOFFR. (<i>Platycerus</i> no. 5). Hist. Ins. I. p. 64.—PREYSSL. Verz. böhm. Ins. I. p. 6. t. 1. f. 1 (1790).	
<i>piceus</i> SCHALLER, Act. Hall. I. p. 319 (1783)	America.
<i>planus</i> QUENSEL, Diss. inaug. p. 19 (1790)	Barbaria.
<i>striatus</i> FOURCROY, Ent. par. I. p. 3 (1785)	Gallia.
var. <i>nitidus</i> HORN, loc. cit. [Proc. Ac. Phil. 1862] p. 83.—CF. REITT. loc. cit. [Verb. nat. Ver. Brünn.] p. 79 (16)	Philadelphía.

COMMON NAMES

Tenebroides mauritanicus has few common names, "cadelle" appearing to be, on the whole, most generally satisfactory. This is the name by which the larva was popularly known to the French, according to Olivier (23, p. 242) in his paper published in 1790. Taschenberg (32, p. 16-18), in 1879, called the cadelle the "bread beetle" because he had found it in bread. In like manner Johnson (14), in 1896, proposed to call the cadelle "the bolting cloth beetle" because it eats holes in bolting cloth in flour-mill machinery. Since the names "bread beetle" and "bolting cloth beetle" do not embrace the varied activities of the insect, the writers have selected the more generally accepted name, cadelle.

ECONOMIC HISTORY

References to the destructiveness of the cadelle to grain began to appear shortly after it was described as a new species by Linné (20) in 1758. Dorthes (8), in 1787, wrote of it as destructive to wheat and Olivier (23, p. 242), in 1790, stated that the insect was common throughout France, attacking wheat in granaries. Some 20 years later, in 1812, Kirkup (17) gave the first real contribution to our knowledge of the life history of the cadelle by recording observations on a specimen which was known to have remained as a larva with a Spanish almond meat for 15 months before transforming to the adult, and to have lived as an adult an additional year and nine months. Kirkup stated that the cadelle was not common in England at that time but was occasionally found on board ships. In

1802 Parmentier (25, p. 355) referred to the damage caused to stored wheat in France, and in 1841 (Harris (11), writing in America, stated that although the cadelle caused considerable damage in Europe, he was "not aware that they have been found in our own garner," probably meaning by this, in the Northeastern States.

In 1860 Curtis (4, p. 332-333) stated that the pest occurred over the greater part of Europe, and that it attacked not only wheat and corn, but bread and nuts, and even dead trees. He records an interesting instance where the cadelle larvæ became established in the rotten floor of a malt house in Cambridge, England. Curtis observed that the damage done to grain by the cadelle is partially offset by its carnivorous attack upon the wolf moth, *Tinea granella* L., also a grain pest. Glover (10, p. 66), in 1871, recommended kiln drying of infested grain to destroy the cadelle. LeBaron (18, p. 64), in 1874, and Thomas (33, p. 93), in 1878, stated as their belief that the cadelle was chiefly carnivorous and fed upon species of *Calandra* and *Tinea* infesting grain. As previously stated, Taschenberg (32, p. 16-18), in 1879, wrote of the insect in Germany and named the pest the "bread beetle," because he found it infesting bread and bake shops in his country. Riley and Howard (28), in 1888, recorded finding a cadelle pupa in a bottle of milk. In the following year Webster (34) discovered specimens that had bored through a cork-stoppered bottle and had then burrowed through powdered white hellebore; and Luggier (21), in 1890, gives an interesting account of the pupal chambers made by larvæ in a book (*Pl. VII, C*). Forbes (9, p. xi-xii), in 1890, mentioned that in Illinois the cadelle larvæ were found boring holes in the sides of a granary for the apparent purpose of transformation.

Plumacher (27), in 1891, recorded the presence of the cadelle in corn in Venezuela, and three years later Riley (29, p. 219) stated that cereals grown in South America and Central America were found, when exhibited at the Columbian Exposition, to be infested by the cadelle. The same year (1894) Riley and Howard (30) recorded the accidental presence of the cadelle in sugar. In 1895, Chittenden (1, p. 290-291) gave a brief account of the cadelle, called attention again to the fact that it often damages many more kernels of grain than it consumes, listed foods eaten by the insect, and established the fact that the cadelle is both predacious and grain-eating. In 1896 (2, p. 122-124), in a chapter on insects affecting cereals and other dry vegetable foods, in a bulletin on the principal household insects of the United States, he stated his belief that the cadelle is of American origin and has one generation annually. He records the larvæ in powdered sugar and suspects that their presence there is due to adulteration of the sugar with flour.

Johnson (13, 14, 15), writing in the American Miller in 1895, 1896, and 1898, gave to the cadelle the name "bolting cloth beetle" because it often cuts the silk bolting cloth in flour-mill machinery. He recorded severe damage by the cadelle to 2,000 bushels of wheat which were found in 1894, on one farm in Illinois, to be swarming with cadelle larvæ. In 1899 he recorded (16, p. 67) that cadelle larvæ bored through the parchment coverings of jam and jelly jars arriving at Baltimore from England, and that the larvæ fed upon the sweets.

Davis (5, p. 21), in 1896, recorded the insect present in beans. Ormerod (24, p. 56-59), in 1900, referred to the presence of the cadelle in bakers' shops, granaries, etc., in England, and expressed the opinion that because of their predacious habit the cadelles, when present in flour or meal, on which so far as she was aware neither the beetle nor its maggot fed, were doing more good than harm; as grain pests, however, she stated that the case was different. R. I. Smith (31, p. 11-12), writing from North Carolina in 1909, after a study of the grain-pest problem there, came to the conclusion that any beneficial result following the attack of the cadelle upon other grain pests was greatly counterbalanced by the insect's direct attack upon the grain.

Dean (6, p. 205-207, figs. 18-19), in 1913, after a study of flour infestation both in America and Europe, established the seriousness of the cadelle infestations in flour and came to the conclusion that the cadelle is one of the most serious of mill pests. Herrick (12, p. 232-236), in 1914, published original data by Slingerland indicating an incubation period of about 10 days for the egg, and a life cycle of about one year's duration.

Zvierzomb-Zubovsky (35) in 1919, McColloch (22) in 1922, and Cotton (3) in 1923, published original biological data that greatly increased our knowledge of the cadelle. Zvierzomb-Zubovsky found that eggs are laid in batches from 18 to 27 in number and hatch in from 7 to 24 days, that the larval stage lasts from 98 to 115 days during which the larva molts five times, and that the pupal stage lasts from 8 to 30 days. Although his work indicated but one generation a year, McColloch found the larval stage to extend over such long periods (from 628 to 1,248 days) that he questioned whether or not the cadelle life cycle might not be much longer than thought by previous writers. Cotton, however, in his paper preliminary to the present paper, gave convincing data on all stages that left no doubt that the cadelle may have two generations each year.

DISTRIBUTION

The cadelle is cosmopolitan in distribution, being found in all parts of the world where grain and grain products are stored. It has been found in all flour mills and manufacturing plants, warehouses, elevators, and farmers' grain bins examined by the writers, no matter whether these were on the Atlantic coast or the Pacific coast, in the North or South. It is easily distributed in grain and grain products and hence is carried with the greatest ease along trade channels. It was abundant in wheat arriving at American ports during the war from Australia, and in rice, peanuts, and other stored products from the Dutch East Indies. Cargoes of corn arriving at New York from South American ports always carry the cadelle. Nut meats arriving in the United States from the Mediterranean regions often are infested. The dunnage of ships frequently carries thousands of cadelles from country to country, and in America, at least, the universal use of breakfast foods carries specimens to nearly every home at some time or other.

NATURE OF INJURY

The association of the cadelle with other grain pests which are more in evidence often aids in obscuring its extremely varied injury. The cadelle larva and adult are both rather restless and do not feed continuously in one place. Both can gnaw holes through sacks, parchments, cardboard (fig. 1), waxed and other papers (fig. 2), and even wooden boards (figs. 3, 6, 7, and 8), and whether they penetrate such substances directly in search of food, or accidentally in making suitable chambers for transformation (fig. 11), the result is the same—the exposure of susceptible foods to hordes of associated pests that might not otherwise have been able to gain access to the food supply.

All who have observed the feeding of the cadelle have noted its preference for the germ of the grains upon which it feeds, and know that the larva and adult may travel from seed to seed and remove the germ from many more seeds than could possibly be completely devoured. The larva, however, is more likely to become embedded in the larger seeds, such as corn, and, half in the seed itself and half in the burrowed-out cob (fig. 4, C), feed upon a seed until little is left except the outer portion. Even small kernels such as those of wheat may be completely devoured except for the outer coverings. On a Maryland farm in 1921 the writers observed cadelle larvæ so abundant in 800 bushels of wheat that the kernels appeared to move, and larvæ could be gathered by the peck. They have also seen larvæ removed by the pailful from rice which had been stored for some time in New York warehouses, and tremendous numbers from flour which was being reconditioned in New Orleans warehouses and wholesale grocery establishments after a season's storage. Dean (6, pp. 205-207) has recorded finding 1,460 and 1,001 larvæ, respectively, in two 140-pound sacks of flour.

In flour mills injury by the cadelle is clearly evident from the holes eaten by both larvæ and adults in the silk cloth used in the bolting

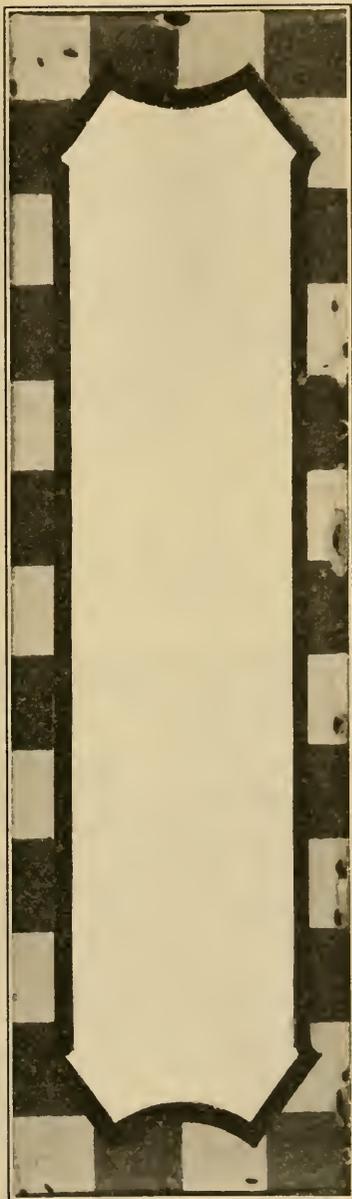


FIG. 1.—Side view of carton of flour showing holes cut in the cardboard by larvæ and adults of the cadelle. Such holes open cartons to the attack of all small grain pests.

machines and in other fabrics from the sifters (fig. 5). Although such injury occurs chiefly while the machinery is at rest, the time required to patch the cloths, or the impaired efficiency resulting from

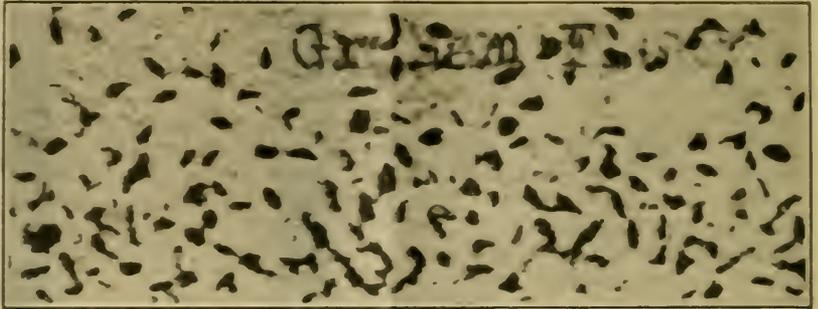


FIG. 2.—Piece of paper taken from top of inside of carton of graham flour. Note perforations made by larvæ and adults of cadelle developing within the flour

the damage, constitutes a real loss. This type of injury is so severe at times that Johnson (14) named the cadelle the "bolting cloth beetle."

The writers believe that the losses brought about by cadelle activity in cartoned foods has been greatly underestimated. Cadelle larvæ have frequently been found in flours, breakfast foods, dried



FIG. 3.—View in hold of grain ship, showing dunnage used to keep sacks of wheat from touching steel sides of ship. Such dunnage used over and over again becomes well infested by the cadelle, and with the assistance of the cadelle becomes also the hiding place for many associated grain pests

fruits, pearl barley, etc., placed on the market in packaged form. A cadelle larva seldom pupates within such a package, but in seeking seclusion for transformation it eats a hole in the carton to effect its escape (fig. 1). It thus opens the carton to all the other chief pests

of cartoned goods and indirectly brings about a loss that is seldom charged to the cadelle itself.

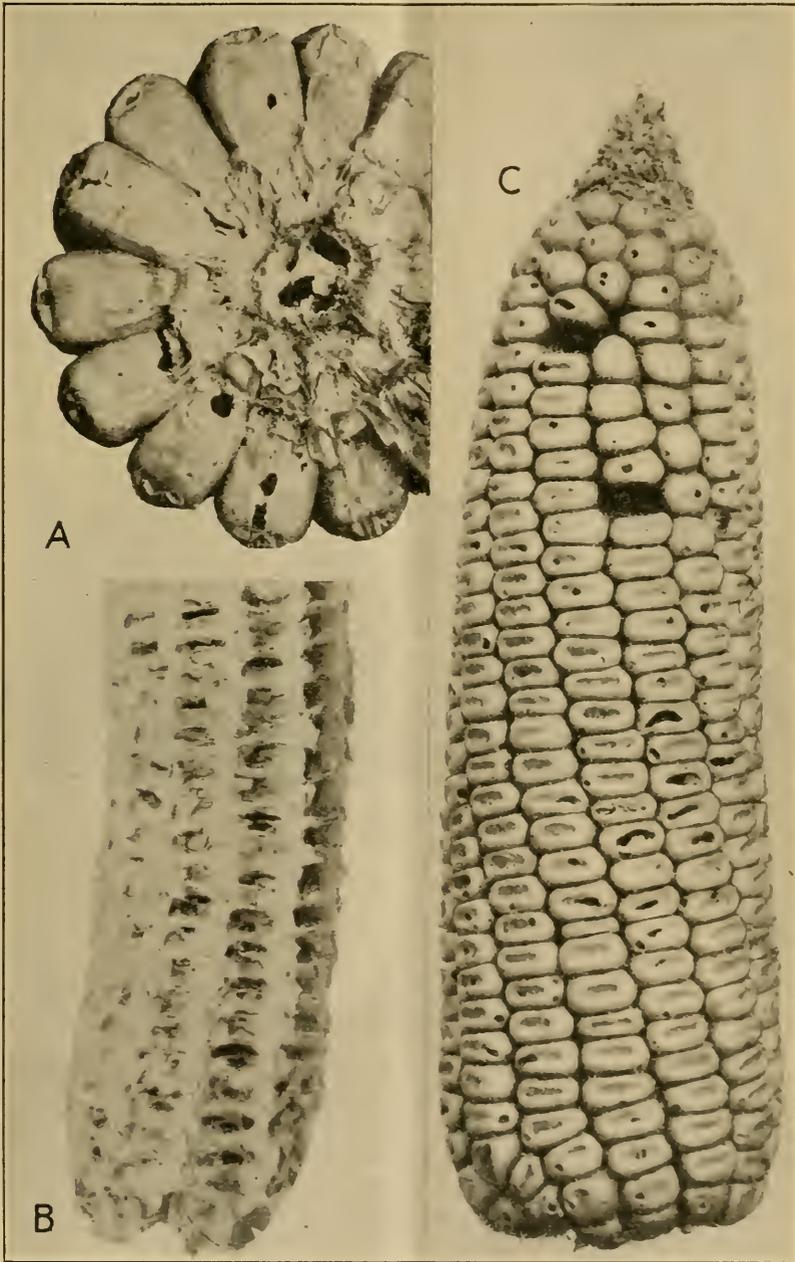


FIG. 4.—A, Burrows of cadelle larvæ in pith of corn cob; B, the dark spots in corn cob indicate burrows of cadelle larvæ which are often found partially concealed in such spots with the remainder of their bodies filling the hollowed-out corn kernel; C, kernels showing evidence of infestation by *Sitotroga cerealella* and cadelle. The large siltlike openings are evidence of cadelle feeding.

In warehouses used for the storage of miscellaneous products the cadelle may cause much annoyance at times. Thus, in a warehouse in Baltimore which had been used the summer before for the storage of grain products but which had been thoroughly cleaned (from a warehouse standpoint) when the grain products were removed during the fall months, adult cadelles appeared in hordes during warm days in March, congregating in numbers between sacks of flour and beans and feeding upon carload lots of potatoes. In some instances as many as 20 adults could be counted about abrasions on potatoes; these had emerged from the wooden floor, in which they had been hibernating during the cold months.

BORING HABITS OF THE CADELLE

The boring habit of both the cadelle larva and the adult is one of the most interesting features of its activities, and enhances greatly its economic importance. Figures 6, 7, and 8 show the ability of the cadelle to bore into wood.

The woodwork about all storage places for grain is more or less penetrated by cadelle burrows. If the wood is very hard, the larvæ may be forced to form pupal chambers between boards, by gnawing



FIG. 5.—Fabric from shifting machine of flour mill showing channels cut in pile by cadelle larvæ and adults. These cuts reduce the efficiency of the machinery and necessitate replacement of fabrics

the adjacent surfaces of the boards. In the case of ordinary dunnage used in grain ships (fig. 3; fig. 6, B, D, E; fig. 8, B), however, the wood of granaries (fig. 6, C; fig. 7, B; fig. 8, A, B), or the woodwork of feed bins in flour mills (fig. 7, A), etc., they have no difficulty in entering the wood by eating out the softer wood of the yearly growths and in becoming established by the thousands. In such places their presence is not usually suspected by the farmer or grain dealer.

Examination by the writers of the dunnage of a grain ship arriving at Baltimore from Australia in 1918 showed the boards used to keep the sacks of wheat from touching the steel sides of the ship to be well perforated wherever a sack of wheat touched the wood. Such borings were of course made during the voyage.

In old farming districts, like that of Montgomery County, Md., where bins built many years ago are still in use for storing wheat, the burrows may be so numerous and may have been so lengthened by the borings of generation after generation of cadelle larvæ and adults that the wood has become well honeycombed. Observe in



FIG. 6.—Cadle burrows in wood: B, D, and E, Sections of 1-inch soft wood; A, excavations made in oak board used as cover for elevator boot in flour mill; C, section of oak timber from granary exposing three long larval burrows

Figures 7, B, and 8, A, longitudinal and cross sections of a 3 by 3 inch oak timber honeycombed by cadelle larvæ. Individual larval

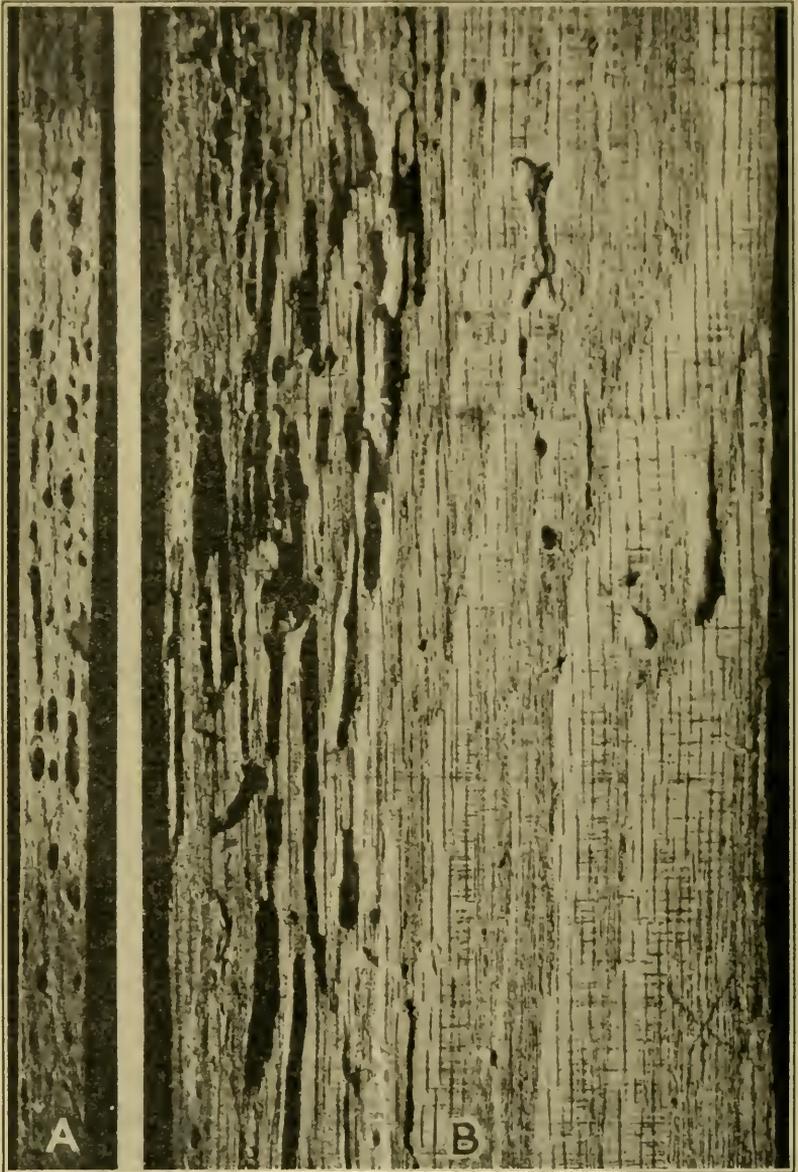


Fig. 7.—Cadelle burrows in wood: A, Quarter-inch strip of soft wood riddled by larvæ taken from bran bin of flour mill; B, longitudinal section of 3-inch oak timber used as rafter in roof of 100-year-old wheat granary on Maryland farm (for cross section see fig. 8, A)

channels may be as long as $2\frac{1}{4}$ inches. One-inch boards of pine are easily perforated. Figure 6, A, shows the excavations made in a hardwood board used as top to a flour elevator in a mill. In one

yellow-pine board 42 by 4 by 1 inch taken from a farmer's bin near Washington, D. C., there were estimated to be 6,160 holes through which larvæ or adults had entered or left the board. The flooring

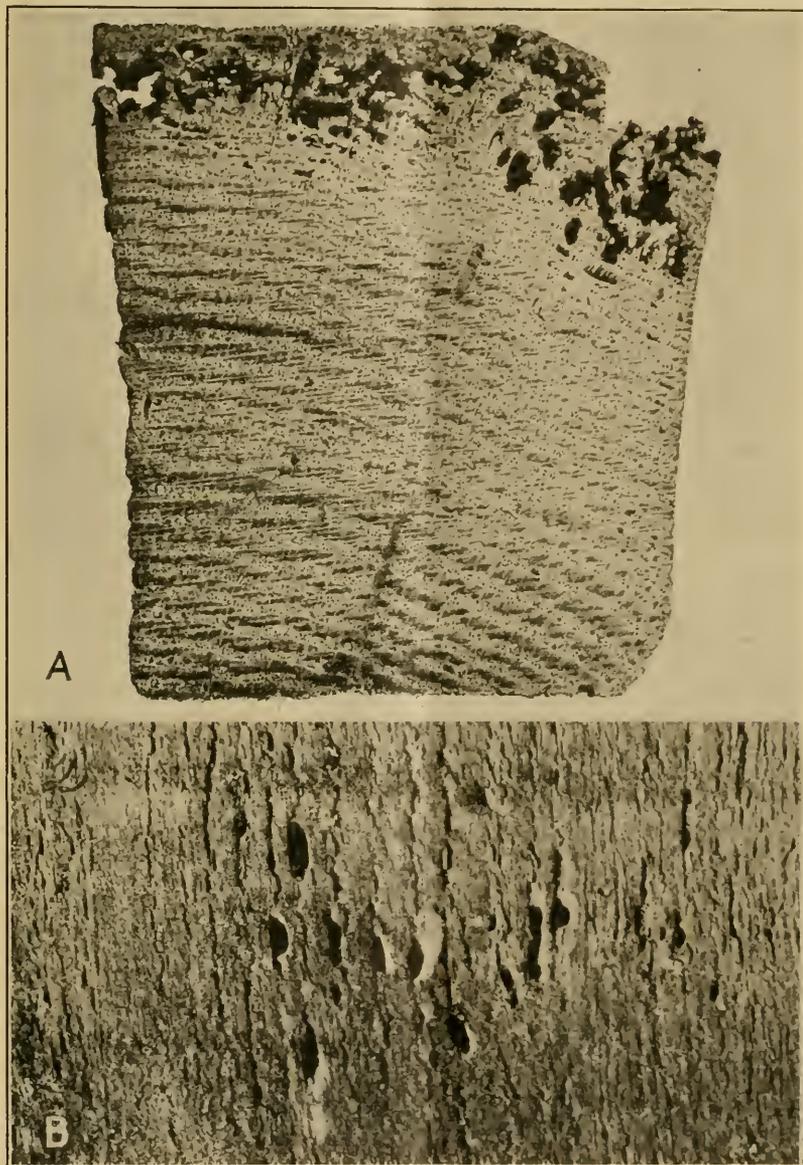


FIG. 8.—Cadelle burrows in wood: A, Cross section of oak timber used as rafter of wheat granary on Maryland farm for over 100 years, showing the exposed surface honeycombed by cadelle larvæ; B, external view of board from side walls of granary, showing entry and exit holes of cadelle larvæ and adults

of another bin which had been in place for many years, and upon which wheat had been placed each year, was found so riddled as to be unsafe. In several old bins the writers have observed cadelle

larvæ burrowing not only into the woodwork of floors and sides of the bins but into the rafters, beneath shingles, and wherever the

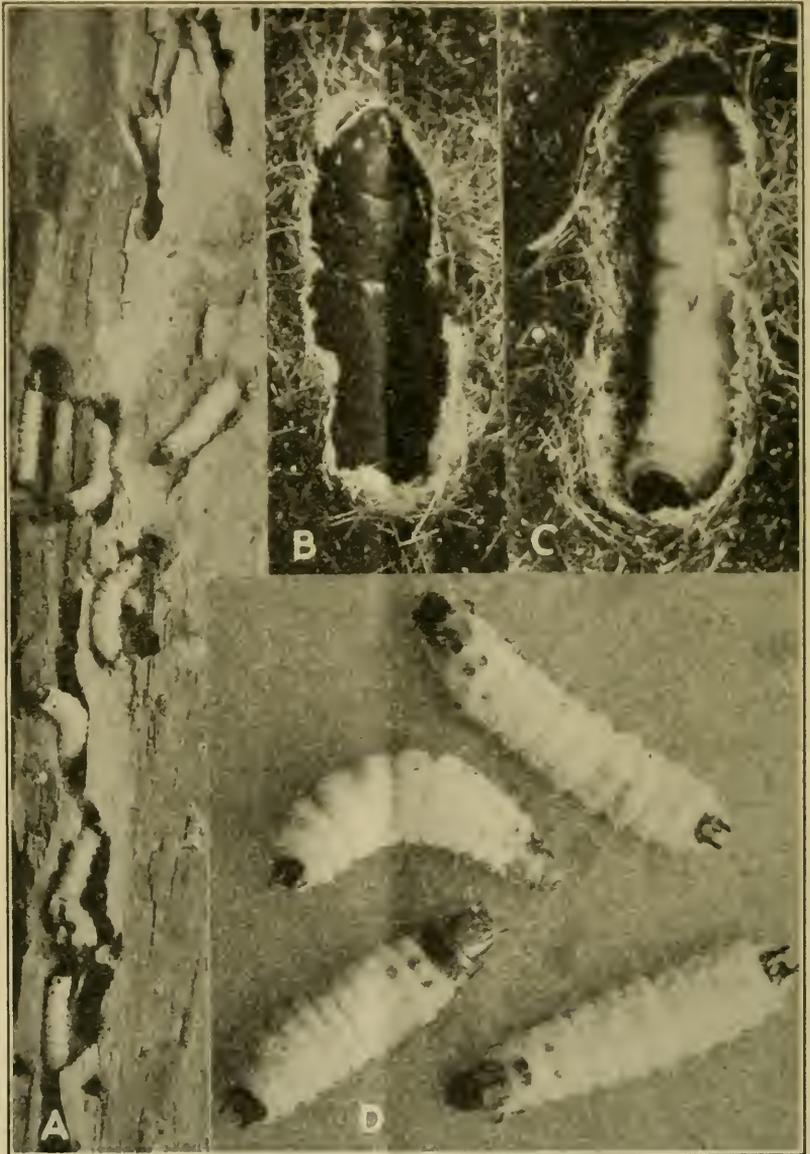


FIG. 9.—Hibernation of the cadelle: A, Sectioned softwood board from granary used for wheat storage, showing numerous larvæ of cadelle using board for protection during winter months; D, cadelle larvæ about to pupate; C, cadelle larvæ hibernating in chamber cut in Wilton rug; B, same as C, only several months later, after larva has transformed to adult

timbers or boards were joined. In warehouses with wooden floors used for the storing of grain and grain products, such as ordinary establishments handling animal feeds, the insects secrete themselves

in large numbers in burrows in the wood itself or between or beneath the boarding.

Since cadelle larvæ and adults may hibernate during the winter months and larvæ may live through a starvation period of from six months to two years, it can easily be appreciated that a warehouse or granary may be cleared of an infested lot of material and thoroughly cleaned in so far as this can be accomplished with broom and white-wash, and yet be so infested with cadelle larvæ and adults that a new supply of grain products, such as cattle feed and cartoned breakfast foods, may be subjected to a truly tremendous onslaught of cadelles as soon as warm weather or transformation permits. In one instance, 800 bushels of wheat, threshed in July and placed in a wooden granary the woodwork of which had been well honey-combed with cadelles, was found so heavily infested with cadelles in September that the kernels appeared to be alive and moving. There was no doubt that the cadelles in the woodwork entered the freshly threshed wheat as soon as it was stored. In the same bin, as soon as cold weather approached, immense numbers of adults and larvæ were observed by the writers to leave the wheat in question and burrow into the surrounding woodwork. Subsequent observation indicated that the farmer sold his wheat before the warm spring weather, but the overwintering cadelles for the most part remained in the wood until the new crop of wheat was placed in the bin the following summer, whereupon they emerged in large numbers and began their attack. Since there is a short summer generation and since the adults are so long-lived and lay so many eggs, the large numbers of cadelle larvæ often found in stored products on the approach of winter weather is easily explained.

As a consequence of its boring habit, the cadelle enters and transforms or hibernates in many substances not attacked as food. An almost endless list of objects thus entered may be expected. The writers found sacks of brown sugar that had been stored on a war ship close by flour, and later removed for storage in a New York warehouse, to contain many lumps in the center of each of which was a hibernating cadelle larva. In another instance larvæ entered rolls of Wilton carpeting and formed pupal chambers by eating away the nap, as shown in Figure 9, B and C. Cadelle larvæ will penetrate an inch of cork stopper in the laboratory if necessary to effect their escape from a bottle. Larvæ will escape from a nest of three pill boxes with the greatest ease. They escape from mailing tubes, and from any cereal cartons known to the writers except those of tin; and paper (fig. 2) and cloth sacks are easily cut. Although escape from a container seems to be the motive for most of the burrowing in food containers in the retail trade, the larvæ can enter ordinary cartoned goods when the cartons are sufficiently close together to allow the larvæ to get a purchase for applying their strength, as, for instance, when the cartons are packed in shipping containers.

LIFE HISTORY AND HABITS

The following data regarding the biology of the cadelle include much that is new. Of special interest are the data dealing with the adult longevity and oviposition and the short and long periods required for larval development.

THE ADULT

A few days before the pupa transforms to the adult (fig. 10), the eyes become dark and the mouth parts and tips of the tarsi begin to color. When first emerged from the pupal skin, the adult is light in color, soft in texture, and very feeble. If exposed it would be unable to protect itself from other carnivorous insects, and therefore it remains within the shelter of its pupal chamber for a week or longer while its tissues are hardening and its color changing to dark reddish brown or black. It then emerges from its cell by eating a characteristically shaped hole (fig. 8, B) through the pupal cell and takes up the struggle for existence.

The beetles prefer darkness to light and usually may be found in dark corners of mills and granaries, between sacks that are stacked close together or in other similar situations.

The food habits of the beetles are very similar to those of the larvæ; but, in addition to eating everything that the larvæ feed on, they will attack and devour the larvæ of almost any insect that they encounter. Beetles were fed in the laboratory with the larvæ of the cheese skipper (*Piophilæ casei* L.) and larvæ of various flour beetles (*Tribolium*, etc.). Observations seem to indicate that oviposition is stimulated by the addition of fresh meat to the diet. Beetles do not hesitate to devour larvæ of their own species, or even a newly emerged adult that is prematurely exposed. The beetles are rather pugnacious, and if confined in restricted quarters they will fight until most of them have lost their legs.

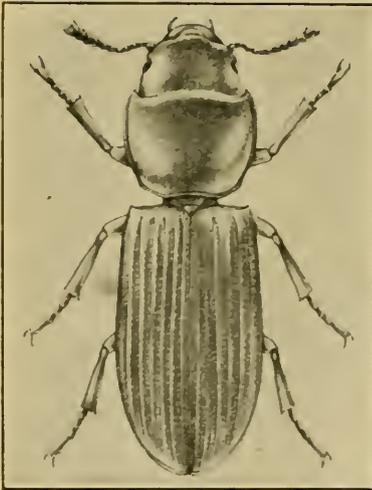


FIG. 10.—The cadelle: Adult beetle. The cadelle is a flattened, black beetle about one-third of an inch long

the data of Table 1 indicate, female beetles reared in the laboratory and given food were all very long-lived and many survived for considerably more than a year, the longest record being 668 days.

AGE AT WHICH MATING AND OVIPOSITION BEGIN

During the week or more that the adult cadelle remains sealed within its pupal chamber, there is of course no opportunity for mating. Mating occurs, however, soon after emergence from the pupal chamber and is repeated at irregular intervals throughout life. In summer egg laying begins about two weeks after transformation to the adult, but in the spring months the preoviposition period appears to be considerably longer. In the case of adults emerging in late summer or early fall, no oviposition takes place until the following spring. Data indicating a preoviposition period of from 15 to 210 days are given in Table 1.

ADULT LONGEVITY

The cadelle adult is usually long-lived. Kirkup (17) records a single specimen that lived for one year and nine months. Slingerland in Herrick (12) observed two adults that lived for about one year. As

TABLE 1.—Data concerning longevity and oviposition of the female cadelle

Female No.	Date emerged	First egg laid	Preoviposition period	Last egg laid	Length of oviposition period	Number of eggs laid	Date of death	Length of life
			Days		Days			Days
1	(1)	July 1, 1922	-----	Sept. 13, 1922	74	530	Sept. 24, 1922	122
2	(1)	-----do-----	-----	Oct. 15, 1922	106	1,190	Dec. 2, 1922	191
3	(1)	-----do-----	-----	Aug. 28, 1922	58	436	Nov. 28, 1922	187
4	Aug. 7, 1922	Aug. 22, 1922	15	Sept. 8, 1923	382	1,311	Mar. 14, 1924	585
5	-----do-----	-----do-----	15	Aug. 8, 1923	351	597	Mar. 28, 1924	599
6	-----do-----	-----do-----	15	Oct. 20, 1923	424	1,087	Dec. 31, 1923	511
7	Aug. 11, 1922	Aug. 27, 1922	16	Aug. 2, 1923	340	990	Nov. 10, 1923	456
8	-----do-----	Aug. 26, 1922	15	Sept. 17, 1923	387	931	Feb. 20, 1924	558
9	Aug. 8, 1922	Aug. 28, 1922	20	Aug. 13, 1923	350	493	June 6, 1924	668
10	Aug. 12, 1922	Feb. 9, 1923	181	July 14, 1923	155	1,319	July 23, 1923	345
11	Aug. 19, 1922	Sept. 18, 1922	30	Sept. 12, 1923	359	987	Feb. 23, 1924	553
12	Aug. 20, 1922	Feb. 27, 1923	191	Oct. 15, 1923	230	1,182	Jan. 11, 1924	509
13	Aug. 22, 1922	Mar. 20, 1923	210	Sept. 9, 1923	173	916	Apr. 10, 1924	597
14	Sept. 28, 1922	Mar. 3, 1923	156	Oct. 7, 1923	218	757	Jan. 29, 1924	488

¹ Emerged prior to May 15.

WHERE EGGS ARE LAID

Previously published accounts give little information regarding the egg-laying habits of the cadelle. The adults deposit their eggs loosely in flour or other food materials, or tuck them into crevices of any sort. They prefer to place them in some protected situation, such as beneath insecurely pasted flaps of cartoned goods, in corrugated cardboards, through the mesh of fabric used as containers for flour or grains, and in floor cracks. The eggs are placed side by side in batches containing usually from 10 to 60 each, although as few as four eggs, and as many as 91, have been found in a single batch. The average number of eggs placed in a batch is 25 (see Table 2). In securing eggs, advantage was taken of the female's preference for oviposition in crevices by offering her small pieces of sheet cork fastened together with paper clips and placed on top of the food in the jar in which she was kept. The beetle invariably placed her eggs in batches between the sheets of cork, hence it was a simple matter to change the cork daily and record the eggs laid. The reader should refer to Figure 11 for photographic records of the manner of oviposition in crevices. In ovipositing into flour, through a cloth covering, the eggs are arranged in many planes.

PERIOD OF OVIPOSITION

With the presentation of the data of Table 2, the writers are able to give for the first time authentic information concerning the period of oviposition of the cadelle.

It will be noted that oviposition, in one instance (No. 6), began August 22, 1922, and ended October 20, 1923. This record, extending over a period of almost 14 months, is the longest known. Other recorded periods of approximately a year's duration were from August 22 to September 8 (No. 4), August 22 to August 8 (No. 5), August 27 to August 2 (No. 7), August 26 to September 17 (No. 8), August 28 to August 13 (No. 9), and September 18 to September 12 (No. 11). In these seven instances (see Table 2) no eggs were laid during the period from September 20 to February 7, inclusive; and in four of the seven records, none until March 2; in two instances

egg laying was resumed the second week in February and continued with fair regularity throughout that and the following months.

In three instances (Nos. 1, 2, and 3) where females emerging before May 15 began ovipositing on July 1, oviposition ended September 13, October 15, and August 28, respectively, and was followed later in the fall by the death of the adults. Ovipositions that began very early in the season, as during February and March, were completed during that year; four such records extended from February 9 to July 14 (No. 10), February 27 to October 15 (No. 12), March 20 to September 9 (No. 13), and March 3 to October 7 (No. 14).

The oviposition period is, then, quite long, with a minimum of about two months and a maximum of about 14 months. Females emerging during the summer months usually lay a portion of their eggs the same year, cease oviposition with the approach of winter, and begin ovipositing once more during February and March (in warm buildings) or later in ordinary warehouses, and continue laying eggs until exhaustion. Since such adults may continue oviposition until the following October, the resulting oviposition periods are the longest. Other females, emerging during late summer or fall, may not begin ovipositing that year but lay all their eggs during the following calendar year, beginning during February or March in warm structures; such females have short oviposition records in spite of their long

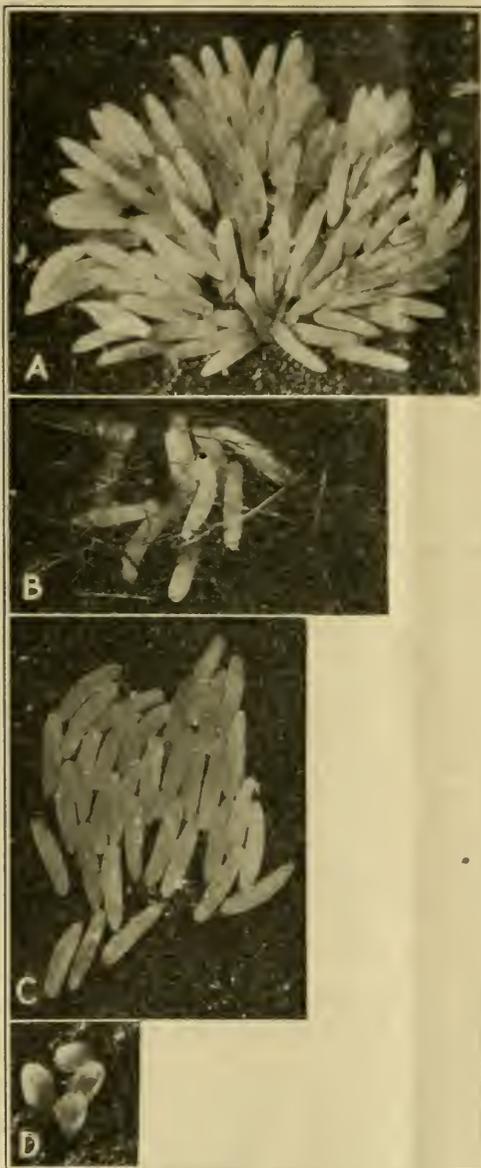


FIG. 11.—Four egg clusters of the cadelle: A, C, Deposited between two flat surfaces; B, in a piece of hat felt; and D, tucked into a hole in a piece of cork

year, beginning during February or March in warm structures; such females have short oviposition records in spite of their long

lives, Certain females which emerge very early in the season (as in the case of Nos. 1, 2, and 3 of Table 2, which emerged that spring before May 15, but did not begin oviposition until July 1) complete their oviposition and die before winter, and these have the shortest oviposition periods of all.

TABLE 2.—*Oviposition records of the cadelle*¹

Date	Number of eggs laid by female No. —													
	1	2	3	4	5	6	7	8	9	10	11	12	13	14
1922														
July 1	30	13	14											
2			32											
3	50	40												
4	30		18											
6	32	24	13											
8	18													
9	22		18											
10	7													
11	11	8												
13		40												
14	6		20											
15		25												
16	27	20	12											
17	16	32												
18		40	34											
20	31	27												
21		10												
22	11													
23	35	14												
25		32												
27	22	24	24											
28		29												
29	17													
30	12	27	48											
Aug. 1		46												
2	9	20												
3	26													
4		21												
6		12	12											
7		19	26											
8		22												
9	17													
11			23											
12	7													
13		12	23											
14	21	8	24											
16		23												
17		12												
18			44											
19		36												
20		34												
21		48												
22	24			7	5	5								
23	11	18		10		11								
24		36			22									
26		59	32	18	7	23		15						
27							12							
28	18		19					9						
29							24							
30				20										
Sept. 31		3												
5		8		45	11									
7	9	49												
8		13												
9				38			9	14						
12		25												
13	11							31						
14		16												
16		43												
17								10						
18		10								11				
19														
20		20						6						

¹ Days on which no eggs were deposited are omitted from the table.

TABLE 2.—Oviposition records of the cadelle—Continued

Date	Number of eggs laid by female No. —													
	1	2	3	4	5	6	7	8	9	10	11	12	13	14
1922														
Oct. 3		30												
5		52												
7		15												
10		23												
15		27												
1923														
Feb. 8											12			
9										7				
10						8								
14										22	18			
16						22								
18											24			
19										25				
21											14			
24											13			
25										58				
27										13	14	30		
Mar. 1				38						22				
2						32					22			
3									33					
4										26				21
6				31					24	32				
7							12				61	18		
9							37	14	6					
10											21			
12												24		
13				16						33				
14					54									
16											16			
18											36			
20											12			6
21							15					34		
22								18						4
25							20							28
27														
28				30							26			
30										17	22			
31												34		
Apr. 2									10				12	
3				33		31					33	31	8	26
5								21						
6				21									56	30
7														
8							64		28	34				
9				46							18			
11								28					53	32
12									4					
13				40									66	
17						20						25		25
18											16			
19				45									20	
20						10								
21									10					
22							55			24	35	30		
24											18			
26									8					
27						10		38		10	28			
28				38								34	20	
29					12									
30								27	20		30			34
May 1				37	15	40								
2									20			6		
4				44								18	30	
5														
6											50			
7													23	
8				64							10	54	5	
9						46		38	17					
11					12									
12								18					12	
13				10	18	24					60			
15								16						
16								54						
17				31	9									
18				40		24		7				16		
19													11	
20								12						14

TABLE 2.—Oviposition records of the cadelle—Continued

Date	Number of eggs laid by female No. —													
	1	2	3	4	5	6	7	8	9	10	11	12	13	14
1923														
May 21				10				30			20			
22												28		
23				48		46		18					27	
26				48			53			9	15		54	
27								32				8		
28													36	
29				64		40	24				22			
31				38			12	36					58	
June 2				32		38	28	50		15		33		40
3											30	20	40	
4				20									32	
5				42		36						48		
6				44			14					32	24	
7				26			34		12	18		32	34	
8					6									
9						10								
10										28				
11										43			52	
12										68		35		
14				40			22	38					38	
15				36								24		
16					40									
18						32	20	28		52	54	36	30	
19				40			34	18		56	14	58		8
20					10					78				
21												45		
22							18			42	12			
23				10					28			16	16	
24								22						
25				26			30			52	32	35	18	
26						37	18	24	16					
28							36	64				16	18	42
29										54				
July 30					16						33			
1				16								28	14	
2					46									
3						56		38				32		
4														22
5				35	44		14	32	32		32	15	40	
6						45		10					18	8
7					20		38					19	24	
9						32		18			16		34	33
10									22	16				
11													26	
12						14	19			25		6		18
14					60					30	32			36
15									39					
16								15						50
17							40				36		64	
18				5				18	56					45
19							18				14			14
20						16							26	
22							11		30		18			
24								32			30			
25									14					12
26						14								
27									16		14			18
29							14	40			23	14	32	
30														72
31							18	25	28			16		
Aug. 1				60							27			
2						18	20		10				28	36
4														48
6														
7											21	16		
8					23	14			17					
13									11				30	
20						15								
21											26			15
25							12							
30									16					
31												41		
Sept. 1				12										
3							22				16	34		
7									30					
8				17										
9						10			32			45	18	
12											29			10

TABLE 2.—Oviposition records of the cadelle—Continued

Date	Number of eggs laid by female No. —													
	1	2	3	4	5	6	7	8	9	10	11	12	13	14
1923														
Sept. 17								16						
18												41		
21												10		
25						31								
27												23		
Oct. 3														16
7						15								10
15						48						12		
20						8								
Total	530	1,190	436	1,311	605	1,087	990	931	493	1,319	987	1,182	916	757

FREQUENCY OF OVIPOSITION

The cadelle female does not oviposit with regularity. Eggs may be deposited daily or every other day during the period of greatest egg-laying activity, although intervals of from 10 to 14 days, more or less, when no eggs are laid, frequently occur even during seasons of favorable climatic conditions. In Table 2, containing data on the oviposition of 14 females, there are only six instances in which eggs were laid each day for periods of three or four days. Thus No. 2 deposited 25, 20, 32, and 40 eggs on July 15, 16, 17, and 18, respectively, 27, 46, 16, and 20 on July 30 and 31 and August 1 and 2, respectively, and 36, 34, and 48 eggs on August 19, 20, and 21, respectively; No. 4 deposited 20, 42, 44, and 26 eggs on June 4, 5, 6, and 7, respectively; No. 12 deposited 48, 32, and 32 eggs on June 5, 6, and 7, respectively; and No. 13 deposited 40, 18, and 24 on July 5, 6, and 7, respectively.

Eggs are frequently laid every other day and sometimes every day during the height of oviposition activity. Thus No. 2 deposited 8, 40, 25, 20, 32, 40, 27, 10, 14, 32, 24, 29, 27, 46, 16, 20, 21, 12, 19, and 22 eggs on July 11, 13, 15, 16, 17, 18, 20, 21, 23, 25, 27, 28, 30, and 31, and August 1, 2, 4, 6, 7, and 8, respectively. A more usual record, however, is that of No. 10, which deposited 22, 20, 61, 24, 16, 36, 12, 50, 22, and 16 eggs on March 1, 3, 6, 9, 12, 16, 18, 22, 28, and 31, respectively. Although egg deposition ceases in most instances during October, November, December, and January, one female (No. 2) deposited 39, 52, 15, 23, and 27 eggs on October 3, 5, 7, 10, and 15, respectively, before stopping oviposition for the winter period. A study of the data of Table 2, in conjunction with other records not included, indicates an irregularity in oviposition that can not be predicted.

NUMBER OF EGGS DEPOSITED BY SINGLE FEMALES

Previous investigators have not determined the egg-laying capacity of the cadelle, hence the records given in Table 2 are the first ever published of females of known age and with oviposition records broken by a period of winter inactivity. The junior writer (*B. p. 62-63, nos. 330, 331, 337*), in a preliminary report, gave records Nos. 1 to 3 occurring in Table 2, which subsequently obtained data

indicate to be fairly trustworthy as complete oviposition records for females emerged before May 25 and reaching their egg-laying capacity before the winter following.

The maximum number of eggs deposited by any cadelle under observation is 1,319; the minimum, 436. The 14 females whose records are included in Table 2 laid 530, 1,190, 436, 1,311, 605, 1,087, 990, 931, 493, 1,319, 987, 1,182, 916, and 757 eggs, respectively. The 10 females depositing the largest number of eggs deposited an average of 1,067 eggs; whereas the average for the entire 14 females of Table 2 is about 910 eggs. The number of eggs laid at a time varied from 3 to 78. In one instance, not recorded in Table 2, a female beetle deposited 91 eggs in a single batch.

THE EGG

The incubation period of the egg varies considerably, being influenced chiefly by the prevailing temperatures. The data of Table 3 indicate the length of the egg stage as determined by the writers under laboratory conditions when the mean temperatures ranged from 69.2° to 85° F. It will be noted that during February and March, 1923, when the mean temperatures ranged from 70° to 71° F., the length of the incubation period was from 15 to 17 days. Later in the spring and in the summer (1922), as the daily means rose, the length of the incubation period became shorter until with an average mean of 80°-85° F., it was reduced to a minimum of 7 days. The data of Table 3 cover those portions of the year when the adult cadelle oviposits in the laboratory at Washington, D. C., and indicate a minimum incubation period of 7 days and a maximum of 17 days.

TABLE 3.—Incubation period of egg of the cadelle

No.	Date egg laid	Date egg hatched	Length of incubation period	Average mean temperature for incubation period
			Days	° F.
1.....	Apr. 27, 1922	May 7, 1922	10	71.4
2.....	May 6, 1922	May 15, 1922	9	74.2
3.....	May 7, 1922	May 16, 1922	9	74.5
4.....	June 5, 1922	June 12, 1922	7	85
5.....	June 6, 1922	June 13, 1922	7	84.3
6.....	June 7, 1922	June 14, 1922	7	83
7.....	June 16, 1922	June 23, 1922	7	80
8.....	July 3, 1922	July 10, 1922	7	80.5
9.....	Aug. 3, 1922	Aug. 11, 1922	8	79
10.....	Oct. 5, 1922	Oct. 15, 1922	10	74
11.....	Oct. 7, 1922	Oct. 17, 1922	10	73
12.....	Feb. 24, 1923	Mar. 13, 1923	17	71
13.....	Feb. 25, 1923	Mar. 13, 1923	16	71
14.....	Feb. 27, 1923	Mar. 14, 1923	15	71
15.....	Mar. 2, 1923	Mar. 17, 1923	15	71
16.....	Mar. 6, 1923	Mar. 22, 1923	16	70.8
17.....	Mar. 22, 1923	Apr. 6, 1923	15	70
18.....	Apr. 2, 1923	Apr. 14, 1923	12	71
19.....	Apr. 6, 1923	Apr. 20, 1923	14	69.2
20.....	Apr. 13, 1923	Apr. 27, 1923	14	70.6
21.....	Apr. 19, 1923	May 2, 1923	13	72
22.....	May 18, 1923	May 28, 1923	10	76
23.....	May 23, 1923	June 1, 1923	9	77.4

THE LARVA

The young larva, after effecting its escape through one end of the eggshell, is almost transparent in appearance and is so small that it is scarcely noticeable to the unaided eye. It is sensitive to light and at once attempts to burrow out of sight within whatever food substance is at hand. If no food is present it will conceal itself within or beneath any object that affords shelter.

FOOD OF LARVA

The larva (fig. 9, A, D; fig. 12) is voracious and, with a favorable environment, will grow rapidly. It will feed on an almost endless variety of foodstuffs but does not thrive equally well on them all. It will feed on all grains and their milled products, such as corn, wheat, oats, barley, rice, all kinds of flours, meals, stock feeds, biscuits, and bread. It feeds freely in many kinds of nut meats and seeds and various dried fruits and vegetables. Although developing more rapidly on the germ of the grain, the cadelle feeds also on the harder portions, and frequently, in the case of wheat, so eats the kernel that nothing is left but a thin shell. In feeding upon corn on the cob (fig. 4, C), the larva eats out the softer germ, thus forming a chamber in which it is frequently entirely concealed and from which it eats a longitudinal channel to the outer end and escapes from the kernel by eating a characteristic slitlike opening well illustrated in Figure 4, C.

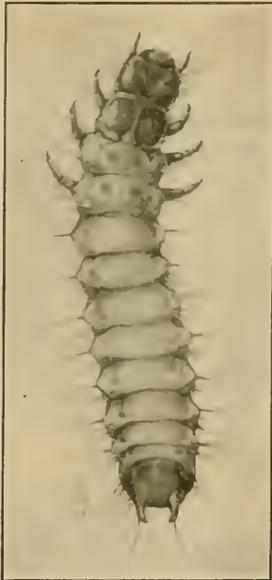


FIG. 12.—The cadelle larva. Commonly found crawling among grain kernels. It may appear glistening white or dull and powdered according to the material in which it is crawling. When full grown it is about three-fourths of an inch long.

Effect of diet upon growth of larva.—During the season of 1922 hundreds of cadelle larvæ were reared in the laboratory in individual vials, and several different foods were experimented with. It was found that the type of food used had a marked influence over the rate of growth of the larva. The larvæ were placed in individual vials and kept under identical conditions as regards temperature and

moisture. Each was supplied with an abundance of food, the only difference being in the kind of food supplied. The foods used were corn, wheat, rough rice, Graham flour, barley flour, and refined white flour. The larvæ fed upon corn, wheat, and Graham flour grew with great rapidity and completed their growth in approximately the same length of time. These larvæ all hatched during the first week in May and completed their growth in about 69 days. Those fed on barley flour did not grow quite so rapidly but a few of them completed their growth about two weeks after the corn, wheat, and Graham-flour-fed larvæ. Those fed on rough rice grew still more slowly and did not transform until the following summer. The larvæ fed upon the refined white flour developed very slowly, many

of them died after living a few months, none completed their development, and the few that were still alive after 18 months were only about half grown. Certain larvæ lived to be about 2 years old without reaching maturity.³

Larva often found in substances upon which it does not feed.—When well grown the larva may migrate from its food in search of a protected place in which to form its pupal chamber and transform to the adult stage. The larva may therefore be found in strange places and foods and cause unnecessary alarm. Thus larvæ may bore into bags of sugar (30) and salt, cornstarch, rolls of carpets and rugs, balls of twine, corrugated cardboard, in soft wood, and have even been found in bottles of milk (28). Of course their presence in such places is accidental and usually is of no economic importance except as they render such foods unpalatable if their presence is noted. In certain instances the cutting of fibers, etc., by the larvæ in forming their cocoons may seriously affect a commodity.

CARNIVOROUSNESS OF LARVA

Much has been said regarding the carnivorous habits of the cadelle larva, and a survey of the literature relating to this insect would lead one to suspect that the larva kills and devours any other insect larva that it chances to encounter. To determine the truth of the matter a large number of cadelle larvæ were confined separately in small glass vials with a small quantity of flour and a number of larvæ of other flour-infesting insects. At the end of a few weeks the vials were inspected and it was discovered that in almost every case all the larvæ were alive and thriving although the cadelle larva must have been in a more or less close contact with some of the other larvæ most of the time. In a few cases some of the other larvæ were found dead and these probably had been killed by the cadelle larva. Further experiments were conducted by placing several cadelle larvæ together in glass Petri dishes with and without food and with or without other insect larvæ. It was found that the cadelle larvæ upon encountering each other would frequently thrash around and inflict wounds with their mandibles which in time caused death to ensue. In this way in the course of a week or two a good many were killed, but the living larvæ made no attempt to feed upon the dead bodies, and it seems quite likely that the mortality was due mainly to the restricted space rather than to any carnivorous proclivities of the larvæ. The other insect larvæ that were confined with the cadelle larvæ fared much better than the cadelles, possibly because of their smaller size and greater activity: a few were killed but the majority escaped and there was no evidence to show that the cadelle larvæ fed upon the remains of the few that were killed. In one instance a cadelle larva was accidentally confined in a vial with the larva of the black carpet beetle (*Attugenus piceus* Oliv.) for several months without food. Upon examination both larvæ were found to be alive and uninjured.

LENGTH OF LARVAL STAGE

The length of the larval stage varies considerably. It is influenced by various factors, the more important of which are the abundance

³This is true in spite of the fact that tremendous numbers of well grown larvæ have been taken from white flour that has been in storage for some months.

and kind of food, the time of year in which the young larva hatches, and the prevailing temperatures.

The effect of the food supply on the duration of the larval growth has been discussed in a preceding paragraph. It was found that when the larva is reared on certain foods such as corn, wheat, Graham flour, etc., growth is rapid and, other conditions being favorable, the larval stage is short, whereas if the larva is fed upon less nourishing foods, growth is correspondingly slower and the larval stage may be considerably prolonged.

Of several hundred cadelles hatched at different times of the year and supplied with an abundance of suitable food a great many completed their growth and transformed within 3 months, a majority within 7 months, and all within 14 months after hatching. (Table 5.) Of a large group fed upon refined white flour none succeeded in transforming, although certain of them lived to be about 2 years old.

The time of the year when the young larva hatches apparently has some bearing on the duration of the larval stage aside from the influence to be expected from changing climatic conditions. Of the larvæ that hatch in the late spring and early summer months, although rearing conditions may be to all appearances identical, a certain percentage have a short larval life and transform the same year, as indicated by the data of Table 7, whereas the rest have a long larval life and do not transform until the following spring or summer, as indicated by the data of Table 8. The rearing records of the several hundred cadelles mentioned in the preceding paragraph show that all larvæ that hatched in March and April completed their growth and transformed the same year: 90 per cent of those hatching in May transformed that year, 40 per cent of those hatching in June, 10 per cent of those hatching in July, but none of those hatching in August transformed the same year. Table 4 contains the data just mentioned and also gives the minimum, maximum, and average lengths of the larval stage for the larvæ that hatch during the different months of the active breeding season. It is interesting to note at this time that of the specimens reared those having the shortest larval life and those having the longest larval life all hatched in June of the same year and were reared under identical conditions.

TABLE 4.—*Influence of time of hatching upon length of larval stage of the cadelle*

Month in which larva hatched	Number of larvæ	Trans- forming same year	Length of larval stage		
			Minimum	Maximum	Average
			Days	Days	Days
March.....	25	100	93	138	100
April.....	15	100	80	104	89
May.....	51	90	60	376	102
June.....	59	40	48	414	209
July.....	47	10	62	346	270
August.....	26	0	233	318	272

Temperature naturally has a marked effect upon the duration of the larval stage but its effect is often modified or vitiated by the nature of the food and time of hatching of the larva. As a general rule, the larval stage becomes shorter as the seasonal temperature increases. Table 5 contains data showing the variation in the

length of the larval stage of larvæ that hatched at different times of the year. It also gives the average mean temperature for each larval period. It may be noted that the average mean temperature for the minimum larval period of 93 days for the larvæ hatching in March was 73° F., for the minimum larval period of 80 days for the larvæ hatching in April the temperature was 79° F., for the minimum larval period of 60 days for the larvæ hatching in May, 80° F.; for the minimum larval period of 48 days for the larvæ hatching in June, 82° F.; for the minimum larval period of 62 days for the larvæ hatching in July, 80° F.; and for the minimum larval period of 233 days for the larvæ hatching in August and extending over winter months, 71° F.

TABLE 5.—Duration of larval stage of the cadelle

No.	Date hatched	Date pupated	Length of larval stage	Average mean temperature for larval period
			Days	° F.
1	May 7, 1922	Aug. 4, 1922	89	80
2	do.	July 29, 1922	83	80
3	do.	Aug. 11, 1922	96	80
4	May 15, 1922	Apr. 22, 1923	342	74
5	do.	July 30, 1922	76	80
6	do.	July 25, 1922	71	80
7	do.	July 14, 1922	60	80
8	do.	Apr. 16, 1923	336	74
9	do.	May 9, 1923	359	74
10	May 16, 1922	July 28, 1922	73	80
11	do.	May 27, 1923	376	73
12	do.	July 26, 1922	71	80
13	June 12, 1922	May 9, 1923	331	74
14	do.	Aug. 7, 1922	56	81
15	do.	do.	56	81
16	do.	Apr. 6, 1923	298	74
17	June 13, 1922	Aug. 1, 1923	414	74
18	do.	Apr. 8, 1923	299	73
19	do.	July 12, 1923	394	74
20	do.	June 25, 1923	377	74
21	do.	June 20, 1923	372	74
22	do.	June 3, 1923	355	73
23	do.	Apr. 6, 1923	297	73
24	June 14, 1922	Apr. 24, 1923	314	73
25	June 17, 1922	Aug. 7, 1922	51	82
26	do.	May 6, 1923	323	73
27	June 20, 1922	June 17, 1923	362	74
28	do.	Aug. 7, 1922	48	82
29	June 23, 1922	Apr. 1, 1923	282	73
30	July 10, 1922	June 9, 1923	334	73
31	do.	Apr. 30, 1923	294	73
32	do.	Apr. 8, 1923	272	73
33	do.	Apr. 4, 1923	268	73
34	do.	Sept. 17, 1922	69	80
35	do.	Sept. 10, 1922	62	80
36	do.	Sept. 24, 1922	73	80
37	do.	June 21, 1923	340	73
38	Aug. 11, 1922	May 3, 1923	265	71
39	do.	Apr. 1, 1923	233	71
40	do.	June 25, 1923	318	72
41	Aug. 14, 1922	Apr. 30, 1923	259	71
42	Aug. 25, 1922	June 3, 1923	282	71
43	do.	May 30, 1923	278	71
44	Mar. 13, 1923	June 19, 1923	98	73
45	Mar. 14, 1923	June 29, 1923	107	74
46	Mar. 17, 1923	June 21, 1923	96	74
47	do.	July 11, 1923	116	75
48	do.	June 19, 1923	94	73
49	do.	Aug. 2, 1923	138	76
50	do.	June 18, 1923	93	73
51	Apr. 14, 1923	July 27, 1923	104	78
52	do.	July 8, 1923	85	77
53	Apr. 26, 1923	July 19, 1923	84	79
54	Apr. 27, 1923	July 16, 1923	80	79

The shortest larval period observed was 39 days from the date of hatching to assumption of the prepupal state, or 48 days to the date of pupation. This larva hatched on June 20, 1922, and pupated August 7, 1922. It was fed on corn.

The longest larval period observed of those reared on favorable food was 414 days. This larva was also reared on corn.

The phenomenally long larval period, noted first by Kirkup (17) in 1812 and more recently by McCulloch (22) in 1922, was probably due to unfavorable food or environmental conditions. Kirkup recorded the case of a single larva which fed for more than 15 months before transforming, its food apparently consisting only of the almond nut in which it was found: how long it had been feeding before discovery can not be predicted but it might have been several months. McCulloch found that larvæ lived from 628 to 1,248 days before transforming, the larvæ being fed wheat, wheat bran, and flour.

NUMBER OF MOLTS

The cadelle larva usually molts either three or four times, although five, six, and seven molts are not unusual when the larval period is long. If for any reason the larval period is prolonged beyond its normal length, many more molts may occur. The writers observed one larva to molt nine times and McCulloch observed another to molt no less than eleven times.

Observations show that the larvæ that hatch in the early spring, if supplied with favorable food, molt only three times. Of those that hatch later in the year, about one-half molt three times and the rest four times, even though food supplies and other conditions are apparently identical. Larvæ that winter over, although apparently fully grown, sometimes start feeding again in the spring and may molt once or twice in the spring before transforming. When possible the larva seeks a sheltered place in which to molt; at other times, when breeding in flour, it comes to the surface to molt.

LENGTH OF LARVAL INSTARS

The different larval instars naturally vary considerably in length at different times of the year, but during the summer months they are more or less uniform. Their average lengths in summer are: First instar, about 11 days; second instar, about 11 days; third instar, about 14 days; fourth instar, about 18 days; and fifth instar, when it occurs, about 11 days. A more comprehensive idea of the relative lengths of these instars and the variation in them can be obtained by a study of Tables 7 and 8, which give complete life-history data of a number of individuals.

PUPATION

After attaining its growth the larva becomes restless and wanders about seeking a place of safety in which to undergo the transformations to the pupal and adult forms. It prefers to burrow into a piece of soft wood, hollow out a small chamber, and close up the open end with a cement made from the borings mixed with a larval secretion. It occasionally crawls between two boards and forms its cell between them, especially if the boards are of hard wood (fig 13).



FIG. 13.—Cadelle pupæ in pupal chambers. Wood sectioned to expose pupæ within chambers. Note burrow made by larva in arriving at place chosen for pupation.

The walls and floor of almost any wooden bin, granary, or warehouse which has been used as a storage place over a period of years for wheat, corn, or other foodstuffs will show evidence of their bur-



FIG. 14.—The cadelle pupa, much enlarged. The pupa is seldom seen as this stage of the cadelle's life cycle is spent in a cell made in an inaccessible place.

rowing. The damage resulting from this habit has been previously referred to. If nothing better is available, the cadelle larva will form its cell in a hollowed-out kernel of corn, filling the openings with the cement; or it will construct a cell out of pieces of grain cemented together. Finally, if nothing suitable is available, it will transform without forming a pupal cell. Larvæ that hibernate usually construct their pupal cells in the fall but do not transform until spring.

Larvæ that were reared in the laboratory were supplied in most cases with small pieces of cork into which they bored and soon disappeared from sight when ready to transform. After a prepupal stage lasting, in summer, from 7 to 17 days (averaging about 9 days), the pupal form (fig. 14) is assumed.

THE PUPA

The insect remains in the pupal stage from 8 to 25 days, the length of this stage being influenced mainly by the prevailing temperatures. Table 6 contains data on the length of the pupal stage and the relation of temperature to the length of the stage. Apparently the cadelle does not pass the winter months in the pupal stage.

TABLE 6.—Duration of the pupal stage of the cadelle

No.	Date pupated	Date adult emerged	Length of pupal period	Average mean temperature for pupal period
			<i>Days</i>	<i>° F.</i>
1.....	1922 July 14	1922 July 25	11	82
2.....	24	Aug. 3	10	82
3.....	25	7	13	81
4.....	29	10	12	80
5.....	Aug. 1	15	14	78
6.....	19	Sept. 1	13	77
7.....	26	8	13	79
8.....	26	9	14	79.5
9.....	Sept. 27	Oct. 14	17	73
10.....	10	Sept. 24	14	76
11.....	17	Oct. 1	14	72
12.....	18	3	15	72
13.....	20	6	16	73
14.....	1923 Mar. 27	1923 Apr. 16	20	69
15.....	28	13	16	73
16.....	30	22	23	72
17.....	Apr. 1	25	24	70
18.....	1	23	22	70
19.....	6	May 1	25	70.5
20.....	8	1	23	70
21.....	8	3	25	70
22.....	11	5	24	71
23.....	24	16	22	72
24.....	27	17	20	73
25.....	30	19	19	73

TABLE 6.—Duration of the pupal stage of the cadelle—Continued

No.	Date pupated	Date adult emerged	Length of pupal period	Average mean temperature for pupal period
			Days	° F.
26.....	1923 May 1	1923 May 21	20	73.5
27.....	6	27	21	74
28.....	9	28	19	74.5
29.....	9	27	18	74
30.....	13	30	17	76
31.....	15	31	16	77
32.....	27	June 8	12	83
33.....	June 3	15	12	81
34.....	10	23	13	81
35.....	17	26	9	85
36.....	21	July 1	10	84
37.....	25	4	9	83
38.....	23	4	11	83
39.....	July 12	21	9	85
40.....	14	22	8	84

LENGTH OF LIFE CYCLE

It has been assumed by previous writers that there is but one generation of the cadelle each year under favorable conditions. These investigations prove that there are often two generations, and that there may be a partial third generation a year in the vicinity of Washington, D. C., with ample evidence that in a tropical climate three generations may normally occur under favorable food conditions. The shortest developmental period from egg to adult observed by the writers was 67 days, from June 13 to August 19, 1922, when the average mean temperature for the period was 81° F. The adult was a female and oviposited for the first time September 18, 1922, completing a life cycle from egg to egg in 97 days. It is not likely that the cycle is ever much shorter than this in the vicinity of Washington, and usually it is considerably longer. In Table 7 are given data on what are termed by the writers the "short developmental period," egg to adult, completed during one season of activity, as compared with the data in Table 8 covering the much longer developmental period, egg to adult, when the insect overwinters as a larva. It will be noted that when the developmental period from egg to adult is completed during a single season of activity, this period varies from a minimum of 67 days to a maximum of 134 days. With life cycles during which the larva hibernates, the egg-to-adult period lasts from 271 to 410 days. When it is realized that should the insect be accidentally placed in cold storage with its food at temperatures ranging from 40° to 50° F., it will remain inactive for well over a year only to resume activity on the removal of its food to ordinary trade channels, one can easily appreciate that the life cycle is capable of tremendous prolongation. In this connection one should not forget the remarkable larvæ reported by McColloch (22) that lived 628 to 1,248 days before transforming.

TABLE 7.—Short developmental period of the cadet, egg to adult, completed during one season of activity

No.	Date egg laid	Date egg hatched	Incubation period	Date of first molt	Length of first larval stage	Date of second molt	Length of second larval stage	Date of third molt	Length of third larval stage	Date of fourth molt	Length of fourth larval stage
	1922	1922	Days	1922	Days	1922	Days	1922	Days	1922	Days
1	Apr. 27	May 7	10	May 23	16	June 3	11	June 20	17	-----	25
2	do	do	10	May 20	13	June 4	15	June 25	21	-----	20
3	do	do	10	May 18	11	do	17	June 20	16	July 13	23
4	do	do	10	May 17	10	June 3	17	June 18	15	July 15	27
5	do	do	10	do	10	June 1	15	June 17	16	July 6	19
6	do	do	10	May 25	18	June 3	9	June 18	15	July 5	17
7	do	do	10	May 22	15	do	12	June 20	17	-----	25
8	do	do	10	do	15	June 7	16	June 23	16	-----	24
9	May 5	May 15	10	May 28	13	June 6	9	June 21	15	July 20	29
10	do	do	10	May 29	14	do	8	June 19	13	-----	26
11	do	do	10	do	14	June 10	12	June 22	12	-----	27
12	do	do	10	do	14	June 17	19	June 29	12	July 14	15
13	do	do	10	May 25	10	June 6	12	June 19	13	-----	28
14	May 6	do	9	May 27	12	June 10	14	June 21	11	July 6	15
15	do	do	9	May 28	13	June 6	9	June 20	14	-----	14
16	do	do	9	May 26	11	June 10	15	June 23	13	July 12	19
17	do	do	9	do	11	do	15	do	13	July 10	17
18	May 5	do	10	do	11	do	15	June 27	17	July 18	21
19	May 7	May 16	9	May 29	13	June 6	8	June 18	12	July 11	23
20	do	do	9	May 31	15	June 11	11	June 27	16	-----	30
21	do	do	9	do	15	do	11	June 25	14	July 11	16
22	June 5	June 12	7	June 24	12	July 4	10	July 15	11	-----	14
23	do	do	7	June 22	10	July 3	11	July 13	10	-----	15
24	do	do	7	June 24	12	July 5	11	July 17	12	-----	12
25	do	do	7	June 22	10	July 3	11	July 13	10	-----	16
26	do	do	7	June 23	11	do	10	July 16	13	-----	13
27	June 6	June 13	7	do	10	do	10	July 18	10	-----	16
28	do	do	7	June 25	12	July 5	10	July 10	11	-----	13
29	do	do	7	do	12	July 6	11	July 19	13	-----	13
30	do	do	7	do	12	July 5	10	July 17	12	-----	15
31	June 11	June 17	6	June 26	9	do	9	July 18	13	-----	11
32	do	do	6	do	9	July 4	8	July 17	13	-----	12
33	June 13	June 20	7	June 29	9	July 5	6	do	12	-----	12
34	July 3	July 10	7	July 20	10	July 31	11	Aug. 16	16	-----	24
35	do	do	7	do	10	Aug. 1	12	do	15	-----	13
36	do	do	7	do	10	July 31	11	Aug. 17	17	-----	17
37	do	do	7	do	10	July 28	8	Aug. 13	16	-----	20
38	do	do	7	do	10	July 31	11	Aug. 12	12	-----	23
39	July 4	July 11	7	July 21	10	do	10	Aug. 16	16	-----	19
	1923										
40	Feb. 25	Mar. 13	16	Apr. 12	30	May 1	19	May 20	19	-----	18
41	Feb. 27	Mar. 14	15	Apr. 11	28	Apr. 30	19	May 22	22	-----	22
42	do	do	15	do	28	do	19	May 20	20	-----	18
43	Mar. 2	Mar. 17	15	Apr. 12	26	May 1	19	May 21	20	-----	17
44	do	do	15	Apr. 11	25	do	20	do	20	-----	17
45	do	do	15	May 5	49	May 20	15	June 10	21	-----	9

No.	Date of formation of prepupa	Length of fifth larval stage	Date of pupation	Length of prepupal stage	Date adult emerged	Length of pupal stage	Length of period from egg to adult	Average mean temperature of period from egg to adult	Food of larvæ
	1922	Days	1922	Days	1922	Days	Days	° F.	
1	July 15	-----	July 25	10	Aug. 7	13	102	79	Graham flour.
2	do	-----	July 24	9	Aug. 6	13	101	79	Do.
3	July 23	10	Aug. 4	12	Aug. 17	13	112	79	Do.
4	July 19	4	July 29	10	Aug. 10	12	105	79	Do.
5	July 15	9	July 26	11	Aug. 7	12	102	79	Do.
6	Aug. 3	29	Aug. 11	8	Aug. 24	13	119	79	Corn.
7	July 15	-----	July 25	10	Aug. 7	13	102	79	Do.
8	July 17	-----	July 24	7	Aug. 3	10	98	79	Do.
9	July 28	8	Aug. 4	7	Aug. 17	13	104	79	Do.
10	July 15	-----	July 30	15	Aug. 11	12	98	79	Do.
11	July 19	-----	July 29	10	Aug. 10	12	97	79	Do.
12	July 21	7	July 31	10	Aug. 13	13	100	79	Do.
13	July 17	-----	July 27	10	Aug. 8	12	95	79	Do.
14	July 15	9	do	12	do	12	94	79	Do.
15	July 4	-----	July 14	10	July 25	11	80	80	Do.
16	July 23	11	Aug. 3	11	Aug. 17	14	103	79	Do.
17	July 19	9	July 29	10	Aug. 10	12	96	79	Do.

TABLE 7.—Short developmental period of the cadelle, etc.—Continued

No.	Date of formation of prepupa	Length of fifth larval stage	Date of pupation	Length of prepupal stage	Date adult emerged	Length of pupal stage	Length of period from egg to adult	Average mean temperature of period from egg to adult	Food of larvae
	1922	Days	1922	Days	1922	Days	Days	° F	
18	Aug. 10	23	Aug. 26	16	Sept. 8	13	126	79	Barley flour.
19	July 18	7	July 28	10	Aug. 8	11	93	80	Wheat.
20	July 17	-----	July 26	9	Aug. 7	12	92	80	Do.
21	do	6	July 29	12	Aug. 11	13	96	80	Do.
22	July 29	-----	Aug. 7	9	Aug. 20	13	76	81	Corn.
23	July 28	-----	Aug. 5	8	Aug. 19	14	75	81	Do.
24	July 29	-----	Aug. 9	11	Aug. 22	13	78	81	Do.
25	do	-----	Aug. 7	9	Aug. 19	12	75	81	Do.
26	do	-----	do	9	do	12	75	81	Do.
27	do	-----	do	9	Aug 20	13	75	81	Do.
28	do	-----	do	9	Aug. 19	12	74	81	Do.
29	do	-----	do	9	do	12	74	81	Do.
30	Aug. 1	-----	Aug. 10	9	Aug. 23	13	78	81	Do.
31	July 29	-----	Aug. 7	9	Aug. 20	13	70	81	Do.
32	do	-----	do	9	Aug. 19	12	69	81	Do.
33	do	-----	do	9	do	12	67	81	Do.
34	Sept. 9	-----	Sept. 27	18	Oct. 14	17	163	78	Do.
35	Aug. 29	-----	Sept. 10	12	Sept. 24	14	83	79	Do.
36	Sept. 3	-----	Sept. 17	14	Oct. 1	14	90	78	Do.
37	Sept. 2	-----	Sept. 18	16	Oct. 3	15	92	78	Do.
38	Sept. 4	-----	Sept. 21	17	Oct. 7	16	96	78	Do.
39	do	-----	Sept. 20	16	Oct. 6	16	94	78	Do.
40	June 7	-----	June 19	12	June 27	8	122	74	Graham flour.
41	June 13	-----	June 29	16	July 11	12	134	75	Do.
42	June 7	-----	June 21	14	July 1	10	124	74	Do.
43	do	-----	do	14	June 28	7	118	74	Do.
44	do	-----	June 19	12	June 27	8	117	74	Do.
45	June 19	-----	June 29	10	July 11	12	131	75	Do.

TABLE 8.—Long developmental period of the cadelle, egg to adult, with insect overwintering as larva

No.	Date egg laid	Date egg hatched	Incu- bation period	Date of first molt	Length of first larval stage	Date of second molt	Length of second larval stage	Date of third molt	Length of third larval stage	Date of fourth molt	Length of fourth larval stage
	1922	1922	Days	1922	Days	1922	Days	1922	Days	1922	Days
1	May 5	May 15	10	June 1	17	June 13	12	July 6	23	July 24	18
2	May 6	do	9	June 12	28	June 29	17	July 15	16	Aug. 3	19
3	May 7	May 16	9	May 31	15	June 10	10	June 25	15	July 13	18
4	June 6	June 13	7	June 27	14	July 8	11	July 19	11	Aug. 7	19
5	do	do	7	June 25	12	July 5	10	July 16	11	Sept. 23	69
6	June 19	June 26	7	July 9	13	July 20	11	Aug. 1	12	Aug. 17	16
7	July 3	July 10	7	July 23	13	Aug. 2	10	Aug. 22	20	Sept. 18	27
8	do	do	7	do	13	Aug. 3	11	Sept. 2	30	1923 May 10	250
9	do	do	7	July 26	10	July 28	8	Aug. 7	10	1922 Aug. 25	18
10	do	do	7	July 19	9	July 27	8	Aug. 8	12	Sept. 23	46
11	do	do	7	July 21	11	Aug. 2	12	1923 Mar. 19	229	-----	-----
12	Aug. 3	Aug. 11	8	Aug. 23	12	Sept. 4	12	1922 Sept. 20	16	-----	-----
13	do	do	8	Aug. 26	15	Sept. 6	11	do	14	-----	-----
14	Aug. 7	Aug. 14	7	Aug. 24	10	Sept. 4	11	Sept. 19	15	-----	-----
15	Aug. 18	Aug. 25	7	Sept. 7	13	Sept. 21	14	Oct. 14	23	1923 Mar. 11	118
16	do	do	7	do	13	Sept. 20	13	Oct. 19	29	Mar. 12	144
17	do	do	7	Sept. 6	12	Sept. 22	16	Oct. 10	18	Mar. 14	155
18	do	do	7	Sept. 4	10	Sept. 18	14	Oct. 18	30	Apr. 6	170
19	do	do	7	do	10	Sept. 19	15	Oct. 28	39	Mar. 10	133
20	do	do	7	Sept. 5	11	Sept. 20	15	Oct. 18	28	Apr. 16	180

TABLE 8.—*Long developmental period of the cadelle, etc.*—Continued

No.	Date of fifth molt	Length of fifth larval stage	Date larva entered hibernation	Date pupated	Length of last larval and pre-pupal stage	Date adult emerged	Length of pupal stage	Length of period egg to adult	Food of larva
		Days	1922	1923	Days	1923	Days	Days	
1	Sept. 25	63	Oct. 14	May 9	226	May 27	18	387	Barley flour.
2	-----	-----	Aug. 23	Apr. 22	262	May 16	24	375	Corn.
3	Sept. 18	67	Oct. 23	May 27	251	June 7	11	396	Broken wheat.
4	-----	-----	-----	-----	-----	-----	-----	-----	-----
	1923								
4	Apr. 20	256	Aug. 23	July 12	83	July 21	9	410	Corn.
5	-----	-----	Oct. 22	Apr. 6	195	Apr. 29	23	327	Do.
6	-----	-----	Aug. 29	Mar. 20	215	Apr. 6	17	291	Do.
7	-----	-----	Oct. 7	Apr. 8	202	May 3	25	304	Do.
8	-----	-----	Sept. 27	June 10	31	June 23	13	355	Do.
9	-----	-----	Sept. 22	May 13	48	May 30	17	331	Do.
10	Mar. 26	213	Sept. 27	Apr. 3	192	Apr. 27	24	298	Do.
11	-----	-----	Aug. 29	June 21	94	July 1	10	363	Do.
12	-----	-----	Oct. 10	Apr. 8	200	May 1	23	271	Do.
13	-----	-----	Oct. 12	May 8	230	May 27	19	297	Do.
14	-----	-----	Oct. 19	Apr. 27	220	May 17	20	283	Graham flour.
15	-----	-----	Oct. 27	May 30	80	June 10	11	296	Corn.
16	-----	-----	Oct. 25	June 5	85	June 15	10	301	Do.
17	-----	-----	do.	June 8	86	June 22	14	308	Graham flour.
18	June 1	56	Oct. 29	June 21	20	July 1	10	317	Do.
19	Mar. 30	20	Nov. 2	June 3	65	June 15	12	301	Do.
20	June 10	55	Oct. 22	June 29	19	July 12	13	328	Do.

SEASONAL HISTORY

The cadelle passes the winter months in the adult or larval stage. The data of Tables 7 and 8 indicate that the time spent by the insect in its egg and pupal stages is fairly short, but great variations may be expected during the larval stage, which may be as short as 48 days or, according to McCulloch (22), as long as 1,248 days. Furthermore, the adult itself has been known to live almost 22 months and may lay eggs over a period of more than one year (Table 2). Taking these facts into consideration, together with the influence of the time of hatching upon length of larval life (Table 4) the reader can appreciate that the generations become hopelessly confused. In warehouses and granaries the adults overwintering have their numbers greatly augmented during late spring and early summer by the newly emerged adults developing from the overwintering larvæ. It therefore happens that at this season of the year the adults are especially abundant in climates having a cold winter. The overwintering adults begin ovipositing early in the spring (often as early as February in warm buildings) and continue oviposition throughout the summer. Eggs laid during early spring hatch and develop through to adults by the end of June or early July. These midsummer adults lay eggs the larvæ from which usually winter over in all degrees of maturity; many become full grown by fall, and a few transform to the adult at that time. The larvæ that winter over transform in the spring and the emerging beetles lay eggs all through the summer and hibernate during the following winter. In subtropical and tropical climates it seems probable that development is more or less continuous and that there is much overlapping of generations.

TECHNICAL DESCRIPTION

THE BEETLE

Elongate oblong, subdepressed. Shining, dark reddish brown or piceous above; under surface, antennæ, and legs dark reddish brown. Thorax slightly wider than long, widely emarginate at apex, narrowed behind the middle, surface finely and evenly punctate. Elytra twice as long as wide, with base distinctly separated from that of thorax, sides nearly parallel, tips rounded; surface striate, intervals with two rows of fine punctures. Length 6.5 to 10 mm.

The original description of Linné (20) follows.

"*T. niger subtus piceus, thoracis marginibus antice posticeque dente angulatis. Similis praecedenti, sed quintuplo minor, supra totus niger, subtus, pedibus antennisque, piceus. Elytra striata. Thoracis margo antice dente utrinque prominulo, & postice dente obsoleto.*"

THE EGG

Slender, elongate, spindle shaped, often somewhat curved; milky white in color, opaque. Length 1.15 to 1.5 mm.; width 0.25 to 0.34 mm.

THE LARVA

FIRST STAGE

The young larva upon hatching measures 1.5 to 1.6 mm. in length and 0.3 mm. in width. It is slender, elongate, and flattened in form; white, almost transparent, in color with eyes and mouth parts darker. Body provided with a few long, stiff hairs. A little later the head capsule, thoracic and anal shields, and cerci turn to a light brown; still later the thoracic and anal shields become nearly black.

Width of larval head 0.23 to 0.28 mm., width of cerci about 0.11 mm.

SECOND STAGE

The second-stage larva is very similar in appearance to that of the first stage but larger and with the thoracic and anal shields darker in color. Length from 3 to 4.6 mm.; width from 0.54 to 0.9 mm.; greatest width of head 0.35 to 0.43 mm.; width of cerci 0.22 to 0.26 mm.

THIRD STAGE

Similar to preceding stage but larger. Length of body 5 to 8 mm.; width of body 1 to 1.5 mm.; greatest width of head 0.55 to 0.80 mm.; width of cerci 0.35 to 0.54 mm.

FOURTH STAGE

Similar to preceding stage but larger. Length of body 7 to 14 mm.; greatest width of body 1 to 2.5 mm.; greatest width of head 0.9 to 1.3 mm.; width of cerci 0.60 to 0.88 mm.

FIFTH STAGE

Mature larva (fig. 15, E) muddy white, elongate, flattened, sides nearly parallel, widest at third to seventh abdominal segments. Maximum length 19 mm., maximum width 3.5 mm. Thoracic segments each with a pair of five-jointed legs. Body soft-skinned. Prothorax with a large chitinized shield composed of two plates separated in the middle by a narrow suture that widens triangularly posteriorly, mesothoracic and metathoracic segments each with a pair of small, chitinized, dorsal plates. In each plate of the mesothorax and metathorax there is a peculiar, small, light spot, probably of glandular nature. Mesothoracic and metathoracic segments and abdominal segments 1 to 8 each with a small, fleshy papilla on alar areas. Abdominal segments 1 to 8 each with a pair of dorsal ampullæ. Body moderately hairy. Nine abdominal segments visible, ninth dorsally carrying a chitinous plate terminating in a pair of heavily chitinized cerci (pseudocerci).

Head (fig. 15, G, H) free, porrect, flattened, quadrate, about as wide as long, occipital foramen posterior and nearly vertical. Frons (fig. 15, G, f)

distinctly limited, large, triangular, extending to posterior margin of cranium, provided with four setae on each side. Clypeus (fig. 15, G, *c*) distinct, broadly

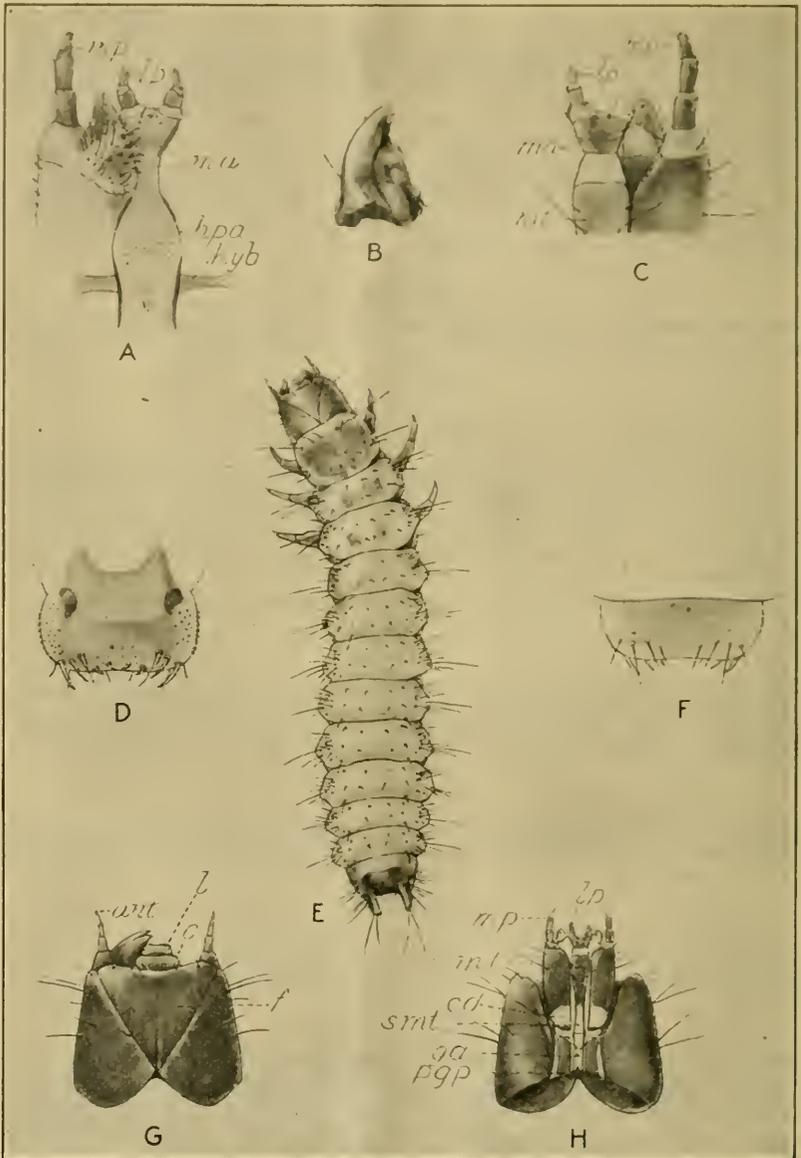


FIG. 15.—Details of fifth-stage larva of the cadelle; A, ventral mouth parts, dorsal view; B, mandible; C, ventral mouth parts, lateral view; D, under side of labrum; E, larva; F, upper side of labrum; G, head capsule, dorsal view; H, head capsule, ventral view. Explanation of abbreviations: *ant*, Antenna; *cd*, cardo; *f*, frons; *ga*, gular area; *hpa*, hypopharyngeal area; *hyb*, hypopharyngeal bracon; *l*, labrum; *lp*, labial palpus; *ma*, maxillary mala; *mp*, maxillary palpus; *mt*, mentum; *pgp*, paragular plates; *sm*, submentum

transverse, about twice as wide as long, not chitinized, leathery, posterior margin with two setae on each side. Labrum (fig. 15, F; G, *l*) subquadrate, considerably broader than long, lateral margins curved and provided with

minute spines, dorsal surface with four setae on each side, and with two pairs of sensory spots.

No epicranial suture, epicranial halves separated by gular area, the ventral epicranial margin from mandibular articulation of mandible to cardo slightly concave, and somewhat larger than rest of epicranial margin. Gula composed of a longitudinal, membranous gular area (fig. 15, II, *ga*) between a pair of paragular plates (fig. 15, II, *pgp*) which probably are separated from the posterior epicranial margin. The gular area bears a pair of large setae. Epicranial setae about six in series along lateral margin of cranium, one near frontal suture on disk of epicranium, one opposite to this near lateral margin, and four small setae near occiput; one seta on ventral surface near base of antennae, three small and one large setae along anterior ventral epicranial margin, and one near lateral margin of cranium. Ocelli five, near base of antennae, an anterior group of three and posterior group of two.

Antennae (fig. 15, G, *ant*) well developed, three-jointed, semiretractile, basal membrane large and semiglobular. Basal joint slightly broader and shorter than second joint which bears a small, fleshy, supplementary appendage and several small setae at distal end. Distal joint slender and bearing one long and two short terminal setae.

Mandibles (fig. 15, B) subtriangular, large, powerful, fitted for biting, bifid at tip, no molar part, a heavy spinelike process split up like a brush on inner margin near base, with two setae dorsally and near exterior margin. Ventral mouth parts (fig. 15, C) retracted, no maxillary articulating area. Cardo (fig. 15, II, *cd*) small, with posterior chitinization transversely placed at base of the equally well chitinized stipes. Stipes almost as long as frons, elongate, subrectangular, about three times as long as wide and much larger than cardo, connected with mentum along its entire inner margin.

Maxillary mala (fig. 15, A, C, *ma*) single, flattened, composed of two not joint-like, triangular pieces one above the other, the dividing line clearly indicated on ventral side, indistinct toward the buccal cavity; tip obtuse. On anterior margin just outside line which separates proximal and distal halves a stout, short, and pointed seta. Ventral surface of terminal piece bearing one large seta. Buccal surface of mala profusely covered with setae, on proximal half about seven very large, hooklike, and obtuse setae that look and work like a rake.

Maxillary palp (fig. 15, A, C, H, *mp*) three-jointed, carried by a membranous, subannular palpiger maxillae bearing two setae on ventral surface and dorsally a tuft of four hairs. Basal and second joints of maxillary palp with a group of minute hairs at tip, second and distal joints each with a seta. Submentum (fig. 15, H, *sm*) between cardines, entirely membranous, anteriorly sharply set off by chitinous mentum, posteriorly by a suture separated from gula. Mentum (fig. 15, C, H, *mt*) chitinized, elongate, subrectangular, bearing on its anterior half two pairs of setae, one smaller pair in front of the other large pair. Stipes labii much smaller than mentum and free, carrying two pairs of setae; no separately chitinized palpiger labii: labial palp (fig. 15, A, C, H, *lp*) two-jointed, basal joint with a tuft of hairs at tip. Ligula not developed, floor of buccal cavity soft skinned without any hypopharyngeal chitinization or paragnathal structures but both areas covered with minute asperities. Hypopharyngeal bracon (fig. 15, A, *hyb*) present, hypopharyngeal area (fig. 15, A, *hpa*) with two or three minute chitinized specks.

Epipharynx (fig. 15, D) carrying a pair of chitinized epipharyngeal plates fused in the middle. In front of these there are a pair of minute setae, a group of six asperities, and two sensory spots. Along the distal margin of the epipharynx are five thickened setae on each side.

Thorax: Dorsal areas undifferentiated. Prothoracic tergal region almost completely covered by tergal shield. Prothoracic tergal shield with seven pairs of small setae and one pair of large setae approximately arranged in three transverse rows. Each lateral margin outside tergal shield bearing six large and three small setae. The preepipleurum is small, the postepipleurum well developed. Hypopleurum with four setae and well developed prephepipleural chitinization. Presternal area marked by a pair of rounded, subtriangular plates each with two setae. Sternum large, composed of preensternum and ensternum, medianly covered with a large, heart-shaped, chitinous sternal plate. This plate is pointed anteriorly and has a large triangular indentation posteriorly, giving to it the heart-shaped appearance. The sternum carries several large setae. Poststernellum present and bearing a small, chitinous, subtriangular shield.

Mesothorax and metathorax subequal, each with two transverse rows of six small setae on tergum and each tergal margin with about nine setae. Preepileurum and postepileurum well developed, preepileurum of mesothorax bearing a large spiracle, hypopleurum with prehypopleural and posthypopleural chitinizations. Presternum, a larger sternum, a faintly indicated sternellum, and a well developed poststernellum present. Presternum with three setae on each side, sternum with four parts of setae and with a faintly indicated sternal plate. Sternal plate of mesothorax subrectangular and about twice as long as that of the metathorax which is quadrate.

Legs five-jointed, chitinized, tarsus and claw fused, tarsus with one seta, other joints each with several setae.

Abdominal segments dorsally divided into prescutum, scutum, scutellum, and postscutellum. Prescutum with six small setae. Scutum with a pair of setae. Alar area large, bearing a bifore spiracle, a small fleshy papilla, and one long, two smaller, and several minute setae. Epipleural lobe bearing two long, three smaller, and several minute setae. Hypopleural lobe bearing one long and three small setae. Coxal lobe bearing five setae. Sternum large, with two pairs of setae; sternellum without setae.

THE PUPA

Pupa uniformly creamy white in color; length from 7 to 10.5 mm., width from 2.5 to 3.5 mm.

Head subquadrate, provided with about 12 pairs of setae; clypeus with two pairs of setae and labrum with three pairs.

Prothorax subquadrate, provided with two pairs of anteromarginal, eight pairs of lateromarginal, two pairs of posteromarginal, and usually three pairs of dorsal setae.

Mesonotum and metanotum usually each provided with two or three pairs of minute, dorsal setae.

Abdomen with nine distinct dorsal tergites, the ninth being very much reduced and terminating with a pair of short, chitinized, pleural spines. Ventrally the ninth segment bears a pair of prominent fleshy processes. The tenth abdominal segment is small and ventral.

Median area of abdominal tergites 1 to 8 each provided with a pair of setae, lateral area of each tergite with a pair of setae, and pleural areas with a pair of long setae and several minute setae.

Tips of wing pads usually attaining the fifth abdominal segment; tips of metathoracic tarsi extending to tips of wing pads.

RESISTANCE TO STARVATION

The adults of the cadelle are fairly resistant to starvation even under normal conditions and particularly so when kept at a moderately low temperature. Adults kept in a warm room, with an average mean temperature of about 68° F., survived without food for 52 days. Others kept without food in a refrigerator, with a temperature ranging from 40° to 50° F., survived for a period of 184 days.

The larvæ are very resistant to starvation, much more so than the adults. Of a small lot of larvæ kept without food at room temperature, half of them survived for 4 months, several for 9 months, and one for 10 months. Another lot of larvæ were placed without food in a refrigerator with a temperature ranging from 40° to 50° F.; 10 per cent of these were still alive after 24 months of starvation, but succumbed soon thereafter.

With such powers of resistance to starvation it is easy to see how the cadelle is able to exist over the sometimes considerable periods that the grain bins are empty.

RESISTANCE TO LOW TEMPERATURES

The eggs and pupæ of the cadelle are rather easily killed by low temperatures and these two stages are never found during the win-

ter in the vicinity of Washington, D. C. The larvæ and adults, on the other hand, are very resistant to low temperatures and, protected as they normally are in granaries and storehouses, are able to survive very cold weather. Both larvæ and adults have survived exposure to a temperature of from 15° to 20° F. for a period of several weeks, and will even withstand a temperature of 0° F. for several hours without apparent injury.

CONTROL MEASURES

Cleanliness in the storehouse and granary is one of the most important factors in control. The habit of the larvæ of burrowing into wooden floors, partitions, and walls of bins, storehouses, and ships, accounts for much of the loss occasioned by fresh supplies becoming infested when placed in storage space formerly occupied by infested material. The substitution of concrete for wood whenever possible is one of the best means of preventing the rapid infestation of fresh supplies. On farms where grain bins are usually constructed of wood, hardwood should be used in preference to soft wood, and the construction made as tight as possible. Bins should be inspected annually and any badly burrowed woodwork removed.

The cadelle in all stages can be killed by fumigation with carbon disulphide, from 6 to 8 pounds per thousand cubic feet of bin space being used where bins are tight. In loosely constructed bins even 20 pounds per thousand cubic feet of space might not kill all cadelles in the grain and woodwork. Carbon tetrachloride, alone or in combination with ethyl acetate, has the advantage over carbon disulphide in that its vapor is nonexplosive and noninflammable, but it has the disadvantage of being about one-half to one-third as effective and must therefore be used in greater dosages.

Hydrocyanic-acid gas is effective in killing all stages of the cadelle. It has the disadvantage, however, of not penetrating bulks of grain and flour sufficiently to reach all cadelles. For this reason the cadelle, along with other beetles found in flour mills, can be better killed by the use of heat, as shown by Dean (7). Since the cadelle is nearly always associated with other common grain pests, any treatment applied for the control of grain pests in general will be effective against the cadelle.

SUMMARY

The cadelle, *Tenebroides mauritanicus* L., is a very common and destructive cosmopolitan pest of grains and grain products and was first described in 1758. It is usually associated in its attack upon food products with other grain pests. In the case of cartoned goods, such as breakfast foods, the economic importance of the cadelle is much enhanced by the holes it bores in the cartons, thus giving other and smaller pests avenues of attack upon foods that otherwise might remain immune from infestation. The cadelle prefers darkness and secretes itself in both larval and adult stages beneath any object or between sacks of flour or other containers of its food. It therefore is less often seen by the casual observer than other grain pests, even when rather abundant. Both adult and larva are restless feeders and consequently move about feeding here and there, preferring the

germ of the kernel and damaging many more seeds than they can consume. The habit of the larva of crawling into any substance in search of a protected place in which to hibernate or pupate results in the presence of the cadelle in many supplies upon which it does not feed. Since the larva and the adult may bore into wood for hibernation or transformation, the woodwork of granaries and the dunnage of grain ships may harbor thousands of cadelles, which can remain in hiding for months and be ready to swarm out to attack the next consignment of a food commodity that may be stored near them.

The adult cadelle is both predacious and granivorous and appears to produce more eggs if given animal food. Many adults live to be over a year old; one has been known to live almost 22 months. The length of the preoviposition period depends upon the time of year the adult emerges. Observations show that it may be as short as 15 days and as long as 210 days.

The eggs are laid loosely in flour or other food materials, or are tucked into crevices of any sort which offer protection. They may be laid daily or every other day, or more often at irregular intervals with 10 to 14 days or longer frequently intervening. The longest egg-laying period known covered almost 14 months, the first egg having been laid in August of one year and the last in October of the following year. Oviposition periods extending over one year are common, but such records are usually made by females that hibernate during the winter. Adults emerging early in the spring may complete their oviposition before winter. The largest number of eggs deposited by a single female was found to be 1,319; the minimum, 436.

The incubation period was found to range from a minimum of 7 days, when the mean temperature was 80° to 85° F., to a maximum of 15 to 17 days, when the mean temperature for the period was 70° to 71° F.

The larva is not considered to be predacious. Larvæ grow best when fed upon corn, wheat, and graham flour, when they may complete their growth in about 69 days. Those fed on rice grow more slowly. Those fed upon refined white flour develop very slowly. When given the most suitable food and normal surroundings, a great many larvæ complete their development and transform to pupæ within 3 months, a majority of them within 7 months, and all within 14 months. All larvæ hatching in March and April at Washington completed their growth and transformed the same year: 90 per cent of those hatching in May transformed that year, 40 per cent of those hatching in June, 10 per cent of those hatching in July, and none of those hatching during August or later transformed the same year. Reared larvæ having the shortest larval life and those having the longest larval life all hatched in June of the same year and were reared under identical conditions. Under less favorable conditions a larva has required as long as 1,248 days for development, but such long developmental periods are abnormal.

When about to transform, the larvæ form pupal chambers, usually by burrowing into some substance like wood. Once the chamber is sufficiently large it is sealed with borings mixed with a larval secretion. After a prepupal stage averaging about 9 days, the pupal form is assumed. The pupal stage lasts from 8 to 25

days. Apparently the cadelle does not pass the winter months in the pupal stage.

The shortest developmental period from egg to adult observed by the writers was 67 days, when the average mean temperature for the period was 81° F. The adult was a female and oviposited for the first time September 18, completing a cycle from egg to egg in 97 days. It is not likely that the cycle is ever much shorter in the vicinity of Washington, and is usually considerably longer. When the development from egg to adult is completed during a single season of activity the length of the cycle may be from 67 to 134 days. With life cycles during which the larva hibernates, the egg-to-adult period may last from 271 to 410 days.

The cadelle passes the winter months in the adult or larval stage. In warehouses and granaries the adults overwintering have their numbers greatly augmented during late spring and early summer by the newly emerged adults developing from the overwintering larvæ. Adults are, therefore, especially abundant during late spring and early summer in climates having a cold winter. Since overwintering adults begin ovipositing in spring, often as early as February in warm buildings, and continue to oviposit throughout the summer, and since the eggs laid during early spring hatch and develop by the end of June or early July, to adults that in turn lay eggs, the larvæ from which usually winter over in all degrees of maturity (although certain ones may produce adults by fall), the generations become thoroughly confused. In tropical and subtropical climates it seems probable that development is more or less continuous and that there is much overlapping of generations.

Cadelle adults at about 68° F. may withstand starvation as long as 52 days, or for 184 days at 40° to 50° F. Larvæ are more resistant and have survived starvation in warm rooms for 10 months. Certain other larvæ held at 40° to 50° F. without food were still alive after 24 months, but succumbed shortly thereafter.

The eggs and pupæ are easily killed by low temperatures and neither stage has been observed during the winter at Washington, D. C. Larvæ and adults are very resistant: both have survived exposure for several weeks to 15° to 20° F. and will withstand a temperature of 0° F. for several hours without apparent injury.

Among the control measures are cleanliness, fumigation, and the use of heat.

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UNITED STATES DEPARTMENT OF AGRICULTURE



DEPARTMENT BULLETIN No. 1429



Washington, D. C.



January, 1927

THE PARASITES OF POPILLIA JAPONICA IN JAPAN AND CHOSEN (KOREA) AND THEIR INTRODUCTION INTO THE UNITED STATES

By

CURTIS P. CLAUSEN, Entomologist

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Japanese Beetle Investigations, Bureau of Entomology

CHO TERANISHI, Assistant

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A female *Centeter cinerea* in the act of ovipositing upon *Popillia japonica* female

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THE GENERAL PROBLEM

The foreign work² in regard to the natural enemies of the so-called Japanese beetle (*Popillia japonica* Newm.) represents one phase of the general problem dealing with the control of this rapidly increasing insect. The work in Japan was initiated in the early spring of 1920, with headquarters at Yokohama, and investigations have been in progress continuously since that time, being confined for the first two years to Japan and extended in 1922 to Chosen. It is expected that importations of the various parasites found will be continued until establishment is certain, or it is demonstrated that environmental and other factors do not permit of its accomplishment.

¹ Valuable assistance was rendered in this work by Kaku Sato, who has been engaged on the project for the last three years. Yoshiro Ouchi also joined the force in 1923.

² During the writers' sojourn in Japan they were most courteously received and aided by all the Japanese Government departments, particularly by the department of agriculture and commerce. Special appreciation is felt for the great help rendered in many ways by S. I. Kuwana, director of the Imperial plant quarantine station, and his staff. Thanks are also due to S. Matsumura, professor of entomology at the Hokkaido Imperial University, for the use of the university collections; to H. Okamoto, entomologist of the Government general agricultural experiment station at Suigen, Chosen; to S. Kuwayama, entomologist of the Hokkaido Agricultural Experiment Station; and to the directors of the two last named stations, where laboratory facilities were kindly provided during the course of the field work.

To Baron Iwassaki and the directors of his estate at Koiwai grateful acknowledgements are made for working quarters during three seasons and for privileges which permitted an extended investigation of the most important area, from the point of view of *Popillia* parasites, thus far found in Japan.

Determination of species and descriptions of those which proved to be new have been made by J. M. Aldrich of the United States National Museum and S. A. Rohwer of the Bureau of Entomology, the former dealing with the Diptera and the latter with the Hymenoptera.

Popillia japonica was first found in the United States near Riverton, N. J., in the summer of 1916. The beetles no doubt entered this country in soil surrounding the roots of Japanese nursery stock shipped into Burlington County, N. J., at a date shortly prior to 1916. When first found the infestation covered an area of approximately one-half square mile and the beetles were exceedingly scarce, only about a score having been taken at that time. The increase in the area infested has been so great that the pest now (1925) covers some 6,047 square miles. The beetle is an omnivorous feeder and in recent years has caused serious destruction to both cultivated and native plants within this area, and to fruit and shade trees.

In the central portion of the infested area the numerical increase has been incredible, as is shown by the following statement from a recent publication by L. B. Smith, in charge of the Japanese beetle laboratory at Riverton:

During July, 1923, in an orchard of one hundred fifty-six 10-year-old Red-bird peach trees, thirteen 16-gallon tubfuls of beetles were shaken from the trees and collected early one morning, in somewhat less than two hours. The next morning the beetles were apparently as numerous on these trees as before.²

Popillia japonica entered the United States apparently free from its natural enemies, and its increase has been due not only to this fact, but to an acceleration of development in a new and apparently ideal environment. Under these circumstances it has become one of the major insect pests of the sections in which it now occurs. American parasites and predators thus far seem to be a negligible factor in preying upon it, and mechanical and cultural control methods are so far not wholly effective. In view of these facts the necessity for an attempt at control by the biological method is evident.

THE FIELD OF INVESTIGATION

The investigations in Japan were begun in 1920 at Nagasaki in the south (fig. 1) and extended northward as the season advanced. On account of existing agricultural conditions and methods in the southern half of the country and the absence of waste land, it was almost impossible to conduct extensive scouting for grubs in the soil. During the first 10 weeks of search only 76 grubs of *Popillia japonica* were found, even though beetles were later fairly common. With so small a number of grubs available, it was evident that the chance of finding parasites upon them would be very slight, and that extensive experimental tests with the various Scoliidæ and other parasitic species collected as adults in the field would be impossible. It was only on the arrival of the writers at Koiwai, in northern Japan, on July 12 that beetles and grubs were found in sufficient numbers to give hope of success in the search for parasites. It was in these northern sections that the greater number of parasite species were eventually obtained.

Although *Popillia japonica* itself was not found in Chosen, the presence of other species of the same genus gave promise of additional parasites of value. The five species of the latter found there substantiated this conclusion, since it was determined that none of these species was specific in its choice of hosts, but would reproduce equally well upon *P. japonica*.

² Smith, L. B. Service and Regulatory Announcements, Federal Horticultural Board, U. S. Department of Agriculture, October-December, 1923, p. 159.

In July of 1923 a scouting trip was undertaken through the central portions of Manchuria, extending from Antung on the Chosen border to Harbin in the north. The greater part of this area is very flat and almost entirely devoid of trees and shrubs. Only two species of *Popillia* (*P. castanoptera* Hope and *P. mutans* Newm.) were found in

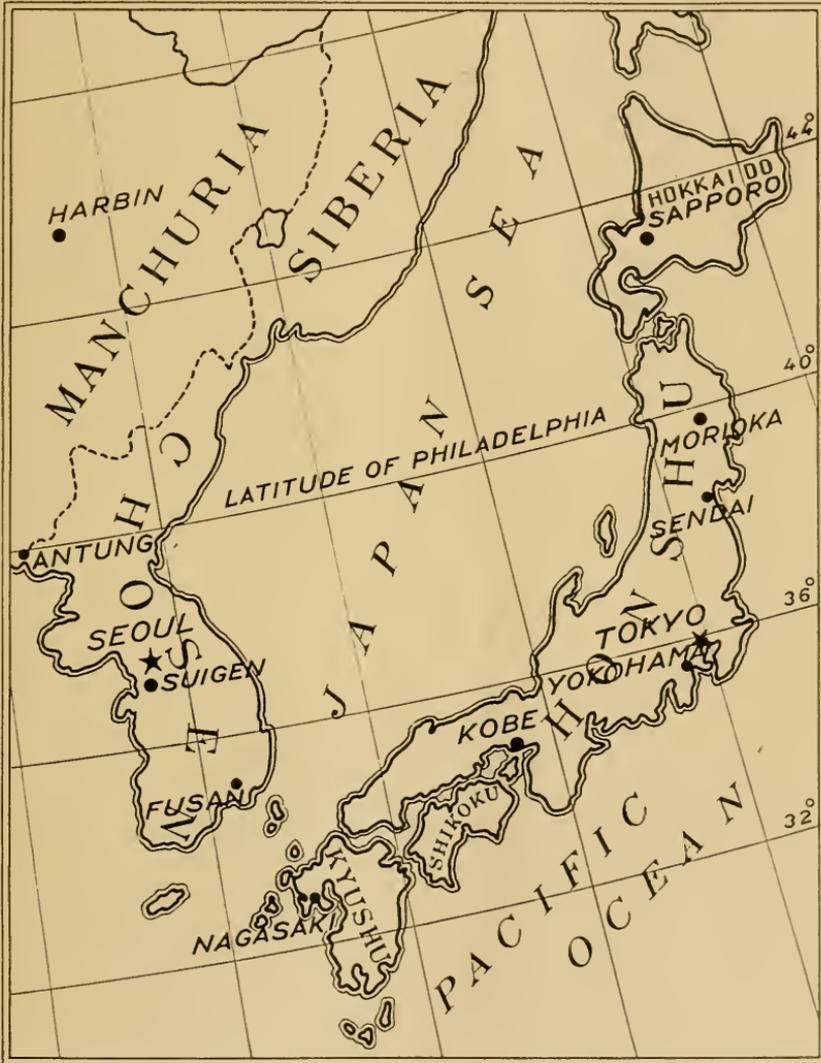


FIG. 1.—Map of Japan and Chosen (Korea) showing the main areas in which *Popillia japonica* and its parasites were studied

this section, and in such very small numbers as not to admit of parasite investigations.

THE PARASITES AND THEIR BIOLOGY

In the course of the investigations nine parasites of *Popillia japonica* and related species were found and their relations to the host species determined. In addition, one predator was studied in some

detail, and extensive shipments were made. The complete list is here given, those starred being found under natural conditions parasitic upon *P. japonica* itself.

Parasites of the adult beetle:

- **Centeter cinerea* Aldrich (Diptera, Tachinidae).
- **Eutrizopsis javana* Townsend (Diptera, Tachinidae).
- **Ochromigenia ornoides* Townsend (Diptera, Tachinidae).

Parasites of the larva:

- **Prosenia siberita* (Fabricius) (Diptera, Dexiidae).
- Dexia ventralis* Aldrich (Diptera, Dexiidae).
- Campsomeris annulata* (Fabricius) (Hymenoptera, Scoliidae).
- **Tiphia popillivora* Rohwer (Hymenoptera, Scoliidae).
- Tiphia vernalis* Rohwer (Hymenoptera, Scoliidae).
- Tiphia koreana* Rohwer (Hymenoptera, Scoliidae).

Predator:

- Craspedonotus tibialis* Schaum (Coleoptera, Carabidae).

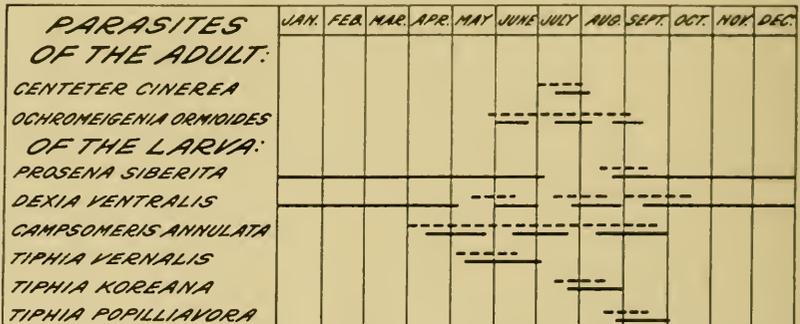


FIG. 2.—The sequence of parasites of *Popillia japonica* and related species. The dotted line represents the period during which adults may be found in the field, and the solid line indicates the time during which living parasitized hosts may be found.

In Figure 2 is given a representation of almost the entire series of parasites as regards their time of appearance and the stage of the host attacked. It is seen that all the species with the exception of the two dexiids pass the winter in the puparium or cocoon stage, these two species carrying over as early-stage larvæ within the host grubs.

In a consideration of this chart, it must be borne in mind that the periods given are as they occur under Japanese or Chosen conditions, which in some cases differ greatly from those in the infested area in America, and certain of the parasites are upon host species which have a different life cycle from that of *Popillia japonica* in the latter locality. The bearing of these factors upon the possible usefulness of the species in America will be discussed in detail in the account of the individual species.

CENTETER CINEREA Aldrich¹

The first evidence of parasitism of adult *Popillia japonica* by *Centeter cinerea* (fig. 3) was secured by the senior author on July 12, 1920, at Koiwai, Iwate-ken, about 300 miles north of Tokyo. Here the beetles were found abundantly feeding upon the foliage of itadori (*Polygonum Reynoutria*) (fig. 4) and other weeds, and a considerable proportion of them bore tachinid eggs upon the thorax.

¹ Determined by Doctor Aldrich as a new genus and species, and described under the above name. Aldrich, J. M. Two Asiatic muscoid flies parasitic upon the so-called Japanese beetle. Proc. U. S. Natl. Mus., Vol. 63, pp. 1-4. 1923.

The number of eggs present indicated that the attack was more than incidental. Observations were extended to the various sections north of Koiwai and to Hokkaido, the northern island. Here, at Sapporo, the proportion of beetles bearing these tachinid eggs approached 100 per cent. It was evident that this was a parasite capable of exerting a marked check upon *Popillia japonica*, and that it might well be of equal value if introduced into America.

Arrangements were at once made to study the species both at Koiwai and at Sapporo, to determine its life history, its method of parasitism, and other points in its biology which might prove of value in determining its relation to the host. Ways and means of breeding and handling were also sought in order that its importation into the United States in the living condition might be assured. These studies were continued for some 10 days, and a small number of parasitized beetles collected and confined in cages for observation, when the sudden and unexpected disappearance of both the host and parasite at Sapporo, and of the latter only at Koiwai,

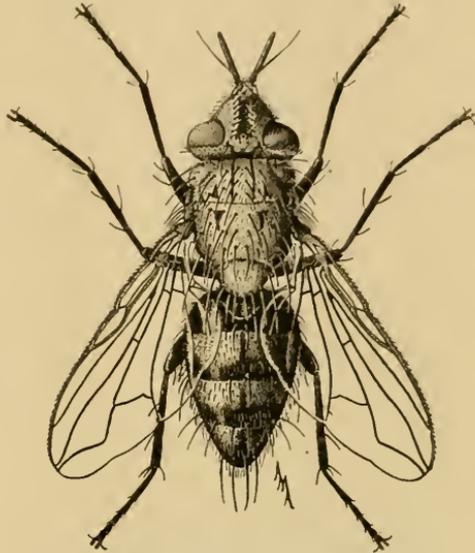


FIG. 3.—*Centeter cinerea*, female



FIG. 4.—Clumps of itadori (*Polygonum Reynoutria*), a favorite food plant of *Popillia japonica*, Koiwai, Japan

interrupted the work for the season. This was a development which was entirely unexpected, since the beetle itself had been present in numbers for not more than two weeks and it was

presumed that the activities of the parasite would be extended over a greater period of time.

No further studies upon the species being possible that season, attention was turned to the finding of other natural enemies of *Popillia japonica*. Observations were renewed in 1921, and in that and the following year studies and collections were made both at Koiwai and at Sapporo immediately upon the appearance of the first beetles of the season. In 1923 final observations and collections were made at Sapporo only, since at this place conditions for the work were nearly ideal, the area infested by the beetle being of considerable extent, the parasites abundant, and collectors available in unlimited numbers (fig. 5). Although the parasite is usually found in most localities north of Morioka, the greater part of the work was conducted at Sapporo because of the favorable conditions prevailing there.



FIG. 5.—Children engaged in collecting *Popillia* beetles parasitized by *Centeter cinerea*, Sapporo, Japan

As is pointed out in the account of the life history of *Popillia japonica* in Japan, there is for the most part a pronounced two-year life cycle in Hokkaido, resulting in an abundance of beetles every second year (1921 and 1923), with a lesser number during the alternate years. At Koiwai, although some of the grubs carry over for two years, the number of beetles emerging each year is fairly constant. This point is elaborated in the discussion of the life history of the host. Such deviation from the normal one-year cycle has had a pronounced influence upon the parasite itself as will be shown later.

FIELD OBSERVATIONS

Centeter cinerea was under close observation during the years 1920 to 1923, inclusive, and its behavior over this period has given a fair indication of its possibilities. Figure 6 shows the relative abundance of the beetle at Sapporo during the period mentioned, and the percentage of parasitism effected by *C. cinerea*. In 1920 the beetles were relatively scarce; the parasitism of the females exceeded 90

per cent during the time immediately following emergence, resulting in an abrupt reduction in numbers and the complete disappearance of the beetles by about the end of July, much earlier than would normally have been the case.

In 1921 this state of affairs was somewhat reversed, the beetles being approximately three times as abundant as in the previous year, whereas at no time did more than 31 per cent of the females bear eggs. The 1922 season practically duplicated that of 1920 in beetle scarcity and parasite abundance, whereas in 1923 the conditions of 1921 were repeated. The numerical abundance of *Centeter cinerea* is therefore in an inverse ratio to that of the host, the parasite being abundant when the host is at its lowest point, and vice versa. In the years of beetle scarcity there is a great duplication of oviposi-

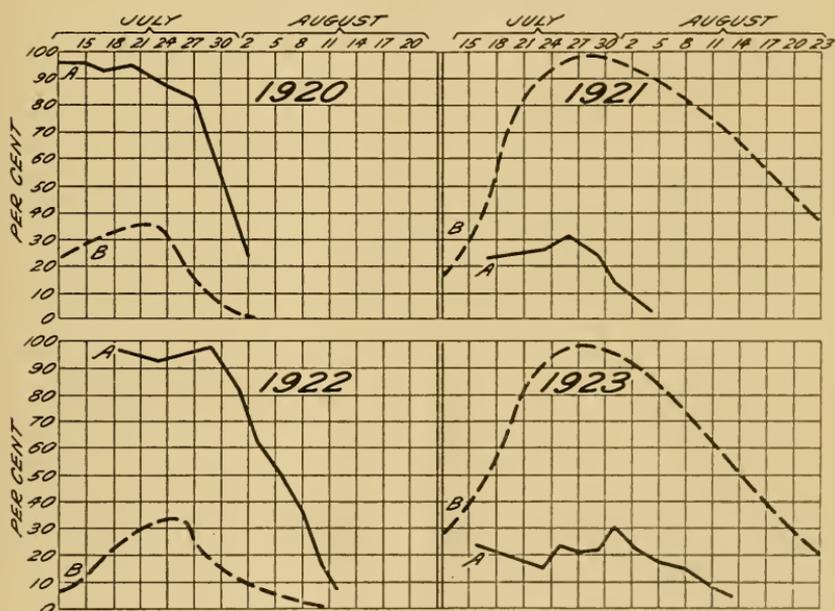


FIG. 6.—Curves showing the biennial broods of *Popillia japonica* at Sapporo, Japan, for 1920 to 1923, inclusive, and the relative parasitism of the female beetles by *Centeter cinerea*: A, percentage of beetles parasitized by *C. cinerea*; B, seasonal curve for abundance of adults of *P. japonica*, that for 1921 and 1923 being considered as approximately 100 per cent

tion by the parasite, female beetles having been found bearing as many as 14 eggs upon the body, whereas the average for 1,135 parasitized females was 4 eggs. Inasmuch as only one individual normally develops in a single host, it is evident that at this point a considerable proportion of the potential rate of increase is lost. The final result is that the following year sees a reduction in the actual number of flies available to parasitize the much greater number of beetles. In consequence, very little oviposition duplication occurs, as is shown by the fact that of 401 beetles bearing eggs, the average number of eggs borne was 1.1 per parasitized female. As a direct result of this a much greater proportion attain maturity than in the preceding generation, and thus the biennial cycle once more begins.

It may be well to consider the data obtained by counts made in the field during the years 1921 to 1923, inclusive, at Sapporo and Koiwai.

This is given in Table 1. At Koiwai the beetles were present in about equal numbers each year, and consequently conditions in this respect more nearly approach those found in New Jersey and Pennsylvania. Few actual counts were made in 1920, and none in 1923, so that data for only two years are available. It is known, however, that the general parasitism in 1920 approximated that of the following two years. It may be explained that in taking these data mating pairs were collected in the field and the number of eggs borne by each sex recorded. In this way a representative series of each sex was secured, and the figures are felt to be a fairly accurate representation of field conditions at the time the observations were made. The general averages cover the period from the appearance of the beetles in numbers to the cessation of oviposition by the parasite.

Reference to the tabulated data for Koiwai shows that in 1921 (Table 1) 42.1 per cent of the female beetles observed bore *Centeter cinerea* eggs, with an average of 1.4 per parasitized female. The males, on the contrary, were attacked only to the extent of 1.1 per cent. Of all eggs, 95.9 per cent were deposited upon female beetles. An explanation of this will be given later in the discussion of the manner of oviposition of the parasite. During 1922 the parasitism was somewhat higher than in the preceding year, the percentage being 58.4 for the females and 16.2 for the males, and the proportion of the egg total on the former 85.9 per cent.

TABLE 1.—Field parasitism by *Centeter cinerea* at Sapporo and Koiwai, Japan, 1921–1923

	Sapporo				Koiwai			
	Females		Males		Females		Males	
1921								
Total number of beetles examined.....	812		812		1,584		1,985	
Total number bearing <i>C. cinerea</i> eggs.....	158	19.5	32	3.9	667	42.1	36	1.8
Total number of eggs present.....	190		32		934		40	
Proportion on each sex.....		85.6		14.4		95.9		4.1
Maximum parasitism.....		22.6		4.7		53.2		6.3
Maximum number of eggs on one beetle.....	4		1		5		2	
Average per parasitized beetle.....	1.2		1.0		1.4		1.1	
1922								
Total number of beetles examined.....	1,292		1,292		500		500	
Total number bearing <i>C. cinerea</i> eggs.....	1,135	87.8	670	51.9	292	58.4	81	16.2
Total number of eggs present.....	4,507		1,096		614		101	
Proportion on each sex.....		80.4		19.6		85.9		14.1
Maximum parasitism.....		100.0		84.3		62.0		25.0
Maximum number of eggs on one beetle.....	14		6		6		2	
Average per parasitized beetle.....	4.0		1.6		2.1		1.2	
1923								
Total number of beetles examined.....	2,122		2,071					
Total number bearing <i>C. cinerea</i> eggs.....	401	18.9	22	1.1				
Total number of eggs present.....	475		22					
Proportion on each sex.....		95.6		4.4				
Maximum parasitism.....		30.5		1.5				
Maximum number of eggs on one beetle.....	4		1					
Average per parasitized beetle.....	1.2		1.0					

At Sapporo, with its biennial periodicity in beetle abundance, in 1921 there was an average parasitism in the females of 19.5 per cent, of the males 3.9 per cent, with 85.6 per cent of the egg total on female beetles. The following year revealed a parasitism of female beetles to the extent of 87.8 per cent, of the males 51.9 per cent, and the proportion of eggs on female beetles was 80.4 per cent. The third year, 1923, revealed 18.9 per cent of female beetles bearing parasite eggs, 1.1 per cent of the males, and 95.6 per cent of the egg total on the former. It is thus seen that conditions in 1921 and 1923 were practically identical and, though lacking exact figures for 1920, it is known that the parasitism for that year was approximately equal to that for 1922. These four years may therefore be taken as illustrating the normal cycle of *Centeter cinerea* at Sapporo.

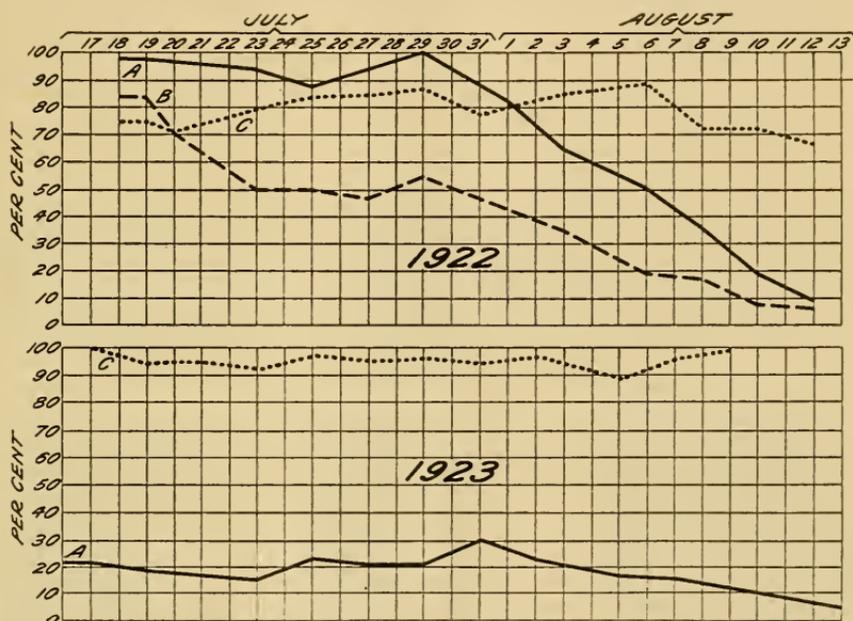


FIG. 7.—Curves showing the percentage of parasitism of *Popillia japonica* by *Centeter cinerea* at Sapporo, Japan, in 1922 and 1923: A, parasitism of female beetles; B, parasitism of male beetles; C, proportion of eggs laid upon female beetles

In Figures 7 and 8 are given in graphic form the data on parasitism at Sapporo in 1922 and 1923, and for 1921 at Kōiwai, these being the years when most extensive data at these places were obtained. The most striking difference in the graphs for Sapporo is that for the parasitism of the males, which in 1923 never exceeded 1.5 per cent, and therefore was too low to be represented on the chart, in 1922 attained a maximum of 84.3 per cent. In both years the graphs representing the proportion of eggs on female beetles remained approximately constant throughout the season, as it did also at Kōiwai.

The full effectiveness of this parasite is not indicated by the figures previously given, but is in reality somewhat greater. Life-history studies have shown that the beetles are killed within a period of six days after the parasite eggs are deposited; consequently practically all beetles bearing eggs on any given date are dead within six days thereafter, and the parasitized beetles in the field at the latter date

represent an additional percentage of the total. To illustrate this point, the graph representing the parasitism of female beetles at Koiwai during 1921 (fig. 8) may be cited. On July 14, 35 per cent bore eggs, these being replaced on the 20th by 45 per cent of the remainder, the latter in turn being replaced by 48.5 per cent of those



FIG. 8.—Curves showing the percentage of parasitism of *Popillia japonica* by *Centeter cinereus* at Koiwai, Japan, during 1921: A, parasitism of female beetles; B, parasitism of male beetles; C, proportion of eggs laid upon female beetles

remaining on the 26th. Thus, theoretically, the parasitism effected was 35 plus 29 plus 17 per cent, successively, during the period of abundance, totaling approximately 81 per cent of the entire infestation. The actual host mortality, however, was lower than this figure, since the mortality in the early stages of the parasite has not been taken into account.



FIG. 9.—*Popillia* parasitized by *Centeter*, in process of packing for shipment to the United States, 1921

COLLECTION AND SHIPMENT

Very extensive collections (fig. 9) of parasitized beetles were made at Sapporo and Koiwai in 1921 and at the former place only in the following two years. Two hundred and ninety-six thousand were secured during this period. As many as 200 men, women, and children

were engaged in collecting at one time. They were shown specimens of the beetle bearing eggs of *Centeter cinerea* and offered 50 sen (25 cents) per hundred for all brought in. In this way as many as 56,000 were secured in a single day during 1922. Since the beetle is killed within six days after the deposition of the egg it was evident that the feeding period of the host itself was very short, and consequently elaborate arrangements for providing food in the cages were not necessary. Cardboard boxes of about one-third cubic foot capacity were used, each being filled loosely with grape or *Polygonum* foliage, and from 500 to 1,000 beetles were placed therein. These boxes were set aside without further attention for six days, after which they were opened and the beetles still alive were permitted to escape, as the parasites of these had died without effecting the death of the



FIG. 10.—*Spalangia* sp., a parasite of *Centeter cinerea*

host. Had these beetles been permitted to die in the boxes their putrefying bodies would have exerted a detrimental effect on the larvæ and puparia present. It was found that the foliage in the boxes maintained a fairly high moisture content for a considerable period, so that pupation was effected without difficulty. Upon the completion of this the dead beetles containing the puparia were screened out and packed in moderately moist sphagnum moss for shipment to America.

From the shipments thus far made a large number of adults have been obtained. In 1922, however, only 700 adult flies were reared at the Riverton laboratory, but in 1923 approximately 7,000 were secured. These were liberated in the field, and beetles bearing *Centeter* eggs were found one week later. This colony survived the winter in good condition, for in the summer of 1924 beetles bearing eggs were found 2 miles from the point of the previous year's liberation, or covering an area of approximately 12 square miles.

SECONDARY PARASITISM

In the large shipment of *C. cinerea* material forwarded from Japan in 1921 there was contained a considerable infestation of several species of chalcid secondaries, the more important one being *Spalangia* sp. (fig. 10). The first trace of this hyperparasitism was found at Koiwai in an examination by dissection of a portion of the Sapporo-collected material shortly prior to shipment. The laboratory at Riverton, N. J., was immediately advised of this

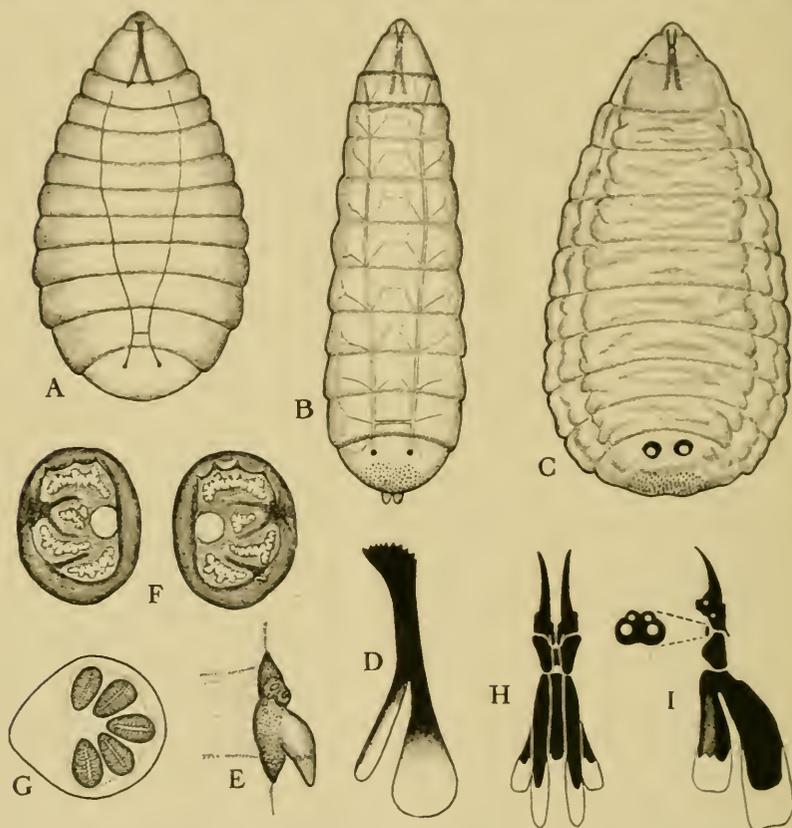


FIG. 11.—*Centeter cinerea*: A, first-stage larva; B, second-stage larva; C, third-stage larva; D, mouth parts, first-stage larva, lateral view; E, caudal spiracle, second-stage larva; F, caudal spiracle, third-stage larva; G, right anterior spiracle of same; H, third-stage larval mouth parts, dorsal view; I, same, lateral view

development and it was thus made possible to guard against the escape of the species at the time of emergence. The proportion of the puparia attacked in the two main shipments was approximately 10 per cent.

LIFE HISTORY OF CENTETER CINEREA

Hatching of the egg.—After having been laid, usually on the thorax, the egg develops rapidly, and the young larva is fully mature within 36 to 48 hours after oviposition. Unlike many tachinids this species does not hatch externally, but while still inside the eggshell drills

directly downward through the shell into the body of the host. The penetration of the heavy exoskeleton of *Popillia japonica* by so minute a larva is made possible by a modification in the structure of the tip of the mouth parts (fig. 11, D), which is provided with a row of heavy teeth forming a "rasper" by means of which a hole sufficiently large to permit of the passage of the body is made (fig. 12). The process of penetrating the thoracic wall is complete in 6 to 12 hours after its commencement, provided the temperature is reasonably high.

In the case of eggs deposited on other parts of the body, the larvæ in many cases are unable to effect entrance into the body proper.

About half of those deposited ventrally on the thorax fail to penetrate on account of the extreme thickness of the exoskeleton at this point. When placed on the elytra few ever reach the body cavity, for having passed completely through the wing cover, they still lie free on the outer surface of the body. Under these conditions they are unable to drill the necessary hole in the derm and soon succumb. Eggs are occasionally placed upon the legs, and of these the ones placed upon the femora are capable of reaching the body cavity, but those on the tibiæ very seldom do.

The larval stages.—In considering the development of the larvæ from the time of hatching onward, only those developing from eggs placed dorsally on the thorax will be dealt with, since this is the normal position. After penetration of the thoracic wall the young larvæ move about somewhat in the thoracic cavity, and the first molt takes place in this portion of the body. Migration to the abdomen occurs almost immediately after the first molt. In the second stage the spiracles are each equipped with a strong hook (fig. 11, E), and dissections of living beetles containing these larvæ indicate that the hooks serve to perforate and to attach the body temporarily to one or more of the numerous air sacs within the host, and that respiration is effected in this way.

After leaving the thorax the larva gradually works its way back to the tip of the abdomen, after which it turns and once more enters the thorax. The death of the female host occurs just prior to this point. The entire contents of the thorax are then consumed, the larva turns once more, enters the abdomen, and completes its feeding, usually devouring the entire body contents with the exception of some of the fully mature eggs. In the case of male beetles the second molt of the parasite takes place in the abdomen rather than in the thorax, and death of the host does not occur until the third stage is reached. Pupation takes place within the dead body of the beetle, with the head closely appressed to the tip of the abdomen. This occurs about four days after the death of the host.

Molting of both of the early stages takes place by means of an anterior split in the derm rather than by its sloughing off in fragments, as occurs in many tachinid species. The process is very readily observed by placing living larvæ of various stages in a normal saline solution, in which they will live for a considerable length of time.



FIG. 12.—Cross section of egg of *Centeter cinerea* upon the heavily chitinized thoracic wall of *Popillia japonica*, showing the aperture made by the first-stage larva in entering the host body

At first it might be supposed that the males, having a smaller quantity of food material in the body, would succumb to the attack of the parasite more quickly than the females, but this is not the case. The vital organs of the female are attacked sooner than those of the male and consequently death takes place earlier. A series of females under observation averaged 5.2 days from the time of deposition of the egg until death, whereas the males averaged 5.8 days, with a maximum of 6 days for the former and 8 days for the latter.

The time elapsing between oviposition and the pupation of the parasite was 9.1 days for the females and 9.2 days for the males. It is thus seen that the early stages of this parasite are of extremely brief duration. Shortly prior to its death the beetle host buries itself in the soil and thus the parasite, being within the body, is provided with an air-filled chamber within which to pass the dormant period.

The number of eggs deposited upon single beetles led to observations to determine if it were possible for more than a single individual to reach maturity in each host. In the case of excessive duplication of oviposition—that is, with five or more eggs upon the body—it was found by dissection that the surplus larvæ were killed in the second stage, whereas with less than that number the mortality occurred largely in the third stage. Two mature larvæ have been found in a single beetle, but the weaker of these is usually killed and the other pupates normally. In the laboratory, occasional instances have been noted of two puparia being produced in a single host.

Pupal stage.—Of a quantity of beetles collected bearing only one parasite egg each, 88 per cent eventually produced puparia, the remaining 12 per cent having died in the egg or first larval stage, and before any effect was produced upon the host. This loss resulting from mortality in the early stages is largely offset in the field by duplicate oviposition.

The mature fly.—The duration of the pupal stage averages about 10.5 months, and emergence is effected during the latter part of June at Sapporo. The cap of the puparium is broken off, the dorsal portion of the two caudal segments of the beetle abdomen pushed away, and the fly then works its way up through the soil into the open air. Emergence occurs largely during the early morning hours. Mating has not been observed.

Feeding occurs principally in the afternoon upon aphid honeydew and at the nectar glands of various plants, particularly itadori (*Polygonum Reynoutria*). At Sapporo large numbers of males and some females were collected on aphid-infested elm foliage. In the breeding cages honey or sugar water served very satisfactorily as food materials.

In the field the flies were found most commonly along roadsides, pasture borders, and streams, where more or less wild vegetation was present and where cultivation did not interfere with the puparia in the soil. In general it may be said that conditions suitable for the development of the host are also nearly ideal for the parasite. The degree of parasitism in the field was unusually uniform throughout all the types of habitat favored by the beetle.

Oviposition does not occur extensively during the cool days frequently prevailing in mid-July in Hokkaido, or upon the days of unusually high temperatures. The optimum condition for oviposition is a temperature of about 85° F. with a fairly high humidity

and the sky somewhat overcast. Under these conditions the beetles remain upon the foliage throughout the day, in contrast with their disappearance about noon on days when the temperature is high and the sunlight intense. This gives the fly a greater opportunity to oviposit, and its own inclination to continue this throughout the day rather than to remain quiescent on the foliage results in a much increased deposition of eggs.

The manner of oviposition is very unusual in that it leads to the placement of the egg on a restricted portion of the host body. In case the beetles attacked are feeding singly upon the foliage they take alarm immediately a fly alights in the vicinity, and a closer approach leads them to drop to the ground. For this reason oviposition normally takes place upon mating pairs, since these do not take alarm so readily. The female fly may stand about on the leaf for some time, apparently watching the beetles, after which she makes a dash for the pair, running diagonally across the thorax of the female and pausing only for an instant to place an egg thereon. About 98 per cent of all eggs laid are so placed and, under normal conditions such as prevail at Koiwai, about 85 to 96 per cent are upon female beetles. This has a very important bearing upon the effectiveness of the parasite.

Oviposition occurs at times on other parts of the beetle body. Occasionally a fly will approach the host from the rear, in which case the egg is placed upon the elytra, or from the side, when it may be laid on one of the legs. The greater proportion of misplaced eggs, however, are ventrally on the thorax, these having been so placed by oviposition through a hole in the leaf. Instances have been observed of female flies alighting directly upon the beetles from flight, and here there is no uniformity in the position of the egg. Occasionally a pronounced struggle may take place between the fly and the beetle, and both may drop to the ground. In this event, however, the attempt to oviposit is seldom successful.

The rate and duration of oviposition under laboratory conditions were observed in a series of 24 females collected in the field sufficiently

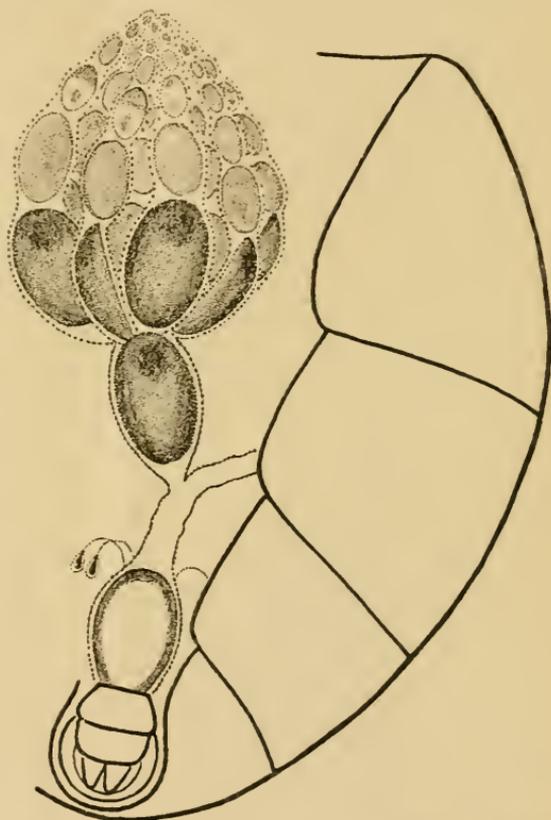


FIG. 13.—Reproductive organs of female *Centeter cinerea*

early to preclude the possibility of any extensive oviposition having previously taken place. The greatest number of eggs secured from a single individual was 62, and the maximum for one day 21. None of the females lived longer than eight days in captivity, this certainly being much less than the normal under field conditions. In the field, oviposition ranges over a period of about two weeks, and exceeds 100 eggs.

Dissections of gravid females showed that each of the large, spherical ovaries (fig. 13) consisted of an average of nine follicles each. The number varied from 6 to 11, and in the greater propor-

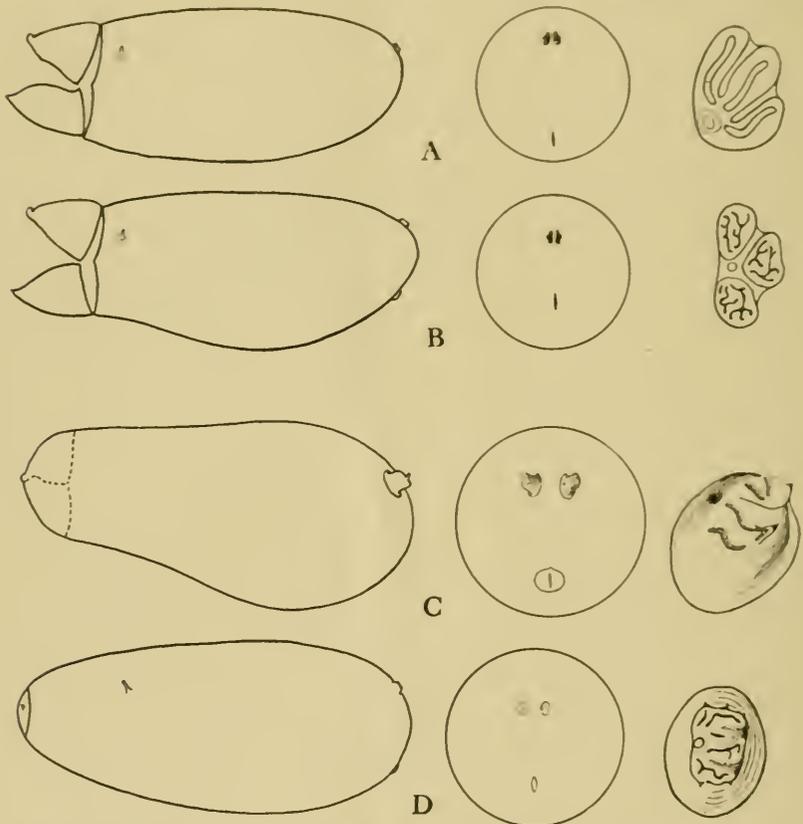


FIG. 14.—Dexiid and tachinid puparia, showing their distinguishing characters: A, *Dexia ventralis*; B, *Prosenia sibirita*; C, *Ochromyenia ormioides*; D, *Centeter cinerea*

tion of individuals was the same in each ovary. An average of 11 mature eggs was found in the gravid females examined. A single egg was always present in the ovarian sac, one in one or both of the ovarian tubes, and a varying total in the follicles. Each follicle normally contains one fully developed egg, one slightly more than half size, and a series of buds of diminishing size.

It appears from the observations made that a follicle is capable of developing a single egg daily, and that consequently the number of follicles present determines the potential daily rate of oviposition, those with a total of only 14 follicles being capable of producing only

that number of eggs, whereas one with 22 follicles yields a correspondingly greater number. This conjecture is borne out by the subsequent examination by dissection of the ovaries of the particular females under observation.

CHARACTERS FOR DETERMINING THE IMMATURE STAGES OF CENTETER CINEREA

First-stage larva (fig. 11, A).—Length approximately 0.7 mm.; color white. Mouth parts modified for rasping, as shown in D. Visible tracheal system consisting of two longitudinal trunks; caudal spiracles small and inconspicuous.

Second-stage larva (fig. 11, B).—Posterior spiracles fairly prominent, with a hooklike projection, as shown in E. The main tracheal trunks fairly heavy, with two main transverse commissures connecting them at the fourth and eleventh segments. Posterior half of last segment and hind margin of the eleventh segment bearing numerous short but stout spines. There are two prominent lobes at the anal opening.

Third-stage larva (fig. 11, C).—Length 8 to 10 mm.; color white. Mouth parts as shown in H and I. Anterior spiracles with five openings, as in G. Posterior spiracles as in F. Posterior area of the caudal segment bearing numerous stout spines.

Puparia (fig. 14, D).—Length 5 to 7 mm.; color brown, surface striate, reflections dull. Shape elongate-oval. Thoracic spiracle present, in the form of an elevated tube; posterior spiracle as in D.

OCHROMEIGENIA ORMIOIDES Townsend

GENERAL OBSERVATIONS

Adults of *Ochremeigenia ormioides* were first obtained from *Popillia japonica* collected at Yokohama in June, 1921 (fig. 15). It was later found as far north as Koiwai, Japan, and at Suigen, Chosen. The species was first described by Townsend from collections made in Java, and it has also been recorded from western China. As far as known it is a parasite of adult Scarabaeidae only.

Apparently this species is more or less periodic in its occurrence on *Popillia*. In the summer of 1920 empty puparia were found in the breeding cages, which later proved to belong to this species. The number obtained at this time was small, indicating an exceedingly low percentage of parasitism. In 1921 collections yielded less than 1 per cent of parasitized beetles. However, collections in 1922 in the vicinity of Tokyo and Yokohama ran as high as 35 per cent, and this was followed in 1923 with a 6 per cent parasitism.

Ochremeigenia ormioides has three broods of adults per season, the first two of which parasitize *Popillia* and the third develops in other Scarabaeidae.

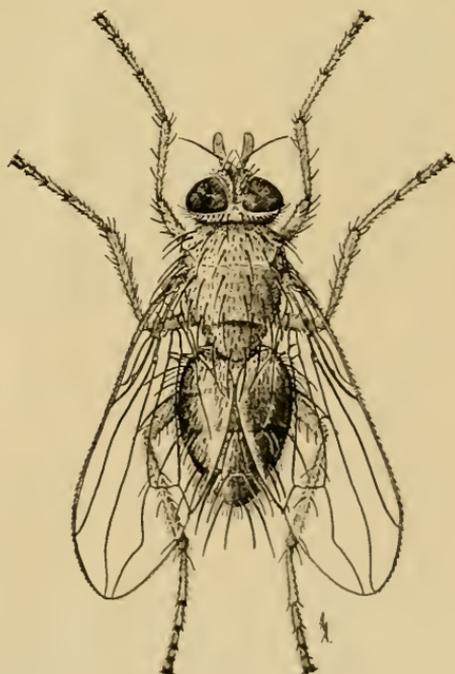


FIG. 15.—*Ochremeigenia ormioides*, female

SHIPMENTS

Shipments of this parasite were made by collecting large numbers of *Popillia* in the field and forwarding them without delay. During the ocean voyage this material is held in cool storage at a temperature of 40 to 50° F. The transcontinental shipments are made by express, at normal car temperature, from Seattle, Wash., to Riverton, N. J. Material in refrigeration between these two points has given poor results as compared with material shipped at normal car temperature. On June 27, 1923, 4,000 beetles were shipped from Yokohama, 5 per cent of which were parasitized. Shipments made in 1924 proved successful and from these about 100 adults have been reared and liberated.

LIFE HISTORY

This tachinid is nocturnal in its habits, remaining quiet during the day concealed on the under surface of foliage of low-growing plants

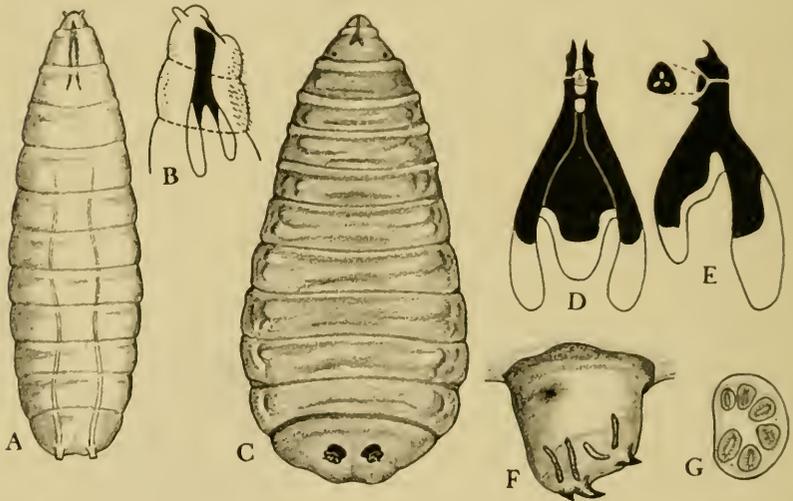


FIG. 16.—*Ochromygenia ormioides*: A, first-stage larva; B, lateral view of head showing mouth parts, first-stage larva; C, mature larva; D, mouth parts, mature larva, dorsal view; E, lateral view of mouth parts, mature larva; F, right posterior spiracle, mature larva; G, right anterior spiracle, mature larva

and in dense undergrowth. In large cages the flies frequently rest on the upper woodwork 5 feet above the ground. They become active at 6.30 to 7 p. m. during July. On account of their nocturnal habits and their attraction to light it is difficult to observe their normal actions. In nature this fly has been observed to feed on honeydew.

The females deposit larvæ rather than eggs. The exact method of placement of these in regard to the host and the manner of penetration of the larvæ into the host have not been determined. Female flies when in cages with *Popillia* beetles manifest considerable interest in them by following them about with the antennæ erect and abdomen curved slightly under and forward as if preparing to larviposit. Frequently they will sidestep in a circle around a beetle, investigating it with extended antennæ; then they will run up over the beetle,

approaching it from behind. During this performance they always stand high on their legs and curve the abdomen under and forward. However, careful examinations of beetles after these actions have failed to reveal larvæ upon or within them. Living first-stage larvæ of this fly in one instance were deposited on the glass of the breeding tube, but when transferred to beetles they were soon lost. The first-stage larvæ (fig. 16, A) are very delicate and can not stand much exposure to dry air. Examination of the female flies fails to show any piercing organ by which the larvæ could be introduced into the host. It is possible that the larvæ may enter either through the genital or anal opening, or if they gain access to the softer body wall under the elytra they may penetrate there. The mouth parts of these first-instar larvæ (fig. 16, B) are not specialized in any way as in *Centeter cinerea*.

The puparia of this parasite (fig. 14, C) are formed within the beetle in the same position as those of *Centeter*, and like it are buried in the ground within the air cavity formed by the body of the dead beetle. The adults when emerging push away the dorsal portions of the last abdominal segments. The period of pupation ranges from 11 to 13 days, with an average of 12 for the first part of July at Yokohama.

The lack of definite data concerning the time of parasitism of the host makes it impossible to determine exactly the length of the entire life cycle. However, adults have been obtained as late as 20 days after the collection of parasitized beetles.

This tachinid has two, and possibly three, generations a season under Yokohama conditions. Adults have been found as early as May 24 in Chosen and as late as September 3 at Koiwai and September 13 at Yokohama.

At Yokohama this fly has also been reared from adults of *Anomala rufocuprea* Motsch. and (*Anomala*) *Phyllopertha orientalis* Waterh., and in Chosen from *Popillia atrocoerulea* Bates and *P. mutans* Newm.

CHARACTERS FOR DETERMINING THE IMMATURE STAGES OF OCHROMEIGENIA ORMIOIDES

First-stage larva (fig. 16, A).—Length of newly hatched larva approximately 0.5 mm.; color white, pellucid. Sensory papillæ prominent. Mouth hooks present; pharyngeal plates as in B. Visible tracheal system in two parallel tubes; caudal spiracles stalked.

Third-stage larva (fig. 16, C).—Length approximately 9 mm.; color white. Mouth parts as in D and E. Posterior spiracles raised on a disk which bears from three to four hooklike spines; spiracular openings usually four in number.

Puparium (fig. 14, C).—Length 6 mm.; color dark brown, shining. Posterior half swollen. Caudal spiracles elevated and spined as in the larva.

EUTRIXOPSIS JAVANA Townsend

Eutrixopsis javana (fig. 17) was first reared at the Japanese beetle laboratory in June, 1923, from a shipment of *Centeter cinerea* material forwarded from Sapporo, Japan, in 1922, and comprised 210 *Eutrixopsis* out of a total emergence of 6,734 tachinids, or 3.1 per cent of the total. However, since all the beetles collected for this shipment were those bearing *C. cinerea* only, it is not possible from this collection to make any statement as to the status of *Eutrixopsis* in Japan, although it is undoubtedly secondary in importance to the species previously mentioned. Whether it deposits eggs which are

indistinguishable from those of *Centeter*, or produces living larvæ as does *Ochroemeigenia*, is not known.

The life cycle apparently corresponds closely to that of *Centeter*, only one generation a year being produced.

PROSENA SIBERITA Fabricius

GENERAL OBSERVATIONS

As in the case of *Centeter cinerea* and *Tiphia popilliavora*, the first trace of parasitism by this species upon *Popillia japonica* was obtained at Koiwai, this being in early August, 1921, when four grubs were

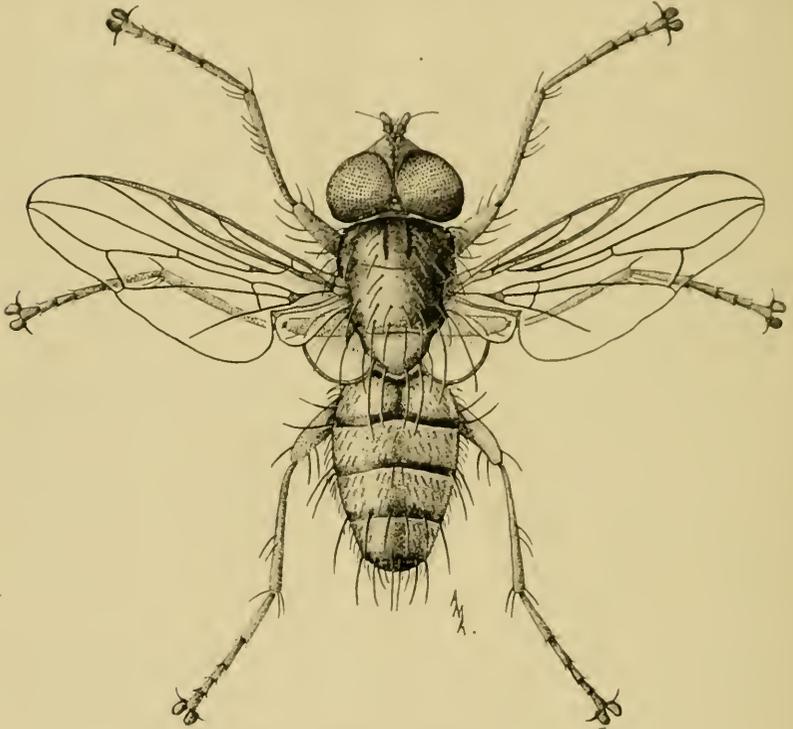


FIG. 17.—*Eutrizopsis jarana*, female

found containing mature larvæ. Breeding experiments were started immediately with adult flies from the field, presumed to be the same species, and the emergence of the adults from the larvæ previously collected later confirmed this conclusion (fig. 18).

Extended investigations on this parasite in Hokkaido revealed it in considerable abundance in several localities, and at Kotoni, a short distance from Sapporo, the field parasitism in 1922 and 1923 was approximately 10 per cent. *Prosenia siberita* is found abundantly throughout northern Japan and, according to literature, occurs also in Europe, continental Asia, and the Oriental region, where it has been recorded from Java.

METHODS OF REARING AND COLLECTING FOR SHIPMENT

Considerable difficulty was experienced in breeding this parasite because of the extreme nervousness of the field-collected females under laboratory conditions, resulting in very early death, and the fact that larvæ were produced rather than eggs. Under normal conditions the young larvæ are deposited on the surface of the soil and they then burrow about in search of host grubs, into which they penetrate very quickly.

An examination of gravid females revealed the ovarian sac as containing upward of 800 eggs and larvæ, the number of the latter being variable, ranging from 50 to 300, and located in the terminal

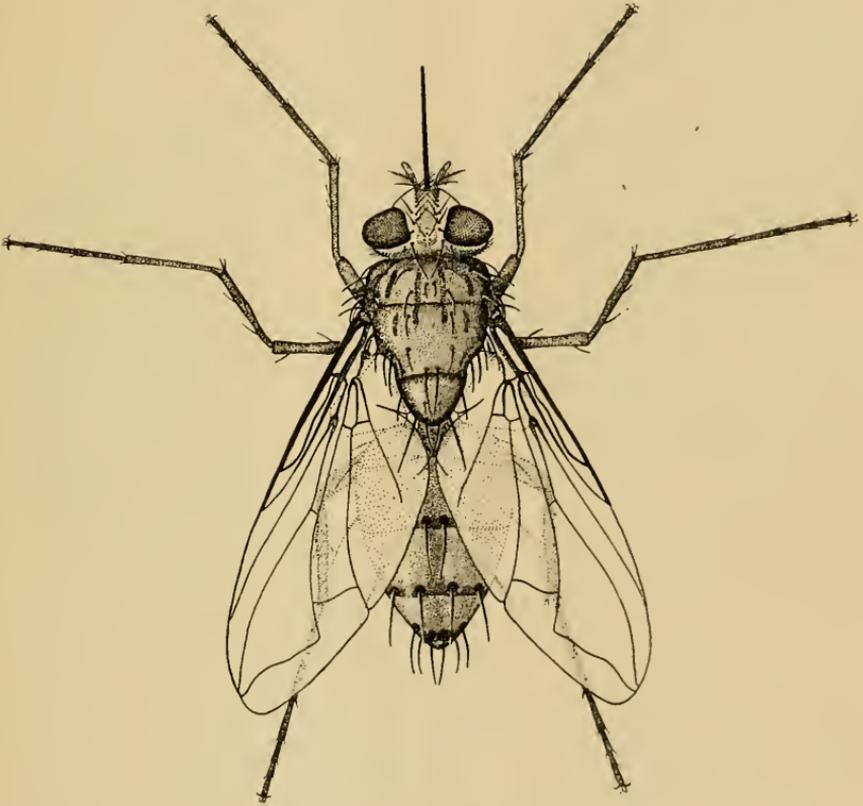


FIG. 18.—*Prosenia siberita*, female

portion of the sac (fig. 19). When the wall of this sac was broken with a scalpel or needle the young larvæ were immediately liberated and quickly crawled away. Experiments indicated that larvæ obtained in this way were normal in every respect and were able to penetrate the host and to develop without difficulty. This brought up the possibility of the use of this method in breeding work, the larvæ to be transferred to the host by means of a fine brush. Results were very satisfactory, and practically 100 per cent effectiveness was obtained from these inoculations. At first the half-grown host grubs were placed in individual vials of one-half inch diameter and five or six *Prosenia* larvæ placed upon each, the vials then being filled with

soil to the depth of 1 inch. Many of the larvæ effected penetration within one or two hours after being placed on the grubs, but ordinarily the vials were set aside for 24 hours to insure a maximum parasitism. In 1922 porous-clay blocks were substituted for the vials, each of

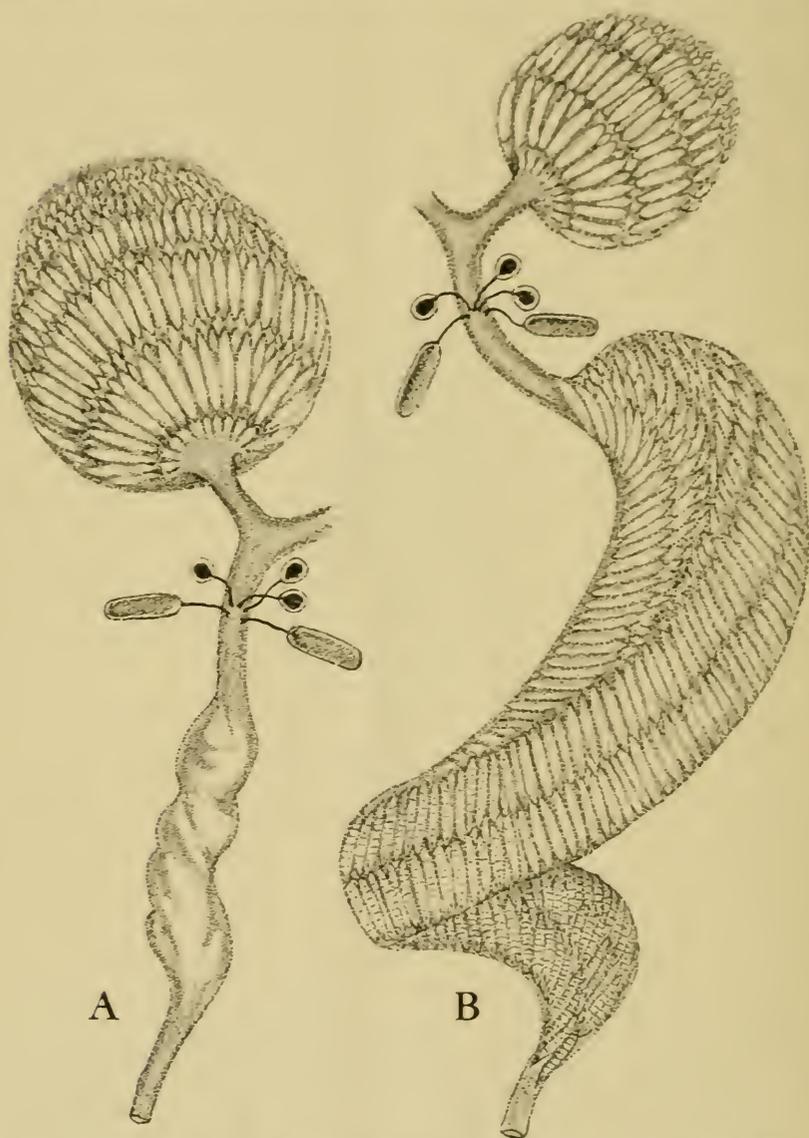


FIG. 19.—Reproductive organs of *Prosema siberita*: A, condition before mating; B, after fertilization, showing eggs and larvæ in the distended egg sac

these blocks bearing upwards of 100 cells of a size suitable to accommodate the grubs used. These blocks were more satisfactory in every way and resulted in a considerable saving in time. With this method it was possible for one person to inoculate more than 1,000 grubs per day, provided a sufficient number of flies were available.

In this manner about 800 grubs were inoculated in 1921 and 7,800 the following year. The greater proportion of the flies collected in the field either contained eggs alone or had already deposited their larvæ, so that the average number procured from each fly did not exceed 50.

Upon completion of the field work for the season the parasitized grubs were forwarded to the Riverton laboratory. It was found as a result of these two years' work that the mortality in shipping from Japan and in holding the grubs under laboratory conditions throughout the winter was so great as to render the general method impracticable. Late in 1922 a locality was found in Hokkaido where adult flies were abundant, and this gave promise of a fair percentage of parasitism in the overwintering grubs in the soil. An examination of the field grubs in April of 1923 revealed an average parasitism of 10 per cent. Collections were consequently made of some 11,000 grubs and these were shipped to New Jersey about the middle of June. At the time of collection it was not possible to distinguish between those parasitized and unparasitized, and consequently it was necessary to forward the entire lot. This method of importation resulted much more satisfactorily, since approximately 70 per cent of the parasite larvæ in the shipment yielded adults during July and August, at Riverton.

LIFE HISTORY

The young larva (fig. 20, F), after being deposited upon the soil, burrows about in search of host grubs, being guided probably by the sense of smell. When the host has been found the larva seeks out a crevice or suture in the integument and commences penetration, this being effected in one to two hours. It now lies free within the host body, surrounded by fluids and masses of fatty tissues. No permanent connection for respiratory purposes is made in this stage either with the tracheal system or through the derm. Early in the second stage, however, the caudal spiracles are attached to a main tracheal trunk near the thoracic or first abdominal spiracles of the host (fig. 21, A). The body is directed caudad, and feeding takes place largely in the mid-abdominal region.

The second molt occurs ordinarily in the early spring, and at this time the dark chitinous respiratory funnel appears as a covering of the posterior segments of the larva. In some cases, where the point of attachment is very close to the spiracle, this funnel is dimly visible externally, but dissection is necessary for verification. Development in the final stage is very rapid, and the body of the host becomes more translucent in color, because of the consumption of the fat bodies which normally are present in large masses. The host remains alive and active until practically all of the body contents, aside from the vital organs, are consumed, though during the week preceding death evidence of life is presented only by a spasmodic twitching of the maxillæ or legs.

After the death of the host the Prosenal larva tears a hole ventrally in the integument of one of the distal segments of the abdomen, then severs its connection with the respiratory funnel, reverses its position, and completes feeding in the thoracic region. This being

accomplished, and the body contents entirely consumed, it again turns and leaves through the aperture previously made. Pupation takes place in the soil 1 or 2 inches beneath the host remains.

The duration of the various stages in the life cycle is not uniform, and the early stages may be greatly prolonged. The newly deposited larvæ are capable of wandering about in the soil for a week or more in

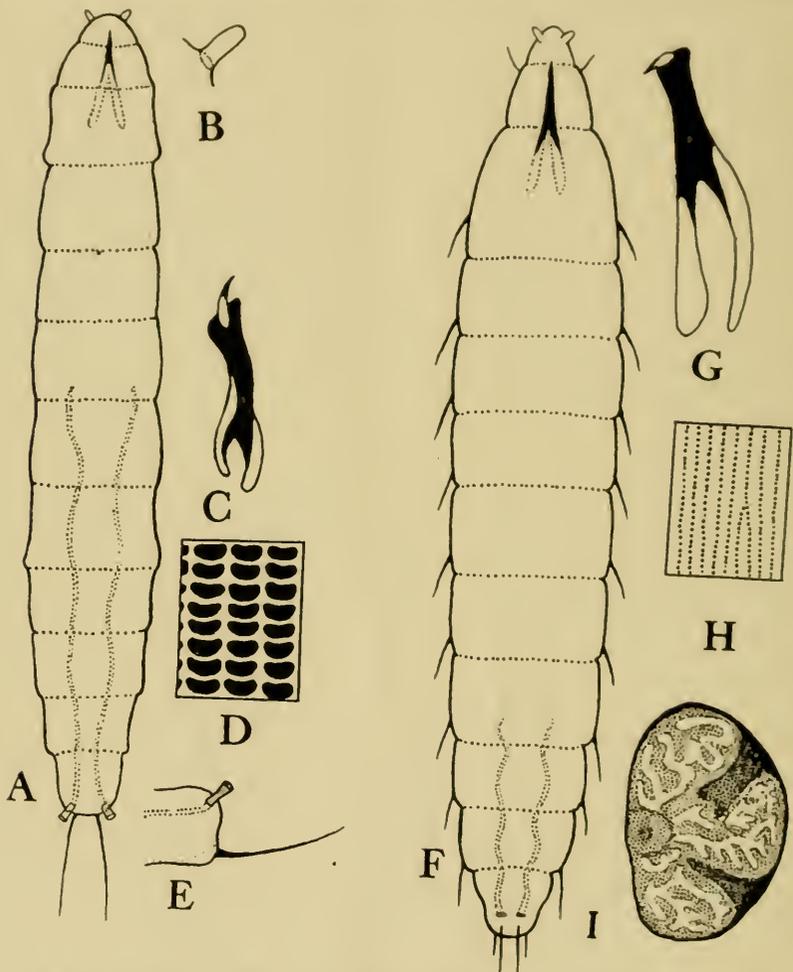


FIG. 20.—A, first-stage larva of *Dexia ventralis*; B, antenna; C, mouth parts; D, enlarged portion of derm; E, lateral view of caudal end of larva; F, first-stage larva of *Prosema siberita*; G, mouth parts; H, enlarged portion of derm; I, posterior spiracle of third-stage larva, *Prosema siberita*.

search of the host, and after entrance is effected the further duration of the stage is dependent on temperature conditions and may be extended to the following spring. Usually, however, the first molt occurs during the fall, and the winter is passed in the early second stage. The third stage is relatively short, as determined by dissections of a considerable series of parasitized grubs during May and June.

At Sapporo the pupation of the earlier individuals begins about the first of July and ranges over the entire month. Under high temperature conditions the pupal stage averages about 22 days, whereas at Sapporo it may extend to 30 days in case the weather is cool. Emergence occurs during the early morning hours.

HABITS OF THE ADULT

The adults are somewhat crepuscular in habit, being active on bright days largely about sunset, but at Koiwai the greatest numbers were always to be found during the rainy periods which occurred almost daily, and practically all collections were made under these conditions. Heavy rains, however, caused them to remain quiescent on the under sides of surrounding foliage. Feeding takes place largely at the blossoms of two umbelliferous plants (*Seseli libanotis* and *Patrinia scabiosaefolia*).

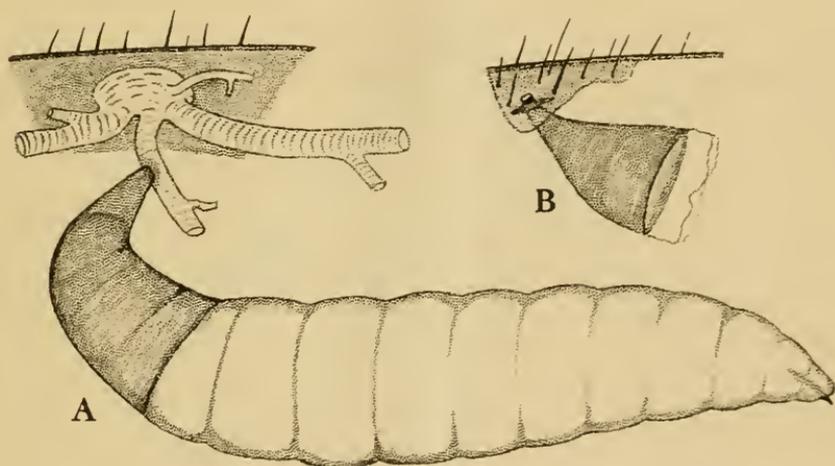


FIG. 21.—A, larva of *Proseña siberita* in situ, with tracheal funnel attached to trachea of host; B, tracheal funnel of *Dexia ventralis* penetrating the derm of host

Mating is effected largely upon the blossoms of these food plants or upon surrounding foliage and at times upon tree trunks. The pairs may remain in copula for a considerable period, and at this time may be captured very readily. Single individuals are very active and take alarm quickly.

CHARACTERS FOR DETERMINING THE IMMATURE STAGES OF PROSENA SIBERITA

First-stage larva (fig. 20, F).—Length of newly hatched larva approximately 1 mm.; color white. Mouth hooks present; pharyngeal plates as in G. Sensory papillae prominent. Derm finely striate. Body segments each bearing a strong lateral bristle; caudal setae four in number. Posterior spiracles sessile.

Third-stage larva (fig. 21, A).—Length 14 mm.; color white. Caudal spiracles as in Figure 20, I. Tracheal funnel always attached internally to the large tracheal trunk of the host near the thoracic or first abdominal spiracles.

Puparium (fig. 14, B).—Length 10 to 12 mm.; color dark brown, reflections dull, surface striate. Posterior spiracles divided into three lobes bearing the branchlike design of the former tracheal openings; thoracic spiracle present in the form of an elevated tube.

DEXIA VENTRALIS Aldrich

Dezia ventralis (fig. 22) is the most common of the dexiids of Chosen, and was first found shortly after the commencement of investigations in that country in late May, 1922. Experiments with it upon grubs of *Popillia japonica* indicated that it would develop satisfactorily in that host, and, consequently, further studies were made upon its biology.

In distribution, this species covers all of Chosen and also the plains area of Manchuria, which latter was scouted during the summer of

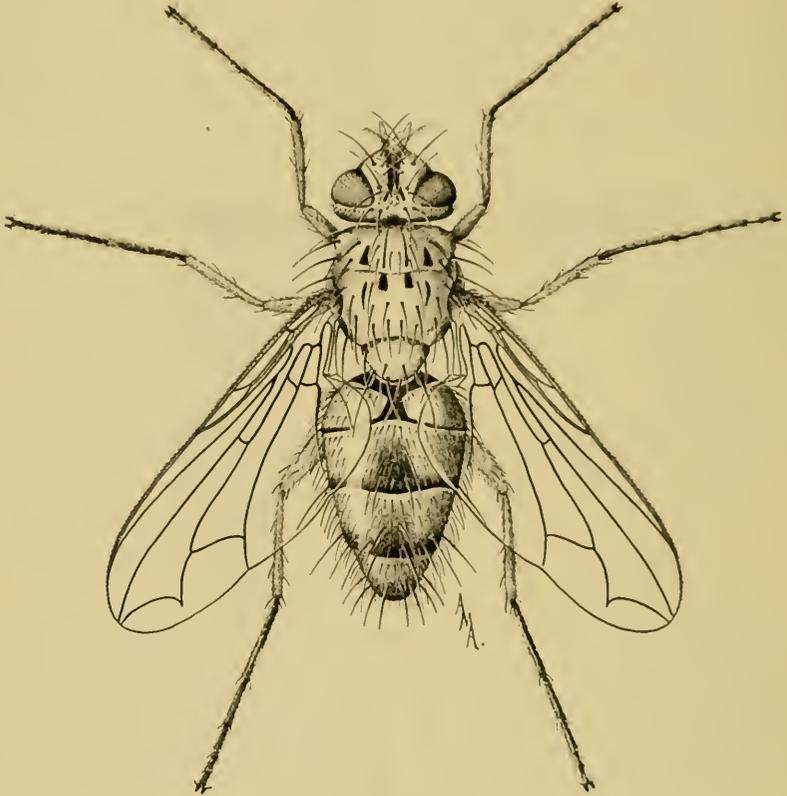


FIG. 22.—*Dezia ventralis*, female

1923; but it is most common in the central portions of the former country. It is also recorded from the Malayan region. Practically all of the breeding and life-history work was done at Suigen, Chosen.

No shipments of this species have been made to America as yet on account of the necessity of first determining certain factors in its biology which have an important bearing upon its potential value under the changed conditions. These various factors will be discussed in detail later. The earlier observations indicated only one generation per year, and since the adults appeared in late May and disappeared within one month it was naturally concluded that the

parasite could not be of value against *P. japonica* in America. The 1923 investigations, however, revealed two additional generations each year, and this fact changed the status of the species markedly as regards its potential value.

LIFE HISTORY

In a consideration of the life history of *Dexia*, the young larvæ produced by the spring generation of females may be taken as the starting point. These burrow about in the soil in search of hosts in exactly the same manner as *Prosenia*, and penetration is effected in the same way. This occurs largely on the dorsal portion of the anterior half of the body. Here the analogy between the two species ends, however, for the young larva upon penetration attaches its caudal end to the aperture in the derm of the host and thus sets up immediately respiratory connection with the outside air. (Fig. 21, B.) The first molt occurs within a few hours thereafter, and consequently the dark-colored respiratory funnel is distinctly visible externally on the same day that the host is entered. This is in marked contrast to the attachment of the respiratory funnel of *Prosenia* in the early second stage to the tracheal trunk of the host, the funnel of which is not visible until the host is almost entirely consumed. Feeding during the early stages is largely upon the fluid contents of the host body, and in the later stages upon the fat bodies, and finally on the vital organs. During this period the parasite body lies with its head directed caudad with respect to the host.

Growth in all of the larval stages is very rapid, the host being dead and the body contents entirely consumed within 10 to 15 days after penetration. A hole is cut ventrally in the wall of the abdomen by the mature larva after the host is killed; it then turns about and feeds in the thoracic regions, and finally emerges and pupates exactly as does *Prosenia*. The pupal period covers seven to nine days. Under field conditions only a single individual reaches maturity in each host, though many grubs have been collected which contained 20 or more first-stage larvæ.

Second generation

The midsummer generation of adults appears during the period beginning about July 25 and extending to August 20, though the greatest numbers are present during late July. The lengths of the various stages correspond very closely to those of the preceding generation.

Third generation

The first of the fall brood of adults appears in the field about September 1, and a maximum abundance is attained by the middle of that month, although females may still be found commonly as late as the middle of October. The temperature during the latter part of this period is very cool, being often below freezing in the early mornings. The progeny produced by these females enter the host and pass the winter in the second larval stage. On account of the lower spring temperatures, the pupal stage is somewhat longer than in the other two generations. The first adults appear about May 22 and persist not later than the middle of June.

Alternation of hosts

The parasite larvæ of the second stage, which carry the species over the winter, are found in three host species, *Miridiba koreana* N. and K., *Popillia castanoptera*, and *Phyllopertha* sp. An examination of field-collected grubs on October 10 revealed the following condition: *Anomala* spp., all *Dexia* larvæ either dead or lost in molting; *Phyllophaga* spp., all *Dexia* larvæ either dead or lost in molting; *Miridiba koreana*, all *Dexia* larvæ in second stage, healthy; *Phyllopertha* sp., all *Dexia* larvæ in second stage, healthy; *Popillia castanoptera*, all *Dexia* larvæ in second stage, healthy; *Popillia atrocoerulea*, all *Dexia* larvæ dead.

The three species which contained living parasite larvæ at this time naturally included the true host. *Popillia castanoptera* may be excluded, since its time of pupation is too late for this generation of parasites. Although it can not be stated as yet with certainty, the available data indicate that *Miridiba koreana* is the major if not the only host of the overwintering generation.

The host of the following generation is also not positively known, but a consideration of the species of beetles of proper size pupating about midsummer points to *Popillia castanoptera* and *P. mutans* as the more probable species.

The third generation of adults emerges exclusively from larvæ of *Serica*, which latter pupate late in the fall and pass the winter in the adult form in the soil. An examination of field-collected grubs obtained August 12 to 27, 1923, gave the following data:

	Number examined	Number parasitized	Percentage of parasitism
<i>Anomala</i> spp. (third stage).....	3,647	51	1.4
<i>Phyllophaga</i> spp. (second stage).....	8,545	863	10.1
<i>Serica</i> spp. (third stage).....	935	129	13.8
<i>Popillia</i> spp. (third stage).....	137	0	0

The counts of parasitized grubs were based upon the funnels visible through the derm, and consequently a portion of the parasites may have been dead at the time of collection without this fact being noticed. Dissections of a representative series were made and the living *Dexia* larvæ found to be in the second stage, though those in *Serica* seemed to be further advanced, and a few had attained the third stage. All the remaining parasitized grubs were set aside in trays for development and were again examined on August 27. Of the 863 *Phyllophaga* grubs, 747 were still in the second stage, and dissections showed all parasite larvæ contained in them to have been killed in the first or early second stage, whereas 116 grubs had transformed to the final stage and had rid themselves of all evidence of parasitism in the process. Among the *Serica* grubs 82 were still alive and contained third-stage *Dexia* larvæ, whereas 37 had already died and yielded puparia.

Rare instances have been observed of this species reaching maturity in field-collected pupæ. In one instance a *Serica* grub containing a late second-stage larva was able successfully to pupate

and later develop into an imperfect beetle. Another succeeded in freeing itself from a second-stage parasite larva 3 mm. in length, but later died from mechanical injuries incident to the withdrawal of the larva through the aperture in the dorsum of the thorax. It is thus seen that the attachment of the parasite by means of its respiratory funnel to the derm of the host larva is very strong, since it is able to withstand the strain exerted by the drawing of the body through a relatively small opening in the newly formed derm of the pupa.

First-stage larvæ from the adults of the first generation were used in a series of experiments upon grubs of *Popillia japonica*. All of the latter which were available were in the advanced third stage and preparing to pupate. An excessive number of planidia effected entrance into each host, as was evidenced the following day by the many respiratory funnels visible underneath the derm. Within a very few days most of the grubs pupated and the parasite larvæ were able to sever their connection with the respiratory funnel, and remained with the caudal end of the body protruding externally. A few maintained the attachment and held the cast skin in position upon the pupal body.

Some of the parasitized larvæ died from injuries incident to excessive superparasitism, and in these instances the third-stage parasite larvæ detached themselves from the funnel and forced the caudal end of the body out through the aperture in the derm. These host grubs then assumed a somewhat mummified condition, but this may be attributed to bacterial and fungus action rather than to any development in relation to the parasite itself. Feeding was continued on the dead body and pupation took place normally and just outside the host remains, which had not been entirely consumed.

The necessity, under Korean conditions, for these different hosts within which the successive generations may develop is due to the fact that the larvæ can reach maturity only in grubs which themselves are undergoing histolytic action preparatory to pupation. This physiological change seems to provide the necessary stimulus for development, a condition which is known to exist in respect to many other parasitic insects, and without which the parasite larva either remains in the early stages or dies. The writers' observations indicate the above state of affairs to exist in all the species of Dexiidae studied; and, although the time of pupation of *Prosenia* would seem to contradict this assertion, the fact is that the presence of the parasite larva in the grub body tends to prevent actual pupation but permits the host to live several weeks or a month beyond the time of normal transformation.

Habits of the adult.—Mating has not been observed in the field, but presumably takes place shortly after emergence. The males appear a few days prior to the females. In the laboratory mating was induced very readily in glass vials or test tubes of 1-inch diameter, and the duration of copulation was normally 10 minutes.

Feeding also has never been observed under field conditions, in spite of the extensive observations made throughout the periods of adult abundance. Unlike *Prosenia*, which has a long, lancetlike proboscis fitted for penetration to the deepest nectar glands of certain blossoms, this species has a very short, fleshy proboscis and is therefore probably a feeder upon honeydew of aphids and other

insects. In the laboratory feeding took place very satisfactorily upon honey or sugar water, and individuals were kept alive for one month under these conditions.

Dexia is decidedly crepuscular in habit and is therefore active largely during the period about sunset and at other times when the sky is overcast and direct sunlight is absent. One of the best places found for the collection of adults of this species was a young pine forest at the summit of a hill near the experiment station at Suigen, Chosen. Here they appeared abundantly resting upon the foliage of the broad-leaved oak, apparently preferring this almost to the exclusion of other types of foliage.

Unlike *Prosenia*, which deposits larvæ exclusively, *Dexia* may at times produce eggs, which have a variable period of incubation externally, depending upon the extent of development attained prior to deposition. Some eggs kept under moist conditions in Petri dishes required two days' incubation, although the average period was much shorter. By far the majority, however, hatch within the ovarian sac and the eggshell is extruded with the larva, in this respect differing also from *Prosenia*, which largely retains the shells.

The larvæ are very evidently scattered promiscuously over the surface of the soil, but observations in the collection of parasitized grubs would seem to indicate that they are deposited in some numbers at each point rather than singly. It was frequently found that grubs within an area of about 1 square yard were very heavily parasitized, whereas those surrounding this area contained practically no parasites, and that these spots of heavy parasitism recurred in greater or less abundance throughout the zone of collection. No locality was found where the parasitism was at all uniform throughout the entire area.

PROBABLE VALUE OF *Dexia ventralis* AGAINST *Popillia japonica* IN AMERICA

A consideration of the life history of *Popillia japonica* and of *Dexia ventralis* in Chosen still leaves open the question of the latter's ability to increase to a point where it will be of value as a check upon this particular host. Climatic conditions in New Jersey and Pennsylvania are not markedly different from those in Chosen, and consequently may be regarded as a minor factor. The major difficulty is the occurrence of three full generations of the parasite per year under normal conditions, probably only one of which could be upon *P. japonica*. It appears probable that the overwintering forms would be contained in grubs of this host, and if such is the case the emergence of the first brood of adults would be delayed until the middle of June, as against a month earlier in Chosen, and the larvæ produced by these females would be able to parasitize such grubs as had not yet pupated. This, however, calls for the utilization of the one host species to carry two generations of the parasite, a condition not conducive in this case to the attainment of maximum numbers of the latter. The following generation must of necessity be upon some scarabæid grub of proper size which pupates about the first of September. This condition is fulfilled principally in the subfamily Sericinae. Full data are not as yet available as to what may be had in the infested regions in this regard, but the general outlook is not good for the development of this species to an important position in the parasite series under course of establishment in America.

CHARACTERS FOR DETERMINING THE IMMATURE STAGES OF DEXIA VENTRALIS

First-stage larva (fig. 20, A).—Length of newly hatched larva approximately 1 mm.; color white. Mouth hooks present; pharyngeal plates as in C. Sensory papillæ prominent. Derm minutely sculptured with rows of reniform elevations. Posterior spiracles stalked. Two long caudal setae.

Third-stage larva.—Although this is not illustrated, the nature of the caudal spiracles may be understood from those of the puparia. Tracheal funnel always attached to the derm of the host (fig. 21, B).

Puparium (fig. 14, A).—Length 8 mm.; color dark brown, reflections dull, surface finely striate. Posterior spiracles divided into three lobes, each bearing an elongate depression of the former tracheal openings.

CAMPSOMERIS ANNULATA Fabricius

GENERAL OBSERVATIONS

Campsomeris annulata (fig. 23) was found rather infrequently at Suigen, Chosen, in August, 1923, and during the following month five



FIG. 23.—*Campsomeris annulata*, female

females were captured in the field. Specimens of both sexes were submitted to S. A. Rohwer, of the Bureau of Entomology, who made the determination. One specimen in the collection of the agricultural experiment station at Suigen bears the name *Elis ventralis* Smith, and under this name is reported by H. Okamoto to be common on Quelpart, a volcanic island lying a short distance off the southeastern point of Chosen. The species is also recorded from Japan as well as oriental Asia.

Experiments were conducted to determine the true host, since the size of the females was such as to permit of development on grubs of *Popillia japonica*. In the first experiments eggs were laid freely upon grubs of *Anomala* sp. and upon *P. atrocoerulea*, and later when mature grubs of *P. japonica* were obtained and supplied to the *Campsomeris* females, oviposition took place as readily as upon the two species previously mentioned. Considering the distribution of

the species, its habits, life history, etc., it appears probable that *Anomala* is the true host of the late generations, although *Popillia* serves equally well when present.

LIFE HISTORY

Since *C. annulata* has been under observation for only a portion of one season, it is not possible at this time to present a complete account of its life history. In breeding experiments it was found that the methods used for *Tiphia* were not at all satisfactory, the females refusing to oviposit under the conditions provided. When placed in glass jars of about 1-quart capacity, which had been nearly filled with well-packed soil, no difficulty was experienced. It appears necessary to provide these large breeding jars and to have the soil firmly packed in order that a well-defined cell may be formed by the grub, this latter apparently being necessary to the wasp at the time of oviposition. It appears also that the grub after being paralyzed is moved about in the soil to a considerable extent by the wasp before the egg is laid. In the field this behavior may be due to the need of the parasite to provide temperature and humidity conditions for her progeny more favorable than are present in the grub cell, which may be close to the surface and very dry.

It has not thus far been possible to obtain oviposition under conditions which would permit of uninterrupted observation of the act, but stinging is probably accomplished in the same manner as by *Tiphia*. However, the paralysis effected is permanent rather than simply for the period required for oviposition, and consequently the paralyzed grubs could be placed in small depressions in moist soil and left without further attention until the formation of the cocoon.

The egg is normally placed medially on the ventral surface of the third or fourth abdominal segment, standing perpendicularly, with the posterior end adhering lightly to the derm. The attachment is very insecure, and in case the host grub is imperfectly paralyzed is usually rubbed off by the slightest movement of the body.

Hatching is effected by an irregular break in the chorion of the anterior end of the egg, and through this aperture the head and thoracic segments of the young larva emerge. The head is then lowered and the feeding puncture made on the median line of the next segment caudad. This feeding puncture is in reality a pronounced hole made in the derm, and is sufficiently large to permit the head to become completely buried within the body. An exudation of the body fluids of the host takes place, and the "neck" of the larva is encircled by a quantity of this fluid external to the puncture.

Molting occurs several times, and feeding continues at the same point throughout all the stages, after which the entire body contents are consumed. The cocoon is then spun, consisting of a dense mass of reddish-brown strands loosely woven together on the outer surface but compact within. It is not noticeably differentiated into layers, as is the case with that of *Tiphia*.

The egg and larval stages prior to the formation of the cocoon cover periods of only 2 and 5 days, respectively, and the time passed within the cocoon only 33 days for the single male thus far reared. This, however, was under relatively low temperature conditions, and is doubtless considerably shortened during mid season. The females

produced from eggs laid August 16 remained in the pupal stage until the following spring. From these fragmentary data it may be surmised that, under optimum conditions, a generation may be produced each six weeks, and that the number of generations per year will depend on the ability of the parasite females to find suitable grubs upon which to oviposit at all times during the season.

CONDITIONS AFFECTING THE DEVELOPMENT OF CAMPSOMERIS IN AMERICA

Since *Campsomeris annulata* is being introduced into America as a parasite of *Popillia japonica*, it is natural that consideration should be given to such factors as are likely to affect its development and increase there. The size of the adult wasp indicates that it is able to produce normal-sized progeny only upon *Popillia* grubs which have reached full maturity, and since these are not present in large numbers during the summer months, two courses of action are open to the parasite. One of these is to seek out some other host upon which to produce the midsummer generation, and the other is for the females to prolong adult life until suitable *Popillia* grubs become available in the fall. Both of these alternatives would result in decreased effectiveness against the major host as measured by the potential rate of increase, and although this may be unavoidable, the parasite may still be of considerable value in its early spring and late fall generations and in conjunction with the various species of *Tiphia* may contribute to the sum total accomplished by the grub parasites.

TIPHIA POPILLIAVORA Rohwer

GENERAL OBSERVATIONS

Tiphia popilliavora (fig. 24), a parasite of *Popillia* grubs, was first found on August 20, 1920, at Koiwai in the identical place where *C. cinerea*, the tachinid parasite of adult beetles, had been located a week previously. Seven species of *Tiphia* were on the wing at that time and fed largely on the same blossoms. These species were successively tested upon grubs of *P. japonica*, and *T. popilliavora* was found to oviposit readily. Subsequent field observations proved the species to be restricted in this locality to the above host alone. Specimens were forwarded to the United States National Museum for examination and have been described by Rohwer as a new species under the above name.

Investigations throughout the seasons of 1920-1923, inclusive, in the various parts of Japan have failed to reveal this scoliid in any abundance other than in the very restricted locality in which it was originally located. However, late in 1923 it was found to occur in small numbers at Suigen, Chosen. Here it was determined experimentally to be parasitic upon *Popillia castanoptera* and *P. atrocoerulea*, the former being the more common host. The major investigations and breeding work were confined to Koiwai entirely and covered the three years 1920 to 1922, inclusive.

T. popilliavora is not of major importance in its native habitat, and at no time did the field parasitism exceed 20 per cent. The inability of the species to adapt itself to varying conditions, as evi-

denced by its extremely localized distribution in Japan and Chosen, would tend to limit greatly its possible usefulness in America.

BREEDING METHODS AND SHIPMENTS

Methods of breeding were largely those used by other workers with this group of parasites. Single females were placed in 3-ounce tin salve boxes which had been filled with soil and into which two or three *Popillia* grubs had been placed (fig. 25). As food for the wasp a drop of honey or sugar water was placed on a leaf on the surface of the soil. These tins were then set aside for a day and at the end of that time



FIG. 24.—*Tiphia popilliarora*, female

examined, the grubs bearing eggs being removed and fresh ones supplied. Those bearing eggs were transferred to cross-section trays which provided a single compartment for each grub, and in which had been placed soil with a small piece of sod to provide food for the grub during the period elapsing before its death from the attack of the parasite larva. The method of handling grubs parasitized by *Tiphia* differs from that used with *Scolia* and *Campsomeris*, because the grubs are not permanently paralyzed as they are in the latter two genera. During the earlier periods of this work, the soil in the trays was kept fairly moist; but it was found that this was responsible for a considerable mortality among the grubs by fungus attack, and consequently in the later work no moisture whatever was applied, and improved results were obtained.

In using the above method it was possible to carry about 500 females through the entire period of oviposition, and this was nearly the maximum number available in the field. In general, it was found that cocoons could be procured to the extent of about 42 per cent of the original number of ovipositions. The loss of more than

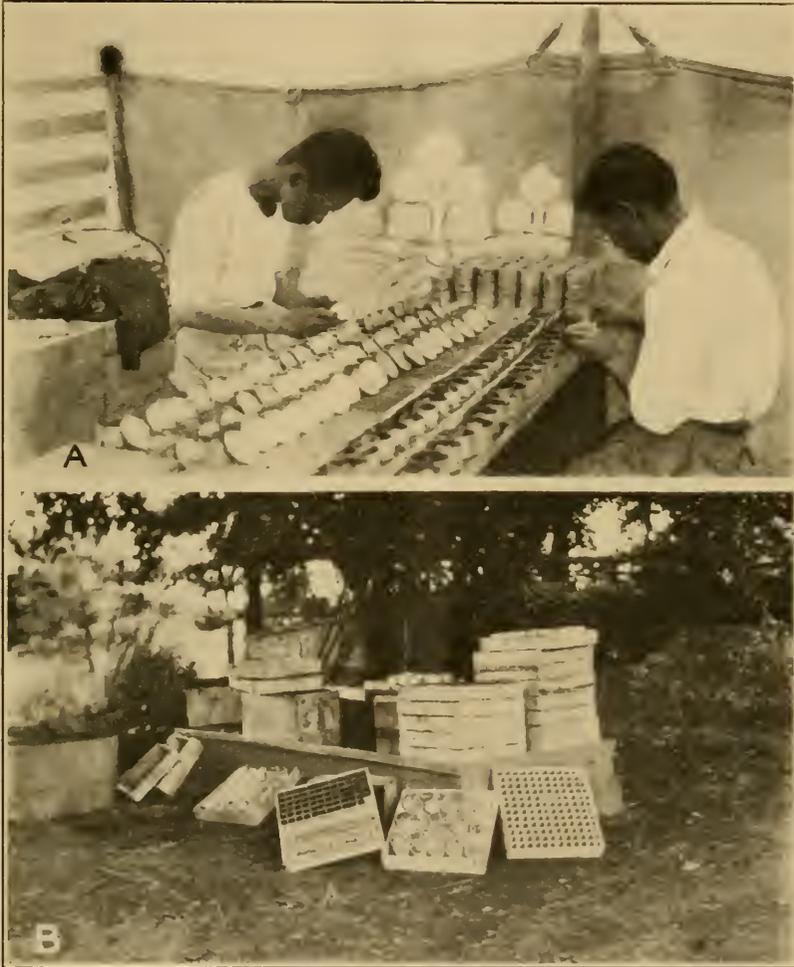


FIG. 25.—Rearing *Tiphia*, Koivai, Japan: A, tins in which female *Tiphia* were kept for oviposition and method of transferring each day to tins containing unparasitized larvæ; B, oviposition tins and cross-section trays in which the parasitized *Popillia* were kept until the *Tiphia* had killed them and spun their cocoons

half during the egg and larval periods may be attributed to several factors, among these being mechanical injury to the grubs, fungous and bacterial attack, and finally, but most important, the rubbing off of the first-stage parasite larvæ by the movements of the host grub in the soil.

In 1920 and 1921 all grubs used for rearing purposes were collected in the immediate vicinity of the place where the *Tiphia* were pro-

cured, but collecting was found to be impracticable there in 1922 and consequently 10,000 were collected in Hokkaido during late July and shipped to Koiwai. The mortality among these grubs during the month from collection to the time of use for breeding purposes was about 50 per cent. A total of 3,350 cocoons have thus far been obtained by the method described above, these being from approximately 10,000 ovipositions. After the formation of the cocoons they were removed from the soil, packed in moss in metal containers, and forwarded to the Riverton laboratory.

LIFE HISTORY AND HABITS

The account of the life history of *Tiphia* may be started from the egg upon the body of the host grub. This is normally placed ventrally between the fifth and sixth abdominal segments,

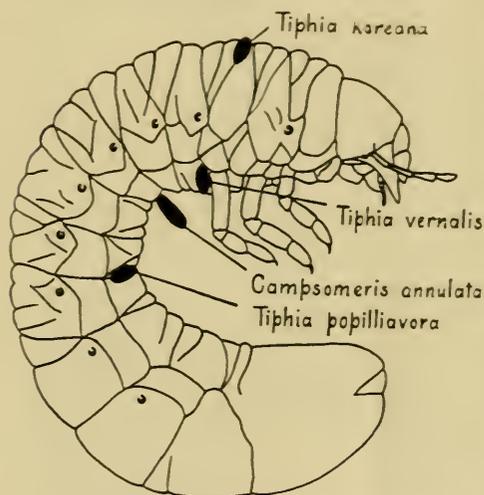


FIG. 26.—A *Popillia japonica* grub, showing the position of the eggs of the four species of Scollidae parasitic upon it

and half way between the median ventral line and the lateral margin (fig. 26). This position may occasionally vary to the extent of one segment either way. The anterior pole of the egg faces inward. It is always placed in the crevice between the segments and is laid with the ventral surface adhering for its entire length to the derm of the host by means of a mucilaginous material provided by the female wasp at the time of oviposition. This adhesive material darkens considerably in color within one or two days after deposition.

The duration of the egg stage varies considerably under different temperature conditions. A series of eggs secured at Yokohama averaged 4.5 days, the temperature during that period ranging from a minimum of 80° up to 97° F. At Koiwai, where the breeding work was conducted, the weather was much cooler and the general duration of the stage was prolonged to about eight days.

Hatching is effected by a vertical split at the anterior end of the egg, the head of the young larva being then thrust out and the integument of the host pierced by the mandibles. Feeding begins almost immediately, and as the body becomes distended the break in the shell enlarges and extends down the median line almost to the posterior tip. The shell remains as a ventral pad beneath the larva, and this serves to maintain its attachment to the host.

The first molt occurs very soon and is effected by a dorsal longitudinal split in the skin, beginning at the first thoracic segment and extending almost to the tip of the abdomen. The head is lifted out of the cast skin, moved forward slightly, and reapplied to the host. The cast skin remains adhering to the ventral surface of the body.

Three additional molts occur before the final larval stage is reached, and at each one the head is shifted forward and a new feeding puncture made. The successive cast skins remain in a leaflike form as a pad beneath the body, serving to attach the parasite larva to the host during these stages. There is thus a total of five larval stages, with the eggshell and four cast skins adhering to the final stage. This is shown diagrammatically in Figure 27.

In the last stage feeding is continued at the puncture hole until after the death of the host, when suctorial action no longer suffices and the mandibles are brought into use. The entire body of the host, exclusive of the head and a portion of the legs, is ordinarily consumed, as well as the cast skins of the parasite itself.

The presence of the egg or early-stage larva on the body causes no appreciable inconvenience to the host grub, but as feeding advances it becomes weakened through withdrawal of the body fluids. Death of the host occurs when the parasite larva is in the fifth instar and the

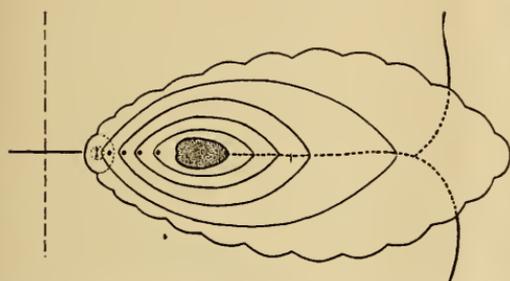


FIG. 27.—Diagrammatic representation of the position of the successive larval stages of *Tiphia* in situ upon the host, showing the mouth parts remaining in the old feeding punctures. Largest outline represents the fifth and last larval stage

formation of the cocoon of the latter takes place within about two days. The duration of the larval stages varies considerably with the temperature conditions, and ranges from 14 days under high temperatures at Yokohama to nearly a month at Koiwai.

Following the completion of feeding, the spinning of the cocoon is immediately begun, and this takes place in situ in the soil cell of the host. The outer covering is of very loose texture, but the succeeding ones are much more compact. The inner surface is very smooth and firm. The meconium of the larva is cast immediately after the completion of spinning and remains as a hard pad at the posterior end. The dormant period is passed in the larval stage within the cocoon, and pupation occurs only a short time prior to the appearance of the adult.

The first adults appear in the field between August 14 and 18, reaching a maximum abundance near the end of the month and disappearing by the middle of September. The period of gestation covers several days to one week, and, consequently, only about two weeks are available for extensive breeding work. The wasps appear on bright days about 10 a. m., the males slightly earlier, and feeding continues until noon. On cool, cloudy days they are present throughout the day, having been observed feeding as late as 6 p. m.

During 1920 feeding by the adults was confined largely to the blossoms and to the nectar glands on the leaf petioles of itadori (*Polygonum Reynoutria*), but in the two years following was almost entirely at the blossoms of two umbelliferous plants, *Seseli libanotis* and *Patrinia scabiosaefolia*. After feeding for the day is complete the females return to the breeding grounds, and there search out

Popillia grubs on which to oviposit. Oviposition occurs largely during the afternoon, but in the warmer periods may continue into the night.

The complete process of egg laying naturally could not be observed in the field, since this takes place entirely underground. In the laboratory, however, visible oviposition was very readily obtained by the use of No. 00 gelatin capsules, a single *Tiphia* female with a medium-sized *Popillia* grub being placed in each. Under confinement in such close quarters, comparable to the grub cell in the soil, the attention of the wasp is centered on the grub. She quickly quiets down after being placed in the capsule and soon begins an examination of the grub. She approaches it from the rear, advances over its dorsum until her own head is near that of the host, and then lowers the tip of the abdomen around the side of the body and up between the legs, after which stinging is effected in the ventral thoracic region, usually between the first and second segments. This may be repeated a considerable number of times before the nerve ganglion is reached, after which the grub becomes almost instantly quiescent. The *Tiphia* then turns to the abdomen and, beginning at the first segment, starts a thorough kneading of the ventral surface with her mandibles. This extends for the entire length of the abdomen but is more thorough on the median segments. From five to seven minutes are devoted to this operation. When it is completed the wasp coils itself transversely about the body in the mid-abdominal region, the mandibles being firmly fastened at the lateral margin, with the body curving over the dorsum and the abdomen extending across that of the host ventrally and almost reaching the point at which the mandibles are attached. The tip of the abdomen is applied to the crease between the fifth and sixth segments and worked back and forth rhythmically for from three to five minutes. This enlarges the crevice somewhat and the rasping of the roughened abdominal tip may also wear away the integument of the host at this point, thus permitting its easier perforation by the young larva. This conjecture is borne out by the fact that, in parasitized grubs, if the body is straightened out between the fingers the point of oviposition is the first to break, and this very readily. The actual deposition of the egg requires only about 15 seconds. It will thus be seen that the entire time elapsing from stinging to the completion of oviposition is from 8 to 12 minutes, but the preliminary examination may prolong the period to half an hour. Within 15 to 20 minutes after it has been stung the grub begins to revive, being then able to move the mouth parts to a certain extent, but movement of the legs and body is not possible within less than 30 minutes. Repeated stinging occasionally brings about the death of the host by mechanical injury.

After oviposition it is a frequent occurrence for the *Tiphia* female to grasp one of the forelegs between her mandibles and bite it until a break in the derm is effected, or the leg entirely bitten off. This being accomplished, feeding takes place upon the body fluids exuding from the wound. Grubs are frequently found in the field showing this type of injury, and the wound is often accentuated by a blackened area caused by bacterial infection.

When a grub which already bears one egg is attacked a second time, the first egg is almost invariably destroyed by the wasp in the course of kneading the abdominal surface with the mandibles, or broken

during the attempted second oviposition. The grub having once borne an egg in the preferred crevice, or one on each side, is thereafter oviposited upon at a different point, either immediately in front of or behind that position. Where egg laying over a considerable period is confined to a single grub and the host then examined, it is found to bear a pair of oviposition scars on each intersegmental crevice from the first to the last on the abdomen, and only a single egg usually remains, this being the one last laid.

The grubs most preferred by *Tiphia* for oviposition are those in the early or middle third stage, for after they pass to the more mature form the body becomes thickened and firm, and thus apparently presents mechanical difficulties to stinging and egg laying. Such grubs are from eggs laid the previous season, and it was only with great difficulty that wasps were induced to oviposit upon them. In the field during early September the grubs from eggs of that season were largely in the second instar, and collected grubs of this stage often bore *Tiphia* eggs and larvæ. Manifestly, grubs in this stage were unable to provide sufficient food to bring the parasite larvæ to maturity, and in many cases observed the resulting cocoons were little larger than those of an average-sized *Apanteles*. The larvæ in these cocoons usually die shortly after the formation of the cocoon. This willingness of the species to oviposit upon grubs of too small size to bring its progeny to maturity indicates a lack of perfect adaptation to a one-year cycle of the host, because of the improper time of emergence for a wasp of this size.

The rate and duration of oviposition in this species were determined in a series of 28 females collected in the field on August 19, which was very nearly the first date upon which adults appeared, and consequently it is reasonably certain that little or no egg laying had taken place up to that time. Records of the 10 best females are given in Table 2, and this is felt to represent very nearly the normal condition in the field.

TABLE 2.—Oviposition records of 10 females of *Tiphia popilliarora*

Female No.	August										September										Total		
	20	21	22	23	24	25	26	27	28	29	30	31	1	2	3	4	5	6	7	8		9	10
1.....	3	2	2	3	2	2	3	3	2	2	2	3	3	3	2	2	4	2	2				47
2.....	1	1	0	1	2	2	3	1	2	3	3	1	2	3	3	3	2	1					34
3.....	0	0	0	0	2	1	2	2	2	3	3	3	3	1	2	3	2	1					30
4.....	1	0	1	1	1	1	2	2	2	2	3	2	3	2	2	3	2	4	3	2			39
5.....	1	1	1	2	2	2	0	2	1	3	2	2	2	1	2	1	2	3	2	3	1	2	38
6.....	2	1	1	2	1	3	1	2	2	3	2	2	1	3	2	2	2						32
7.....	1	1	0	1	0	1	1	1	1	2	3	2	2	2	3	1	2	3	2	3			32
8.....	0	0	1	2	1	1	0	2	2	1	3	3	2	2	1	4	2	6					33
9.....	3	1	2	2	2	3	3	2	2	1	4	1	2	2	5	0	2	1					38
10.....	1	1	1	0	4	2	2	2	2	2	3	2	2	2	3	2	3	1	2				37
Average																							36

It will be seen from these records that the general average per day was approximately 2, with a maximum of 6. In the laboratory, under forcing conditions in capsules as previously mentioned, as many as 8 eggs were obtained within a period of 6 hours, but this was abnormal and is not duplicated in the field.

TIPHIA VERNALIS Rohwer

GENERAL OBSERVATIONS

Tiphia vernalis is a Chosen species which has for its normal host *Popillia castanoptera*. It was found by the junior writer in May, 1922. In establishing the value of this and all other Chosen scoliids, they were first tested out on larvæ of *P. japonica* which were taken from Japan to Chosen for that purpose. If they readily accepted the Japanese *Popillia*, they were considered of economic importance and their study and rearing were continued.

In the studies of several species of *Tiphia* it was found that the group as a whole tends to be limited to a host genus rather than to a single species. *Tiphia vernalis* will accept grubs of *P. atrocoerulea*, but as a rule this host is physiologically unfit, being too near the pupal period to be readily parasitized. On the other hand, *P. japonica* is taken early enough to be suitable. In captivity this *Tiphia* has been reared on four species of *Popillia*.

In the spring of 1922 a few individuals were reared on *P. japonica* (fig. 28), but in 1923 this work was undertaken on a large scale with native hosts. Hundreds of females were collected in the field and brought to the laboratory for oviposition and rearing of larvæ. The same rearing methods were used as for the preceding species. At times as many as 450 females were on hand for this purpose. From a total of 5,785 eggs obtained at Suigen in 1923, 2,350 cocoons were obtained.



FIG. 28.—Larva of *Popillia japonica* parasitized by *Tiphia vernalis*

LIFE HISTORY AND HABITS

The adults of *Tiphia vernalis* are found in the field from May 5 to June 14, with a maximum abundance from May 19 to 25. Feeding takes place largely upon honeydew produced by aphides on pine, oak, and chestnut. The females are most abundant on chestnut foliage from 9.30 to 11.30 a. m. on warm, bright mornings. A low temperature tends markedly to slacken activity.

Although the adults seem to be very local in distribution, the parasitism of *Popillia* grubs in regions where the wasps were not abundant indicates that the species is more generally distributed than is evidenced by the presence of the adults alone.

Tiphia vernalis, although not of prime importance, is well worth introduction. Its occurrence in the spring is timely for *Popillia* in America, and if introduced with the preceding species would form the practical equivalent of a two-brooded species. On June 5, 1923, a count of 100 field-collected grubs gave a 10 per cent parasitism by *vernalis*.

The egg-laying habits of this species are similar to those of *Tiphia popilliavora*, except that the eggs are placed in the suture between the third thoracic and first abdominal segments on either side of the median ventral line (fig. 26), and with the anterior pole directed

toward the lateral margin. The time of oviposition is largely during the afternoon. The eggs are white or yellowish white, and 1 mm. in length. The duration of the stage is from eight to nine days. The hatching and feeding of the larvæ are similar in all respects to those of *T. popilliavora*.

The rate and duration of oviposition as determined for this species are indicated in Table 3. From this it will be noted that the species does not average 1 egg per day during the oviposition period, that the maximum number obtained in one day was 3, and that the average total per individual was 25. This is markedly lower than the records obtained for *Tiphia popilliavora*.

TABLE 3.—Oviposition records of 10 females of *Tiphia vernalis*

Female No.	May																															Total
	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31																
1	1	2	1	0	0	2	2	2	0	1	1	1	1	1	0	0	0															
2	1	1	1	2	1	1	0	1	0	1	0	1	1	1	0	1	1															
3	0	1	1	0	1	0	2	0	1	1	1	1	1	1	2	0	1															
4			2	0	2	0	1	1	1	1	1	1	1	1	0	1	1															
5			1	0	1	0	2	1	1	2	1	2	0	1	1	1	1															
6					1	1	0	0	1	2	1	1	1	0	1	1	1															
7					1	1	1	1	1	2	0	2	1	1	1	1	1															
8					0	1	1	0	1	1	0	1	0	1	0	1	0															
9						1	1	0	1	2	0	1	0	0	0	0	1															
10						0	1	1	1	0	1	2	1	1	0	0	1															

Female No.	June																Total
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	
1	1	2	1	1	1	1	0	1	2	1	1	0	1	0	D	28	
2	2	1	0	1	1	1	1	1	2	1	1	0	0	1	D	26	
3	1	0	1	1	0	1	1	0	1	2	2	2	0	0	D	25	
4	2	1	2	0	1	2	0	1	2	1	1	0	1	1	D	28	
5	2	1	0	0	1	2	0	1	1	2	1	2	1	0	0	D	28
6	2	1	0	1	0	0	1	2	1	2	0	0	1	D	21	28	
7	1	0	1	1	1	2	1	2	2	0	2	1	1	0	D	28	
8	0	1	0	1	1	2	1	1	1	1	2	1	0	0	D	19	
9	2	2	1	0	1	1	0	1	2	1	1	1	0	0	0	D	20
10	1	0	2	1	0	1	1	2	2	1	1	3	3	1	D	28	
Average																25.1	

¹ D indicates death of female.

The period of larval growth from the hatching of the egg to the spinning of the cocoon is 24 days, or slightly longer. In this species the period of growth is much more constant than in the Japanese species, a fact which is no doubt due to the increasing temperature of May and June in Chosen, whereas at Koiwai it decreases rapidly during August and September.

The cocoons are like those of the preceding species. Unlike those of most *Tiphia*, however, the larvæ transform to pupæ in the fall and development advances to an almost perfect imago, in which state the winter is passed.

TIPHIA KOREANA Rohwer

GENERAL OBSERVATIONS

During the middle of August, 1923, there were found in a small locality near Suigen, Chosen, a few individuals of *Tiphia* which, when tested experimentally, oviposited readily upon grubs of *Popillia atrocoerulea* and *Anomala* sp. Later grubs of *P. japonica* were provided, and oviposition and development took place normally upon them. However, field collections of parasitized grubs indicated its true host to be *Anomala* rather than *Popillia*.

The adult wasps were very rare in the field at the time mentioned and only nine females were obtained. Examination on August 12 of field grubs bearing eggs or larvae revealed practically all to be in the first larval stage, though a few eggs had not yet hatched. The proportion of *Anomala* grubs parasitized ranged as high as 76 per cent in small lots brought in by the collectors, the general average being 20 per cent for the area in which the parasite was known to occur. A consideration of the foregoing data would indicate that the period of adult presence ranged from about July 20 to the middle of August, with the peak of oviposition attained in the first week of the latter month, and that the few adults collected represented merely the end of the period rather than an actual numerical scarcity. A small number of cocoons were obtained from field-collected material and forwarded to the Riverton laboratory for rearing and liberation.

LIFE HISTORY

Unlike the other species of *Tiphia* discussed in this bulletin, *T. koreana* places its egg dorsally rather than ventrally upon the host, and in a crevice on the median line of the third thoracic segment. The egg is somewhat dark in color as compared with that of the two preceding species. Under relatively high temperature conditions hatching occurs in five to six days, but the larval stages in the field are prolonged as a result of the rapidly decreasing temperatures in the latter part of August and early September. The winter is passed in the larval stage within the cocoon.

The adults of this species are somewhat larger than those of *Tiphia popilliavora* and *T. vernalis*; in fact, they are the largest of all the species found in Chosen, and this combined with the earliness of their appearance would seem to handicap it considerably against *Popillia japonica* in America. With a largely biennial cycle of the host, as in Hokkaido, mature grubs would be available for parasitism during the period covered by this *Tiphia*, but very few such grubs are available in the American infestation. It is therefore seen that relatively little effectiveness can be looked for from its introduction.

KEY FOR THE DETERMINATION OF TIPHIA ADULTS

In order to facilitate the identification of the introduced species of *Tiphia*, S. A. Rohwer has prepared the following key. However, reference to further detailed description in his papers⁵ is advisable. In this key the specific characters are inclosed in parentheses.

⁵ Rohwer, S. A. Descriptions of three species of *Tiphia* parasitic on *Popillia japonica* (Hym.). In Proc. Ent. Soc. Wash., vol. 25, pp. 87-92, 1924. A new *Tiphia* from Korea (Hym.). In Proc. Ent. Soc. Wash., vol. 29, January, 1927.

1. Inner side of hind basitarsus without a longitudinal groove; propodeal enclosure distinctly narrowing posteriorly, about twice as long as greatest width, the median carina incomplete; about 12 mm. long; (anterior and dorsal margin of pronotum separated by a carina; side of pronotum without a groove; second intercubitus curved; punctures on tergites 3, 4, and 5 small, close, and evenly distributed) — *koreana* Rohwer
- Inner side of hind basitarsus with a longitudinal groove; propodeal enclosure nearly parallel-sided, the median carina strong, complete; about 10 mm. long ----- 2
2. Anterior and dorsal margin of the pronotum separated by a carina; (legs black; basal part of pygidium striato-punctate, the apical part very minutely sculptured); Japan ----- *popillivora* Rohwer
- Anterior and dorsal margin of the pronotum not separated by a carina; (second intercubitus distinctly curved; produced median portion of clypeus slightly emarginate apically); Japan and Chosen --- *vernalis* Rohwer

CRASPEDONOTUS TIBIALIS Schaum⁶

COLLECTION AND SHIPMENT

The carabid *Craspedonotus tibialis* (fig. 29) occurs abundantly in the sandy areas near Miho, a small seacoast village about 50 miles south of Yokohama. It is predacious in both the larval and adult stages, feeding upon a number of insect species, including the Scarabaeidae. Because of this habit it was thought worth while to introduce the species for experimental and study purposes at the Japanese Beetle Laboratory at Riverton, N. J. Consequently, in June and September, 1920, some 1,100 adults were forwarded, and these were followed by shipments of 15,350 beetles in June, 1921.

The beetles were collected by the women and children of the district (fig. 30, A), who became very proficient in locating them. Individual beetles were packed in small wooden safety-match boxes containing damp sphagnum moss. The match boxes were further packed in strong wooden containers which were roped together in sets of six (fig. 30, B).

Shipments were made in cool vegetable storage from Yokohama, but on arrival in the United States they crossed the continent at ordinary temperatures. These shipments reached the laboratory at Riverton with a mortality of approximately 50 per cent. Since a considerable mortality had been anticipated allowance was made for this by shipping unusually large numbers.

LIFE HISTORY AND HABITS

There is one generation annually, and hibernation takes place apparently in the last larval stage. Adults appear in abundance at Miho in June. In the collections made from June 1 to 6 many of the beetles were not completely hardened, indicating that they had very recently changed from the pupal stage.

The adults live in deep tubular burrows 10 to 18 inches in depth and enter the soil at an angle of about 45°. The time spent in these burrows by the female beetle must be considerable, extending through the mating and egg-laying periods. Often at the lower end of the burrow the remains of scarabaeid beetles were found.

The eggs are laid in small cells or chambers one-half inch deep, which angle off in a downward direction from the sides of the main

⁶ The first observations upon the habits of *Craspedonotus tibialis* were made by Frederick Muir, of the Hawaiian Sugar Planters' Experiment Station, and it was through the entomologists of that station that information was obtained regarding the localities in which it could be found in abundance.

burrow. The entrances to the egg cells are filled with sand so as to close them off from the burrow inhabited by the female. As many as 9 to 11 cells are formed, each containing a single egg.

All attempts to establish this species were unsuccessful, these failures probably being due to a decided change in the ecological habitat. In Japan *Craspedonotus* is found only in sandy regions with open vegetation, whereas at Riverton the place of introduction was a heavier soil covered with a dense plant growth. Since this beetle is found in the sandy banks at Koiwai in northern Japan, it would seem

that the temperature factor was not the limiting one in the failure of the species to become established in America.

LIFE HISTORY OF POPILLIA JAPONICA IN JAPAN

As has been previously mentioned, the varying life cycle of *Popillia* as it occurs in Japan has an important bearing on certain of its parasites. When this is compared with the life cycle in the United States it will be seen that further conditions will undoubtedly arise which will have an important bearing on the parasite-introduction problem, and it is therefore important that these points should be further discussed.

Popillia japonica is found on all of the main islands of Japan, but does not extend to the Asiatic mainland. It is most abundant in the northern half of

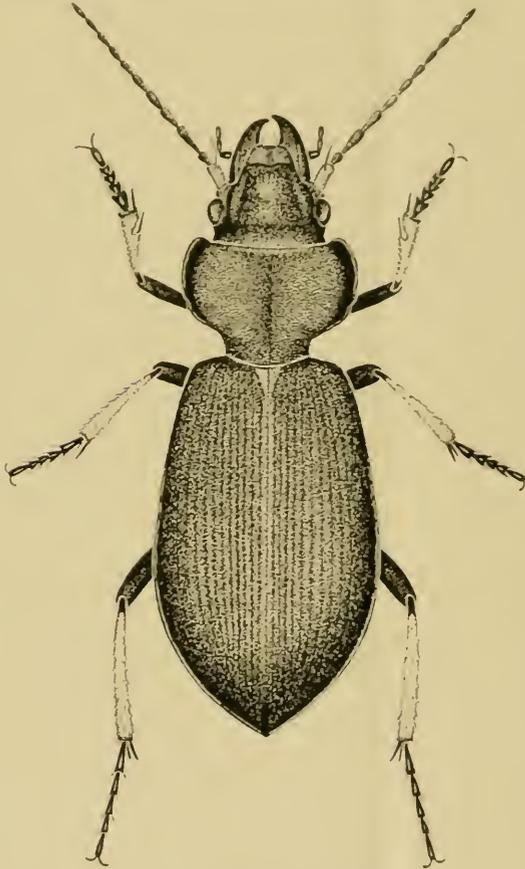


FIG. 29.—*Craspedonotus tibialis*, female

Honshu and all of Hokkaido in the areas where grasslands occur. This northern habitat corresponds somewhat in climate to that of New Jersey and Pennsylvania. Nowhere in Japan is it a pest of much economic importance.

At Yokohama (lat. 35.5° N.) *Popillia* is common but not abundant enough to be of any importance as a plant pest. Here the first beetles of the season appear as early as May 28, the maximum numbers being found in the field about June 20, after which date a gradual decline takes place and by July 25 only a very few stragglers are found.

In this locality one complete generation occurs each year, there being no evidence of larvæ going over a second season; in fact, all reach the third instar by mid-September of the year in which the eggs are laid.

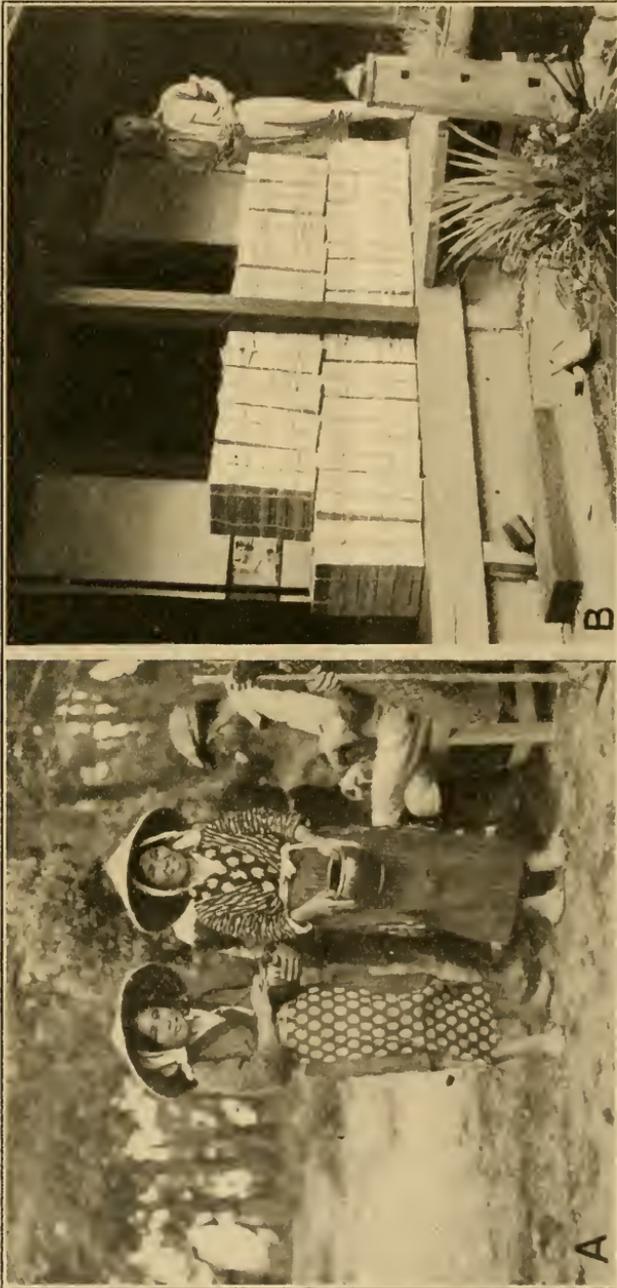


FIG. 30.—A, collectors of *Craspedonotus tibialis* at Miho, Japan; B, 10,000 beetles of *C. tibialis* packed for shipment to the United States from Miho, Japan

At Koiwai (lat. 39.5° N., altitude 1,500 feet), a small village about 10 miles from Morioka and 300 miles north of Yokohama, the

climate is considerably colder than at the latter place, the growing season being confined to June, July, and August. Because of the grass and meadow lands here *Popillia* is more abundant than southward, although it is not an economic pest. The first beetles of the season appear about July 1, increasing rapidly to maximum numbers by July 24, after which the decline is gradual through August, and by September 10 only a few are left. Here approximately 25 to 30 per cent of the beetles undergo a two-year cycle. This condition seems constant in northern Honshu.

At Sapporo (lat. 43° N.), on the island of Hokkaido, and about 520 miles north of Yokohama, *Popillia* is more abundant than elsewhere in Japan, perhaps because of the presence of extensive grass and meadow lands which afford undisturbed breeding grounds. It is said that at times the adults occur in such numbers as to cause damage to the foliage of the soybean, although in four years' observations by the writers no material damage to any economic crop was noted.

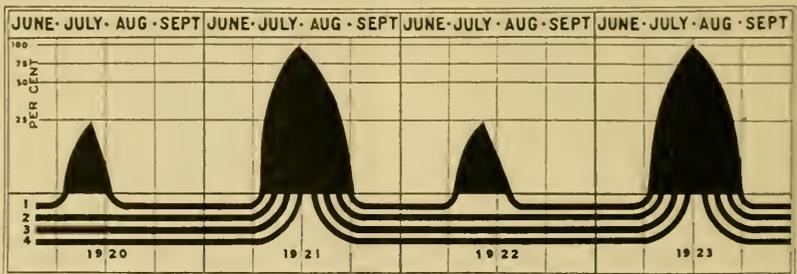


FIG. 31.—Diagrammatic calendar of the fluctuating biennial broods of *Popillia japonica* at Sapporo, Japan. Lines 1, 2, 3, and 4 represent, respectively, 25 per cent of the stages passed in the soil, eggs, larvæ, and pupæ. Solid black curves represent adults as they occur during the seasons. Winter months are omitted for convenience. The years 1920 and 1922 were seasons in which only 25 per cent of the larvæ (No. 1) transformed to adults, larvæ Nos. 2, 3, and 4, or 75 per cent, remaining in the soil to transform the following seasons. The years 1921 and 1923 were seasons in which practically all larvæ transformed into adults. Curves for adults in 1920 and 1922 have their apices about July 20, or 10 days earlier than normal, because of the intensive parasitism by *Centeter cinerea*. Curves for adults in 1921 and 1923 represent normal abundance with apices at the end of July, *C. cinerea* not being abundant enough to affect the decline as in the preceding years. This fluctuating condition seems to be constant for this region.

In this region *Popillia* has largely a two-year life cycle with about 75 per cent of the adults emerging in alternate years (see fig. 31). Thus 1920 and 1922 were years of minimum emergence, comprising about 25 per cent of the beetle fauna. During these years the first adults appeared about July 5, the maximum numbers occurring about July 22, followed by a rapid decline and the disappearance of the beetles by the first week in August. This latter condition is due to the parasitism of the adults by *Centeter cinerea* and is discussed under that head. In the years of greatest abundance (1921 and 1923) the first beetles appeared about July 5 also, and reached the maximum by the end of the month. The decline was gradual through August and by early September all had disappeared.

In the years of adult abundance virtually all larvæ develop into adults, only a fraction of 1 per cent of the total number remaining in the larval stage by the end of July. These doubtless comprise two-year cycle grubs which originated from the 25 per cent of one-year beetles. It is also presumed that a fraction of the progeny of the two-year beetles may revert to the one-year cycle. During the

periods of larval scarcity it is impossible to obtain sufficient numbers for experimental purposes.

As contrasted with the life cycle of *Popillia* at Sapporo and Koiwai, Japan, that in the United States in the infested area of New Jersey is as far as known entirely of one year, corresponding in this respect to the condition existing at Yokohama. At Riverton the first beetles issue in numbers in mid-June, and the maximum emergence is reached from July 10 to 20. From the end of July or mid-August, according to the season, the decline in numbers takes place, coming to a close in mid-September.

FOOD PLANTS OF POPILLIA IN JAPAN

During four years' study of *Popillia* in Japan, the writers have not observed it as a serious pest, although Japanese entomologists have recorded it as at times doing considerable damage to soybean plants. As regards this particular food plant, we may cite the condition existing during the summer of 1921 at Koiwai, where feeding by the beetle was largely upon *Polygonum Reynoutria* growing along the roadside bordering the breeding grounds, and immediately adjoining it was a large field of soybeans. Although the *Polygonum* foliage was almost skeletonized, hardly a single individual was found in the adjoining soybean field. At Koiwai also, where considerable corn is grown, there is no damage to the silks or to green corn. However, at Riverton corn silk and green corn are favorite foods. Likewise wistaria at Yokohama is much fed upon by *Popillia*, yet wistaria at Sapporo is rarely touched. These points illustrate a common feeding habit, namely, that the favorite food plants of one district, although present in another, are often not fed upon by the beetles.

The favorite food plants in the three localities in which observations were most extensive are listed in Table 4.

TABLE 4.—Favorite food plants of *Popillia japonica* at Tokyo, Koiwai, and Sapporo

Locality and botanical name	Common name	Parts of plant eaten
Tokyo, Yokohama region:		
<i>Cissus japonica</i>	Blind grape.....	Leaf and flowers.
<i>Wistaria floribunda</i>	Wistaria.....	Leaf.
<i>Vitis</i> sp.....	Cultivated grape.....	Leaf and flowers.
<i>Castanea</i> sp.....	Chestnut.....	Flowers.
Koiwai:		
<i>Polygonum Reynoutria</i>	Itadori.....	Leaf and flowers.
<i>Rumex</i> sp.....	Doek.....	Do.
<i>Populus nigra</i>	Italian poplar.....	Do.
<i>Pteridium aquilinum</i>	Fern.....	Do.
Sapporo:		
<i>Polygonum Reynoutria</i>	Itadori.....	Do.
<i>Prunus japonica</i>	Hedge plum.....	Leaf.
<i>Populus nigra</i>	Italian poplar.....	Do.
<i>Vitis</i> sp.....	Cultivated and wild grapes.....	Leaf and flowers.

Table 5 gives a more complete list of the food plants of *Popillia japonica*. The list includes a few foreign plants commonly grown in Japan.

TABLE 5.—*Food plants of Popillia japonica in Japan*

FOR THE REGION OF TOKYO, YOKOHAMA, AND SOUTHWARD

Botanical name	Common name	Parts of plants eaten
Trees:		
<i>Castanea pubinervis</i> ¹	Chestnut	Leaf and flowers.
<i>Quercus variabilis</i>	Oak	Leaf.
<i>Quercus serrata</i>	do.	Do.
<i>Populus maximowiczii</i>	Poplar	Do.
<i>Populus nigra</i> ¹	Italian poplar	Do.
<i>Ulmus parvifolia</i>	Elm	Do.
<i>Zelkova serrata</i>	Kiaki	Do.
<i>Tilia japonica</i>	Linden	Do.
<i>Tilia mequieliana</i>	do.	Do.
<i>Alnus japonica</i>	Alder	Do.
<i>Prunus serrulata</i>	Cherry	Do.
<i>Melia japonica</i> ¹	Sendan	Flowers.
Shrubs:		
<i>Rosa multiflora</i>	Rose	Leaf and flowers.
<i>Hibiscus syriacus</i>	Hedge plant, nonindigenous	Leaf.
<i>Dioscorea japonica</i>	Yumanorma	Do.
Vines:		
<i>Vitis thunbergii</i> ¹	Wild grape	Leaf and flowers.
<i>Vitis vinifera</i> ¹	Cultivated grape	Do.
<i>Cissus japonica</i> ¹	Blind grape	Do.
<i>Wisteria floribunda</i> ¹	Wistaria	Leaf.
<i>Smilax china</i>	Smilax	Do.
Herbaceous plants:		
<i>Glycine soja</i>	Soybean	Leaf and flowers.
<i>Phaseolus vulgaris</i>	Common bean	Do.
<i>Polygonum convolvulus</i>	Sendanoki	Do.
<i>Polygonum Reynoutria</i> ¹	Itadori	Do.
<i>Polygonum thunbergii</i>	Mizosoba	Do.
<i>Polygonum nodosum</i>	Omutede	Do.
<i>Asparagus officinalis</i>	Asparagus	Do.
<i>Rumex</i> sp.	Doek	Leaf.

FOR REGION NORTH OF TOKYO TO SAPPORO

Trees:		
<i>Castanea pubinervis</i> ¹	Chestnut	Leaf and flowers.
<i>Populus nigra</i> ¹	Italian poplar	Leaf.
<i>Zelkova serrata</i>	Kiaki	Do.
<i>Prunus japonica</i>	Hedge plum	Do.
<i>Platanus orientalis</i>	Sycamore	Do.
<i>Filipendula kamtschatica</i>	Filipendula	Do.
<i>Berchemia racemosa</i>	Kumayanagi	Do.
<i>Salix purpurea</i>	Willow	Do.
Shrubs and vines:		
<i>Rosa</i> spp.	Wild roses	Leaf and flowers.
<i>Vitis</i> spp. ¹	Cultivated and wild grapes	Do.
<i>Rubus crataegifolius</i> ¹	Kumaichigo	Leaf.
Herbaceous plants:		
<i>Polygonum Reynoutria</i> ¹	Itadori	Leaf and flowers.
<i>Oenothera biennis</i>	Primrose	Do.
<i>Glycine soja</i>	Soybean	Do.
<i>Asparagus officinalis</i> ¹	Asparagus	Do.
<i>Pteridium aquilinum</i> ¹	Fern	Leaf.
<i>Hypericum</i> sp.	St. John's wort	Flowers.
<i>Trifolium pratense</i>	Red clover	Do.
<i>Rumex</i> sp.	Doek	Leaf.

¹ Favorite food plant.

CLIMATIC CONDITIONS IN THE MAIN FIELDS OF INVESTIGATION

A comparison of the climatic conditions in the various regions in which work was conducted with those in the infested area in America is of value from two points of view: (1) In relation to the reactions of *Popillia japonica* itself under varying conditions, and (2) as bearing upon the question of establishment of the oriental parasites in this country.

Figure 32 gives a graphic representation of the mean monthly temperatures throughout the year for Yokohama, Koiwai, and

Sapporo, Japan, and Suigen, Chosen, the four main centers of investigation. These graphs show a considerable uniformity in certain respects, the peak in each case occurring in August and followed by a sharp decline. Sapporo is uniformly 6 to 10° C. (11 to 18° F.) cooler than Yokohama, with Koiwai occupying an intermediate position. In Chosen, on the contrary, the summer temperatures approximate those at Yokohama, whereas during the winter they coincide closely with those of Koiwai and Sapporo.

A comparison of these records with the graph shown in Figure 33, which is for Philadelphia, brings out several interesting points. The winter temperatures at the latter place are 4 to 6° C. (7 to 11° F.) above those of Koiwai, Sapporo, and Suigen, whereas the graph for

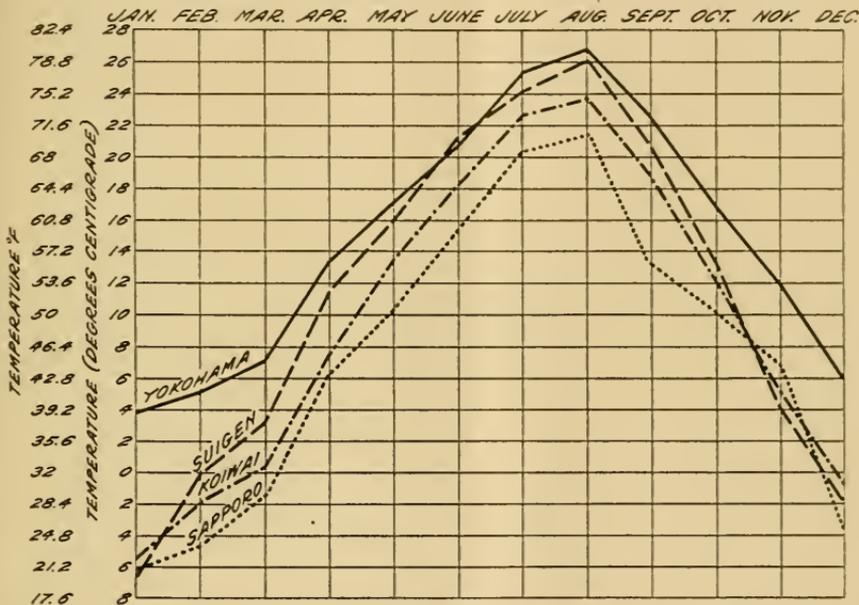


FIG. 32.—Curves showing the range of the mean monthly temperature for Yokohama, Koiwai, and Sapporo, Japan, and Suigen, Chosen. Temperature based on a three-year average, except Yokohama, which is for two years

the spring months follows very closely that of the latter place. The maximum summer temperature is attained in July rather than August, and the decline which follows is more gradual. Thus it is seen that the growing season at Philadelphia is nearly six weeks longer than at Koiwai or at Sapporo, and this in a measure explains the more or less biennial cycle of *Popillia japonica* in northern Japan as contrasted with the normal one-year cycle at Yokohama and in America,

Figure 34 shows the mean monthly precipitation for Yokohama, Sapporo, and Suigen, based on a two-year average, and Figure 33 shows that for Philadelphia on a 50-year average. Unfortunately it was not possible to obtain records for Koiwai, and although those for Morioka, 10 miles away, were available yet these were in no wise comparable to the Koiwai figures. A heavy snowfall occurs in the winter months and fairly heavy rains are not infrequent throughout the remaining portions of the year, in fact daily showers are a rather notable feature.

It is seen by reference to Figure 34 that rainfall at Yokohama was very light in the winter but fairly heavy in the summer months, whereas at Sapporo the heaviest precipitation was recorded in the winter, with the lowest points reached in the early summer months.

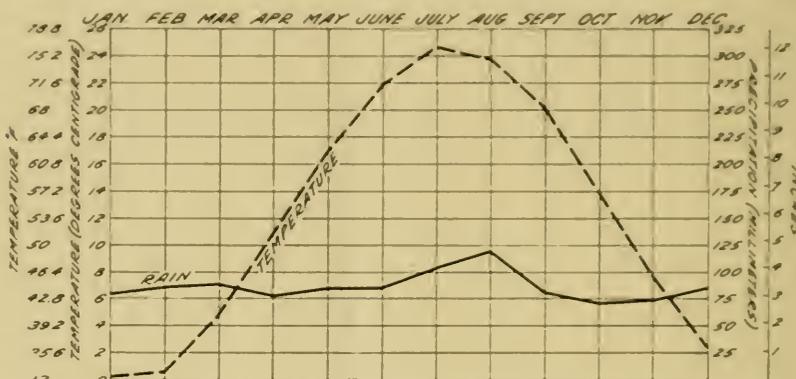


FIG. 33.—Curves showing the mean monthly temperature and precipitation for Philadelphia, based on a 50-year average

At Suigen, Chosen, however, the winter and spring precipitation is very low, followed by a period of exceedingly heavy rainfall during July and August. The rainfall during the 24 hours of July 28, 1922 totaled 11.3 inches. A comparison of these graphs with that of

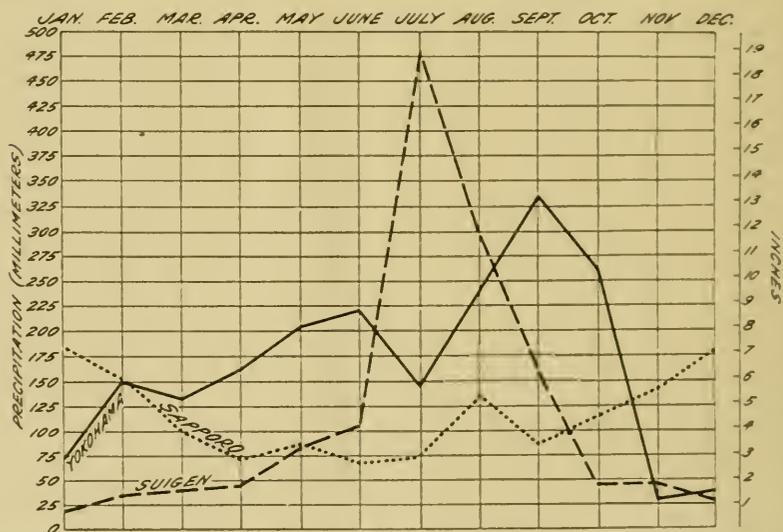


FIG. 34.—Curves showing the mean monthly precipitation for Sapporo and Yokohama, Japan, and Suigen, Chosen, based on a two-year average

Philadelphia shows that Sapporo, and probably Koiwai as well, correspond fairly closely, whereas the heavy summer and light winter precipitation at Yokohama and Suigen are far removed from it.

A consideration of the two factors of temperature and rainfall in the various localities reveals the fact that conditions at Koiwai and

Sapporo more nearly approximate those of the infested area than do those at Yokohama and at Suigen.

AGRICULTURE AND NATURAL LANDS OF JAPAN AND CHOSEN IN RELATION TO POPILLIA

Since agricultural and natural conditions have an important bearing upon the fauna, it is relevant here to make a few remarks concerning them.

The combined area of the main islands—Honshu, Kyushu, Shikoku, and Hokkaido—is 140,000 square miles, or approximately the same as the area of Montana. A large part of this area consists of mountainous country heavily forested with virgin and planted forests. Much of the land is worthless "hara," or rolling prairielike lands at the foot of the higher mountain ranges. These are densely covered with low, persistent bamboo grasses. Sand hills and plains along the coast also form a distinct habitat of considerable extent. About 17 per cent of the total land area is estimated as arable, although only 12 per cent is under actual cultivation.

The limited area of arable land and the food supply demands of this densely populated country have made Japanese agriculture one of the most intensive in the world (fig. 35). Rice is the chief food and it is grown largely in flooded plots called "paddy fields," one-half of the agricultural lands being given over to this crop. The average landholding in this agricultural area is $2\frac{1}{2}$ acres per individual. Where physiographical conditions were originally unfavorable, they have been altered if possible to suit rice growing. This has resulted in the terracing of hill and mountain sides and the cutting up of the lowlands into innumerable paddy fields to accommodate them to the varying water levels. Where it is possible to drain the paddy fields they are immediately prepared for wheat or barley as a successive crop. Areas not suited to rice culture are devoted to dry farming, including the growth of wheat, barley, rye, millet, soybeans, and such vegetables as daikon radishes, eggplants, sweet potatoes, taro (*Caladium colocasia*), and Japanese onions (negi). All these food plants, including such grains as wheat and rye, are cultivated and fertilized intensively during their growing period, and often eggplants, onions, or cucumbers are grown between the rows of grain.

On the island of Hokkaido, natural and agricultural conditions more nearly approach those of our Eastern States. There are large areas of natural forest similar in makeup to our own forests, the trees consisting of species of oak, maple, beech, magnolia, chestnut, birch, and pine. The extent of waste lands in Hokkaido compares with that of Pennsylvania. Agricultural landholdings in this region are somewhat larger than in Honshu and the method of cropping is similar to that in America. Corn, wheat, oats, barley, rye, millet, and some rice are the chief grains grown. Grasslands suitable for grazing are more abundant here than elsewhere in Japan, and dairying and stock farming are resulting industries.

Koiwai, near Morioka on the island of Honshu, is not in the zone of intense agriculture, but is in reality one large estate of 7,500 acres in an old volcanic upland of sufficient elevation for the development of natural grasslands and grains, such as corn, wheat, and oats, and the methods of cropping are like those employed in the eastern

section of the United States. The forest areas here are entirely artificial, consisting for the most part of regular plantings of chestnut, larch, and pine.

These agricultural conditions may be a factor influencing the relative abundance of *Popillia japonica* within certain regions. From Sendai southward is the region of intense cultivation, as

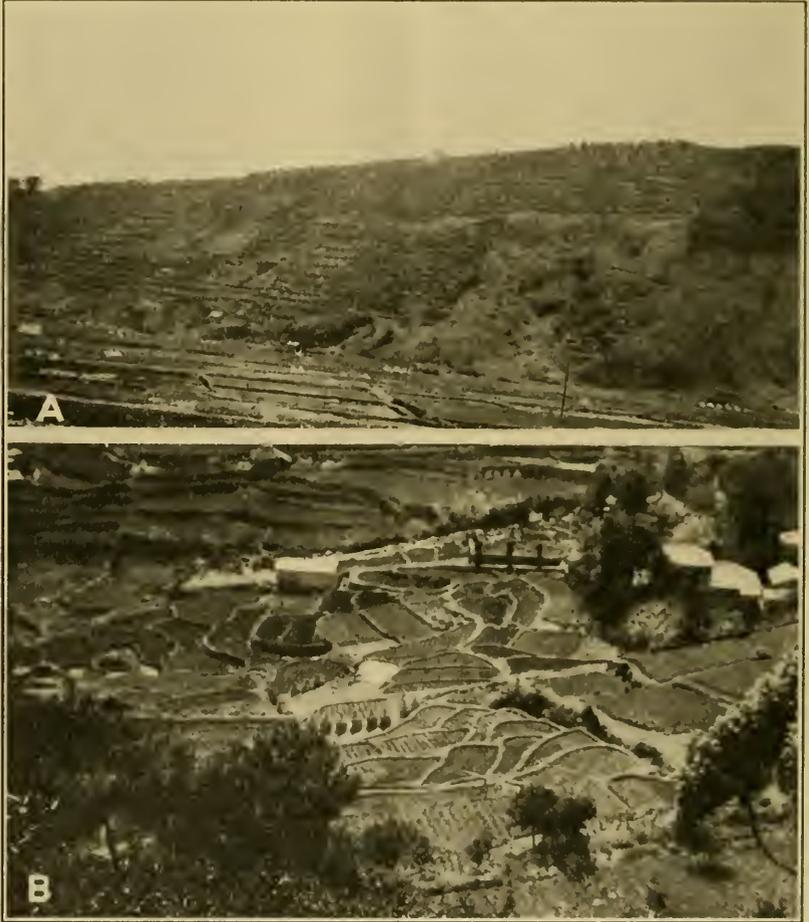


FIG. 35.—A, terraced hillside planted with orange trees, showing intensive agricultural conditions in southern half of Japan; B, rice paddy lands in a valley, illustrating intensive agricultural conditions in central Japan

described in the preceding paragraphs, and within this region *Popillia* is much less abundant than northward. This lack of abundance may be the result of the intense cropping of the soil and the flooding of the paddy fields, practices which are most unfavorable for soil-inhabiting insects. Further, within this region there are very few grasslands other than dense growths of low bamboo grass, these latter being rarely inhabited by *Popillia*. On the other hand, north of Sendai, including Koiwai and the island of Hokkaido, *Popillia* is

more abundant than elsewhere in Japan. Here agriculture is not so intensive, waste lands are more extensive, and sod or pasture lands in which *Popillia* breeds are not uncommon. Food plants suitable for the adults, however, are no more abundant here than in the south.

The foregoing points have been considered for the reason that they are thought by some to be the chief factors influencing the distribution of *Popillia*; but the writers are of the opinion that this insect is more abundant in the north because it is by nature a species which has become adapted to a northern habitat. At Tokyo and Yokohama, where sod lands have been artificially produced in lawns and golf links, *Popillia* does not increase and take advantage of these breeding grounds.

In Chosen agricultural conditions, although similar to those of Japan, are not so intensive. The outstanding feature in that country is the lack of forests. As a result of this forest destruction vast mountain areas have lost their soil and support no vegetation. In the lowlands grasses grow in all the waste places and in these areas the Chosen species of *Popillia* are commonly found.

THE SPECIES OF POPILLIA IN CHOSEN

Of the five or six species of this genus said to occur in Chosen only three are common and widely distributed.

POPILLIA ATROCOERULEA Bates

During the season the first species of *Popillia* to appear is *P. atrocoerulea*. This is a large species measuring from 11 to 13 mm. in length. It is entirely dark blue and has lateral tufts of white hairs on the abdominal segments. A common variety of this same species has the basal half of the elytra marked in deep chestnut brown.

The first beetles appear about the first of June and all disappear by the end of the month. They are most abundant about the time of full bloom of the Chosen chestnut during mid-June.

Only a few individuals have been reared through their life cycle. Egg laying is largely in grasslands, and the duration of the stage averages 12 days. There are three larval instars, the winter being passed in the third stage.

The chief food plants of this species are the flowers of the Chosen chestnut (*Castanea crenata*), leaves of the goumi bush (*Elaeagnus umbellata*), and the leaves of both wild and cultivated grape, the nonpubescent races being more readily eaten. These beetles have a strong tendency to feed on flowers, and are very destructive to roses.

POPILLIA CASTANOPTERA Hope

This species is second in seasonal occurrence. It is a small beetle 8 to 10 mm. in length, with the thorax bright metallic green and the elytra bright chestnut brown.

This is an abundant species and is found from late June to mid-August. The larvæ inhabit sod lands. Hibernation takes place in the third and final instar.

The important food plants of the adult are red straw (*Galium verum*), both leaves and flowers, leaves of *Quercus serrata*, a number of species of smartweed (*Polygonum* spp.), leaves and flowers of chestnut (*Castanea serrata*), leaves of goumi (*Elaeagnus umbellata*), and wild and cultivated grapes.

POPILLIA MUTANS Newm.

This third Chosen *Popillia* is much less abundant than the preceding two. The adults are robust beetles from 11 to 13 mm. in length, entirely deep indigo blue in color, and resembling somewhat the blue forms of *P. atrocoerulea*, but distinguishable from them by the absence of the abdominal tufts of white hair.

This is a late-appearing species, being found from mid-August to mid-September, and at no time is it abundant. Larvæ are found feeding on the roots of grasses. Only a few individuals have been reared through the life cycle, and these hibernated in the second larval instar.

The adults are flower feeders, confining their attention almost exclusively to the flowers of bush clover (*Lespedeza bicolor*), though they occasionally feed on flowers of other clovers.

SUMMARY

Nine species of parasites and one predator of the Japanese beetle (*Popillia japonica*) have been found and studied in Japan and Chosen. These represent three species of tachinids, two dexiidæ, four scoliidæ, and one carabid.

Among the tachinids *Centeter cinerea* is the most promising species, for in its native habitat it is very abundant and exerts a marked control upon *Popillia japonica*. In Hokkaido the largely two-year life cycle of the host interferes with its rate of increase, so that in successive years the percentage of parasitism fluctuates from approximately 20 to 90, respectively. At Koiwai in northern Honshu, where the number of beetles is fairly constant each year, the parasitism averages somewhat above 50 per cent. The climatic conditions under which this species lives correspond fairly closely to those of the infested locality in America.

Ochroemeigenia ormioides is more common in the warmer regions of Japan, though it ranges into Chosen and northern China, which would indicate that it is not limited to mild climatic conditions. This parasite is extremely sporadic in its attacks upon *P. japonica*. In some seasons parasitism reaches 35 per cent in a given locality, but in the following seasons it may fall below 2 per cent. A secondary host is necessary for the overwintering brood. The establishment of the species therefore depends upon its ability to become adapted to a new alternate host in America, if such is available.

Eutrixopsis javana has been obtained only from Hokkaido, and in that locality is of very minor importance as compared with *C. cinerea*.

Of the Dexiidæ two species have been found to parasitize *Popillia* larvæ. *Proscna siberita* occurs abundantly in northern Japan and *Dexia ventralis* in Chosen. Living larvæ are deposited on the soil and these burrow about in search of host grubs, into which they penetrate and upon which they feed. *P. siberita* has but a single brood each year and is well adapted to its host as regards the time of appearance. It effects a field parasitism in Japan of approximately 10 per cent. *D. ventralis* has three broods per year and apparently requires a different host for each one. The establishment of this parasite in America depends upon the presence of additional hosts which pupate at a time favorable to the brood of *Dexia*.

its rate of increase will also depend upon the numerical abundance of these hosts, if such are available.

Four species of Scoliidae have been found which either normally attack *Popillia japonica* or readily accept it as a host. *Campsomeris annulata* readily accepts full-grown grubs of *P. japonica*, but success in establishing it will depend upon the abundance of other acceptable native grubs which will support the broods for which large *Popillia* grubs are not available.

Of the *Tiphia* species, *T. popilliavora* at Koiwai effects a parasitism of 20 per cent upon grubs of *P. japonica*. It is a fall species, occurring during late August and early September. *T. vernalis* is a spring species occurring in Chosen during May and early June. It effects a field parasitism of 10 per cent upon native *Popillia*, and it readily accepts *P. japonica*. *Tiphia koreana* from Chosen is normally parasitic upon *Anomala* sp., but readily accepts *P. japonica*. The average parasitism by this species in the field is 20 per cent, but ranges at times as high as 76 per cent.

Craspedonotus tibialis is the only predator which has been considered for introduction. Large numbers were forwarded, but establishment was not successful.

In the Orient *Popillia japonica* is found only in Japan proper, and in that country it is of very minor importance as an enemy of economic crops. The most striking difference in its life history in Japan is the occurrence of a two-year cycle in 75 per cent of the total *Popillia* fauna on the island of Hokkaido. At Koiwai, in northern Honshu, only 25 to 30 per cent undergo a two-year cycle, whereas for Yokohama and regions southward only a one-year cycle is found.

Three species of *Popillia* occur commonly in Chosen, and the chief importance of these lies in the fact that their special parasites may be of use in combating *P. japonica* in America. The known parasites of these have been tested on the latter host, and in all cases have accepted it readily.

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UNITED STATES DEPARTMENT OF AGRICULTURE**

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UNITED STATES DEPARTMENT OF AGRICULTURE



DEPARTMENT BULLETIN No. 1449



Washington, D. C.



October, 1926

TUMORS OF DOMESTIC ANIMALS

By

ROBERT J. FORMAD, Associate Pathologist, Pathological Division
Bureau of Animal Industry

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INTRODUCTION

A tumor is an atypical, abnormal growth of tissue, developing without apparent cause, having no function, and growing independently of the laws that govern the growth of the body. Until the true cause of tumors is known no satisfactory definition can be given, as can be seen from the fact that every prominent authority on tumors has given a different definition of a tumor, depending on the particular angle from which his studies were undertaken.

Tumors are comparatively common in the domestic animals. They are of considerable interest to the veterinary practitioner and of more

duction. Hauser thus considers the changes in the cells more important than Ribbert's disturbance of tissue tension.

Von Hansemann (7) went even further, considering the increased growth energy of cells due to a gain in the power of independence and coincidental loss of differentiation of chromatin, brought about by chromatic changes in the nucleus with unequal division of chromosomes.

THE THEORY OF NERVOUS INFLUENCE

Disturbance of trophic innervation has been ascribed as the cause of neoplasms, the overgrowth of tissue being the result of local irregularities of nervous influence, particularly in neoplasms that are of nerve origin, formed in the course of nerve trunks. It would be difficult to conceive of the formation of all neoplasms as due to such a cause.

THE PARASITIC THEORY

The parasitic theory accepted in the Middle Ages was revived some time ago, especially by investigators of cancer, but this hypothesis has received less credence than other theories. Protozoanlike bodies with marked degenerative changes of the cells have been found in neoplasms by Thomas (20), Russell (18), Gaylord (6), von Podwyszki (16), and others. This, however, indicates only their accidental presence in a favorable soil produced by the degenerative changes and the accompanying chronic irritation, but throws no light on the causation of neoplasms; moreover, none of these observers describe exactly the same bodies that they consider as protozoan parasites.

In line with the advocates of the parasitic theory are such investigators as Scheurlen (19), Doyen (5), and others, who have found bacteria in neoplasms and described the *Bacillus neoformans* as the cause of cancer. The "Plimmer bodies," which are of blastomycetic origin, are said by Plimmer (15) to be the cause of cancer.

One of the principal objections to the parasitic theory of neoplasms is the difficulty of reproducing the disease by transplantation of fragments of neoplasms of one animal to an animal of another species.

Late experiments by Jensen (10), Loeb (12), and others in the transplantation of tissues have been successfully carried out, but these experiments prove only that the cells of malignant neoplasms of an animal can be transplanted at times to another animal of the same sort and continue to live and grow in the same fashion that a metastatic growth forms a secondary neoplasm. They do not prove the parasitic nature of neoplasms, because in most of them neither protozoa nor bacteria can be found. Benign neoplasms can not be transplanted.

CLASSIFICATION OF NEOPLASMS

Up to the present time no classification embracing all neoplasms has been accepted as satisfactory. Neoplasms may be classified clinically as to their nature, histogenetically as to their structure, or morphologically as to their shape.

CLASSIFICATION BY NATURE (CLINICAL CLASSIFICATION)

Clinically neoplasms are divided into two classes, benign and malignant.

Benign neoplasms are usually harmless and in themselves do not endanger life except by accidental location. They grow slowly from the center and mechanically push aside the surrounding tissues and remain distinct from them. Their slow growth permits a reaction of the surrounding tissues to concentrate around the neoplasm to form a capsule which sharply defines the neoplasm from the surrounding tissue. Even when diffused, benign neoplasms do not infiltrate the surrounding tissues and their growth may be arrested, to be renewed later. The paucity of their cells may account for their slow growth. Though usually small, they may become rather large in certain localities, as, for example, lipomas in the abdominal cavity and myomas in the uterus. They do not recur after complete removal; neither does metastasis occur.

Benign neoplasms, though harmless in their nature, may produce death indirectly by accidental location if in or contiguous to vital organs. A benign neoplasm of the larynx may become lodged between the vocal cords and completely obstruct respiration; when developed in the brain or the spinal cord it produces paralysis by pressure and eventually may lead to death. Benign neoplasms may interfere with the nutrition of vital organs either by pressure, thus limiting the blood supply of the latter, or by obstructing the digestive tract, bringing about a state of ill health commonly referred to as cachexia, resulting in emaciation or even starvation.

Malignant neoplasms are always harmful and usually destroy life in whatever situation they arise. Because of their preponderance in cells and a richer blood supply they grow more rapidly than benign neoplasms. They are frequently softer in consistence and usually have no capsule and are ill defined from the surrounding tissues. They increase by peripheral extension and dissemination of the proliferating cells into the surrounding tissues. They give metastases to internal organs by either the blood vessels, as is the case in sarcomas, or the lymph vessels, which is the common mode of cancer metastasis. They usually recur after removal.

The prominent features of malignancy in neoplasms are metastases, infiltration of the surrounding tissues, and recurrence. Metastasis may take place by direct contact, which is rare but is sometimes observed in neoplasms of the mucous membranes, or by the transmission of particles of the primary growth through the blood or lymph vessels, which is the usual mode of metastasis. These particles in the blood or lymph stream ultimately lodge in either proximate or distal parts of the body, where they grow rapidly in their new environment and deprive the tissues of some of the nutrition by appropriating blood enough for their own existence. Neoplasms when situated near a blood vessel may, during their growth, diminish by pressure the blood supply of an organ and interfere with its functional activity. The entrance of neoplastic elements into the vascular channels is the result of the destructive nature of a malignant neoplasm and is comparable to embolism. Anemia of the organ usually results and may eventually be followed by general anemia of the body, and in the more severe cases by emaciation and cachexia.

The peripheral cells in malignant neoplasms proliferate more rapidly and receive more nourishment from the surrounding tissues than the cells in the interior of the neoplasm. Insufficient nutrition and increased pressure, to which the inner portion is subjected, bring about degenerative changes which are followed by atrophy and absorption of the inner portion of the neoplasm, resulting in the formation of a cavity. The cavity may contain remnants of the degenerated product, or may be filled with an albuminous fluid or serum resulting from negative pressure.

Marked anemia, emaciation or wasting of the body and extreme cachexia are invariably associated with malignant neoplasms (cancers) of the esophagus or the stomach, which interfere with the passage of food, resulting in starvation; some malignant neoplasms (sarcomas) in other locations, though larger in size, may not produce such marked cachexia.

Superficial malignant neoplasms often ulcerate around their periphery. The ulceration may be accompanied by inflammatory changes and offers a favorable soil for bacterial infection, and inflammation. These processes, singly or collectively, may produce soluble substances which are absorbed into the circulation and contribute largely in bringing about cachexia.

Chemical analysis of neoplasms has shown that their composition closely approximates the composition of the structures from which they grow. Glycogen has been found in excess in neoplasms which originated in tissues that normally contain glycogen. Enzymes are likewise present in greater quantity in certain neoplasms than in the normal tissues from which they grow.

During the last few years pathological chemistry has been actively used in research of neoplasms in human-cancer investigations and in the transplantation experiments of malignant neoplasms.

Malignant neoplasms differ in their rapidity of growth, depending on the location and the blood supply of the tissue. They also differ in the extent of their metastatic ability. Some are more prone to metastasis than others, the latter expressing their malignancy by peripheral invasion of the surrounding tissues. Recurrence, which is the chief feature of malignant neoplasms, is also variable, depending on the difference in type. Under exceptional circumstances malignant neoplasms have been known to revert or undergo apparently spontaneous retrogression, resulting in their complete disappearance.

Degenerative changes in benign as well as in malignant neoplasms are very common. Any degeneration that affects an organ or a tissue may likewise affect a neoplasm, as albuminous, fatty, mucoid, or colloid degeneration. Calcification, pigmentation, glycogenous infiltration, necrotic changes, and hemorrhages may also be observed in neoplasms.

CLASSIFICATION BY STRUCTURE (HISTOGENETIC CLASSIFICATION)

The histogenetic classification of neoplasms is based on the structural elements of which the neoplasms are made up. This classification was suggested by Virchow (21) after the development of the cell doctrine and the fact that the animal body is composed of ele-

mentary tissue, which forms every structure, organ, or system of the body.

Virchow's classification is as follows:

1. Histoid. Simple-tissue neoplasms.
2. Organoid. Compound-tissue neoplasms consisting of several tissues like those found in organs.
3. Teratoid. Mixed or congenital new formations, containing such structures as teeth, hair, cartilage, and bone.

The following modified histogenetic classification is used by many authorities:

1. Connective-tissue neoplasms.
2. Epithelial neoplasms.
3. Teratoid neoplasms.

Adami (1) has suggested a modification of the histogenetic classification based on embryonic layer formation, as follows:

1. The lepidic group or lepidomas, comprising the lining membrane tissues or rind neoplasms, which are of epithelial and mesothelial structures deficient in stroma.
2. The hyleic or primitive pulp tissues of undifferentiated material, which are rich in stroma comprising essentially hypoblastic and mesoblastic structures.

A careful study of the minute structure of neoplasms shows that all neoplasms are composed of elements present in the animal body in their adult or in their embryonal state. Neoplasms therefore originate from existing elements in the animal body and reproduce the adult or the embryonal tissue from which they have originated. Neoplasms, like normal tissues, consist of cells and a supporting interstitial ground substance. The cells of neoplasms, although retaining the morphological type of normal tissues sufficiently to be recognizable, are subject to considerable variation in size and shape. The greater their departure from adult cells the more pronounced becomes the embryonal type of structure. The stroma is more abundant in neoplasms which originate from the mesoderm than in the neoplasms originating from the ectoderm or the entoderm, which have a very scanty stroma.

When a neoplasm is composed of a single tissue which is analogous to the tissue from which it started, it is known as a homologous growth, whereas those neoplasms which have departed from the normal tissue are described as heterologous.

The histogenetic classification is followed in the arrangement of this bulletin and the various kinds of neoplasms in each class are discussed in order of their frequency of occurrence.

CLASSIFICATION BY SHAPE (MORPHOLOGICAL CLASSIFICATION)

Morphological classification is used to distinguish neoplasms by macroscopic conformation before the actual structure and nature are determined. It is as follows:

1. Uniform swelling (affecting organs): Golter, lymphoma.
2. Flat tabular swelling (slight elevations above the surface): Keloid angioma, epithelioma, sarcoma of serous membranes.
3. Nodes growing centrally which lie embedded in the tissue: Fibroma, myoma, adenoma.
4. Nodes growing peripherally: Primary sarcoma, primary carcinoma.
5. Tubers (partly protruding nodes): Chondroma, osteoma, osteosarcoma.
6. Fungus (spongy growth): Telangiectatic sarcoma, cavernous angioma.

7. Polyps (pedunculated growth): Myoma, soft fibroma, sometimes also lipoma, adenoma.

8. Papillae (dermic growth): Corns, cutaneous horns.

9. Dendrites (branching or cauliflowerlike growth): Warts, papillom epithelioma.

10. Cysts (saclike or bladderlike neoplasms): Glandular cystoma, papilloma cystoma.

NOMENCLATURE

In naming a neoplasm the root word of the tissue of which the neoplasm is composed is used with the addition of the Greek word "oma," signifying tumor or neoplasm. Thus the names fibroma, myoma, osteoma, neuroma, angioma, and other similar ones are obtained. An exception is made in naming a group of neoplasm which from their resemblance to flesh (sarko) are known as sarcomas, and also in designating another group of neoplasms, having the fanciful resemblance to a crab (karkinos), are called carcinoma.

CONNECTIVE-TISSUE NEOPLASMS

FIBROMA

Definition.—A fibroma is composed of fibrous connective tissue which it resembles in structure and arrangement, but presents some differences in its finer composition. Originating from the mesoderm, the connective tissue has a wide distribution and a marked difference in the arrangement and grouping of the fibers. The bundles may be arranged loosely, as in the areolar tissue and in the submucous tissue in mucous membranes, or the bundles may be very compactly arranged, as in the periosteum, fascias, and tendons.

Seats.—The wide distribution of connective tissue makes it possible for fibromas to start and grow in any part of the body, but there are certain places in which they grow with preference. Some of the more common places are the skin and the subcutaneous connective tissues of the chest. Fibromas are often found in the chest of horses and in the dewlaps of cows.

They may be found at times in the region of the throat and neck in cattle and horses as well as in other animals. The extremities, especially about the knee and elbow, are comparatively common places to find fibromas in cattle, horses, and dogs. The tail in cattle is also a frequent seat of hard fibromas. Care must be taken, however, to differentiate the hard, fibromatous nodules on the tail from nodular formations which may be tuberculous or actinomycotic in nature.

Less frequently fibromas are found in other locations, as the "fibroma diffusum" involving the muzzle of cattle, where it may become as extensive in size as the muzzle itself. Polypoid or pedunculated fibromas are found in the nose, pharynx, and larynx in cattle and horses. In the latter locations they have been known to cause fatal results by obstructing respiration. Other sites for polypoid fibromas are the uterus, vagina, and ovary in cows, mares, and bitches. In these latter localities the neoplasm assumes a more pedunculated shape, is harder, and may be many times larger than the comparatively small, soft, edematous nasal polypi. The tongue is also one of the rare seats of fibroma. The tumor usually grows near the upper surface without encroachment on the mucous mem-

brane, is dense, hard, white, and well defined from the muscle of the tongue. Fibroma in the tongue should be differentiated from actinomycosis, which often has collections of pus, sulphur-colored granules of colonies of actinomyces, and calcified areas. Among the rare locations for fibroma are the esophagus, stomach, intestine, mammary gland, lung, liver, kidney, and spleen.

Structure.—According to the dense or loose arrangement of the fibrous-tissue bundles, fibromas are designated as soft or hard. They may be found in any part of the body where connective tissue is naturally present. A fibroma grows comparatively slowly and is encapsulated and usually poorly supplied with lymph and blood vessels. Exceptionally a fibroma may be very vascular, as the bleeding fibroids, which occur in man, but they are rare in animals. Fibromas are usually single, but they may be multiple, especially in animals.

Macroscopic appearance of hard fibroma.—Hard fibroma is a nodular or lobular firm growth, variable in consistence, circumscribed, and well defined from the surrounding tissues. It is generally encapsulated, light in color, slow growing, and usually small in size, but it may reach enormous size in the body cavities. It is somewhat dry, cutting with tough resistance like a tendon, and is glistening in appearance on the cut surface.

Microscopic appearance of hard fibroma.—On microscopic examination the bundles of fibers are found to be coarse in texture, wavy in their course, frequently interwoven, crossed, and interlaced in a most complex manner, and form whorls around the scanty blood vessels. Between the bundles a fair number of spindle-shaped cells are present. These cells are rather inconspicuous owing to the small amount of cytoplasm. The presence of elastic fibers in fibromas, although doubted by some observers, can be found in the denser forms of fibroma in animals.

Structure of soft fibroma.—Soft fibroma, or fibroma molle, is soft in consistence, rich in cells, poor in fibrillar tissue, and is abundantly supplied with blood and lymph vessels.

Macroscopic appearance of soft fibroma.—The color of fibroma molle is gray or grayish red, in contrast to the glistening white color of the hard fibroma. The shape may be nodular, often lobulated, and not infrequently polypoid or pedunculated when growing from a mucous membrane.

Microscopic appearance of soft fibroma.—On microscopic appearance the connective-tissue bundles are seen to be more delicate and smaller in size and more loosely arranged than in hard fibromas. The cells are more numerous, possessing a considerable quantity of cytoplasm around the oval nuclei. They vary in shape and may be round, oval, spindle shaped, and irregular. Wandering cells, plasma cells, and leucocytes are often present.

Combinations.—Fibromas may frequently combine with other tumors, forming combinations in which the fibroma predominates, and the neoplasm is named by combining the two names, but naming the predominating tissue first, as in fibromyoma or in myofibroma. The more common combinations of fibroma with other tumors are fibromyoma, fibrolipoma, fibrochondroma, fibroosteoma, fibroangioma, fibroadenoma, fibropapilloma, etc.

At times it is difficult to draw a sharp line between the hyperplasias of connective tissue resulting from chronic inflammation as in chronic mastitis, and true fibromata. Diffuse hyperplasias of the viscera, which at times are inflammatory, are generally considered by most authorities as cases of diffuse fibrosis.

Degeneration.—Serious infiltration and mucoid degeneration are often present in polypoid fibroids originating in the submucosa of the respiratory tract. Calcification and ossification have been reported but are rather rare.

Nature.—Clinically, fibromas are benign neoplasms which do not give metastasis to internal organs unless they are combined with malignant growths.

LIPOMA

Definition.—Lipoma or fatty neoplasm is made up of adipose tissue, which it closely resembles in appearance and structure. It may be found in all domestic animals and is rather common.

Seats.—Lipomas may grow wherever adipose tissue is normally present. The more common locations are the subcutaneous tissue in the region of the back, shoulders, breast, knees, inner surface of the thigh, the submucous tissue, and the subserous tissue of the mesentery, omentum, and peritoneal cavity.

The less frequent places to find lipomas are the liver, kidney, lung, mammary gland, ovary, and uterus.

Very rarely lipomas are found in the membrana nictitans in the horse and dog, also in the brain, arising from the blood vessels of either the pia mater or the dura mater.

Macroscopic appearance.—Lipomas are usually single but frequently may be multiple. They are slow growing, at times rather small, but have been known to reach enormous size. They are usually smooth, encapsulated, and can be readily shelled out of the capsule, being well circumscribed from the surrounding tissue. Their shape may be round or oval while they are small, when developed in the subcutaneous tissue, before they are subjected to pressure; but they become hemispherical or dome shaped when the pressure is from one side. When they become large the tension on the skin is sufficient to cause ulceration and even gangrene of the skin. Peritoneal lipomas in the omentum and intestines are often lobulated, especially in cattle, sheep, and hogs. The subserous intestinal lipomas in cattle may also be pedunculated. When the pedicle is stout and elastic a loop of the intestine may wind around it and cause strangulation in the intestine. A more unusual shape of lipoma is the diffuse form. Under this heading may be mentioned lipomatous elephantiasis. Lipomas may be firm or soft. If soft they are flabby. They are white or yellowish white in color, depending on the amount of connective tissue present and the composition of the fat. The fat of cattle, sheep, and hogs contains a higher percentage of stearin than of olein. In these animals the fat is whiter than in the horse. The fat of the horse contains more olein than stearin and is yellower and softer. The resistance varies according to the amount of connective tissue in the lipoma.

Microscopic appearance.—The individual fat cells and the lobules in lipomas are larger than those in normal adipose tissues. The

supporting connective tissue is coarser and contains fewer blood vessels.

Combinations.—Fibromatous change in lipomas is the most common. It is considered by many authorities to be more of a hypertrophy of the supporting fibrous connective tissue than a true combination with fibroma. Myxofibroma is not infrequent and may also be regarded as a fibrolipoma undergoing myxomatous change.

Degeneration.—Ulceration and necrosis in areas of isolated lobules may take place at times on the periphery of large lipomas. More rarely calcification is present, and then only in limited areas.

Nature.—Clinically, lipomas are benign neoplasms which give no metastases to internal organs.

XANTHOMA

In connection with lipomas there may be mentioned the xanthoma, a peculiar form of fatty neoplasm, which is a small, flat elevation, yellowish, found in the skin about the eye and eyelids, and more rarely about the internal organs in man. It is composed of modified fatty tissue resembling embryonal adipose tissue, with large vacuoles containing cholesterin esters (cholesterin and fatty acid clumps) and is supplemented by numerous round cells such as are found in cell infiltrations. Xanthoma has not been described from domestic animals.

MYXOMA

Definition.—Myxoma is a neoplasm composed of mucous tissue which is an embryonic connective tissue similar to that of the umbilical cord, or the jelly of Wharton, or the vitreous humor of the eye. As myxoma originates from a type of connective tissue from which fat develops in the embryo, the relation of myxoma to lipoma and fibroma is very intimate. These growths vary in size from that of a pea to the size of two fists.

Appearance.—Pure myxomas are soft, jellylike, translucent, encapsulated, grayish neoplasms, which are rather rare in their pure state. When their consistence is lacking in softness and gelatinous composition it would be more proper to consider such neoplasms as the myxomatous degeneration of a fibroma, lipoma, or sarcoma, instead of a myxoma. The most characteristic form of myxoma is the soft, grayish-colored, polyp-shaped mass commonly spoken of as nasal polypus. Myxoma may also appear as a hemispherical elevation projecting from a surface, or it may be lobulated, and occasionally it presents a diffuse mass without any definite limits, having no capsule.

Seats.—The mucous membrane of the nasal passages and the uterus of cattle are some of the common seats, also the serous membrane of the heart. Less common are the myxomas found in the mammary gland and those found in the course of the nerve trunks. Rarely myxomas are found in the marrow of bones and in the periosteum, also in the brain and spinal cord.

Structure.—On microscopic inspection myxoma consists of loosely scattered cells, some of which are spindle shaped, but most are star shaped with long processes that frequently anastomose with one another. These cells have a fair amount of cytoplasm and large, oval nuclei. Numerous fine, loose fibers, which are often gelatinous

in nature, are intermingled with the cells. Between the cells and fibers is the gelatinous, homogeneous, interstitial ground substance. A few blood vessels and lymph vessels are invariably present.

Combinations.—Myxoma is sometimes combined with fibroma, lipoma, and sarcoma, but most authorities are inclined to regard these combinations more as a process of mucous degeneration of the above-mentioned neoplasms rather than a combination with the myxoma.

Degeneration.—Myxomas frequently become edematous or undergo degeneration which is followed by the formation of a cyst.

Nature.—Clinically, myxomas are benign, nonmetastatic, slow-growing neoplasms. Their capsule is more delicate than in the fibroma of the lipoma and is often almost entirely absent when the myxoma assumes the lobulated form. At times, however, myxomas may grow rapidly, and the cell processes become absorbed, the interstitial substance is reduced in quantity, whereby the cells are closer together and the neoplasm develops a malignant tendency.

CHONDROMA

Definition.—Chondroma is a neoplasm composed of cartilage and a variable amount of fibrous connective tissue, which forms a capsule on the periphery and penetrates into the interior of the neoplasm.

Chondromas may be found in all domestic animals, especially in sheep, cattle, hogs, and horses, also rather commonly in dogs and domestic fowls.

Appearance.—Chondromas are nodular, lobulated, or rounded in shape, white or whitish gray, translucent when the hyaline cartilage predominates, and of a bluish-white tint on section. The color may be yellowish when elastic tissue predominates.

Seats.—Two distinct forms may be considered: (1) Chondroma proper or enchondroma, and (2) cartilaginous outgrowths or ecchondroma. The first, originating in noncartilaginous tissue, is the more usual form and is associated with the osseous system, starting from the periosteum and less frequently in the bone marrow. The sternum and ribs are frequently subject to injuries in domestic animals and are common seats of chondroma growing from the periosteum. The maxillary bone and the long bones are less frequently involved in the process. More rarely chondromas are found in the thyroid, parotid, and mammary glands, the testicle, and the ovary. In these localities chondromas must be the result of misplaced embryonic cell rests, congenital in origin, and are frequently combined with other neoplasms.

Ecchondromas or cartilaginous outgrowths originate from the perichondrium of the laryngeal, tracheal, and bronchial cartilages of the lung.

Structure.—Under the microscope chondromas usually resemble hyaline cartilage, less frequently elastic cartilage or fibrocartilage. The cells in chondromas are more irregular in shape and size, not only in different growths, but also in different parts of the same neoplasm. Several cells or groups of cells may be present in a lacuna and the capsule is generally absent. Some chondromas are very cellular, others are poor in cells. The smaller cells are always peripheral and the larger cells are central. Between the cells is the matrix, which is usually hyaline and homogenous or apparently

structureless, but may at times contain elastic or fibrous tissue. Chondromas, like normal cartilage, do not contain any blood vessels and derive their nutrition from the perichondrium or the capsule surrounding the periphery. For that reason they are subject to either retrogressive or progressive metamorphosis.

Combinations.—Chondroma frequently combines with sarcoma, myxoma, osteoma, adenoma, or lipoma, occurring in the mixed neoplasms found in the parotid gland, mammary gland, testicle, and ovaries. Of these combinations the chondromyxoma, chondrosarcoma, and osteochondroma are more frequent than the adenochondroma and chondrolipoma.

Degeneration.—Chondromas in domestic animals are very prone to undergo incomplete calcification or even ossification. The ground substance may be affected by mucoid degeneration with the production of softened foci and liquefaction resulting in the formation of cysts, which is less common in animals than in man.

Nature.—The ordinary chondromas are clinically benign neoplasms which give no metastasis and do not recur after removal. Exceptionally, however, metastases may be present even in the ordinary tumor and are always present in combinations of chondroma with sarcoma and in mixed neoplasms, when they become malignant, give metastasis, and recur after removal.

CHORDROMA

Resembling the structure of chondroma and myxoma, the chordroma may be mentioned; it is a rare, diminutive neoplasm of man which is about the size of a pea, occurring usually at the base of the skull in the vicinity of the sphenoid-occipital synchondrosis that corresponds to the upper end of the notochord, of which it is considered an embryonal remnant. It has also been described in the sacrum and coccyx. In structure it consists of cartilage cells, many of which are large and vesicular, and a homogeneous, jellylike, interstitial substance. It is usually benign when small, but more recently a number of cases have been reported in which it grew to a large size infiltrating the brain substance and becoming malignant.

This neoplasm has not been described in the domestic animals.

OSTEOMA

Definition.—Osteoma is a neoplasm composed of bone tissue. In the domestic animals there are a number of osseous deposits which result from injuries or inflammation of the periosteum that are osteoid conditions but are not true osteomas. The true osteomas are usually small and slow-growing neoplasms attached to the bony skeleton. They may occur, however, unattached to bones, as in the lung, testicle, parotid gland, mammary gland, ovary, and uterus.

Osteomatoid conditions, such as small protuberances projecting from the surface of the bone, the exostoses, osteophytes, splints, and spavin are the result of chronic inflammation and should not be considered as osteomas.

Appearance.—Osteomas may be of various shapes. Usually they are nodular, hard, at times lobulated, but always firmly or intimately attached to the surrounding tissue. According to the density of the caseous elements, three varieties may be distinguished: (1) Osteoma

eburneum, of ivorylike hardness and density; (2) osteoma spongiosum, resembling the structure of spongy bone; (3) osteoma medullosum, composed mostly of marrow, supported and reinforced by bone spicules.

Seats.—The tips of the horns in cattle are often the seat of osteomas. Injuries and inflammation to the damaged part may have contributed their share in the formation of horn neoplasms. Large and common osteomas may be found arising from the sphenoid, ethmoid, or the turbinate bones in cattle and horses. The mandible and inferior maxilla are other frequent places, as are any of the bones of the head, especially in the region of the orbits.

Structure.—Osteoma eburneum closely resembles compact bone. It is made up of bone lamellæ, lacunæ, and canaliculi, which are generally short and ill defined. Some of the lamellæ form in a concentric manner around the Haversian canals; these are the Haversian lamellæ. Others unite the Haversian systems; they are the interstitial or ground-bone lamellæ.

The arrangement of the lamellæ in osteoma is like that of normal bone—external or circumferential, Haversian or concentric, and interstitial or ground lamellæ. The Haversian canals are less regular and their course is at right angles to the axis of the bone. The larger canals may contain marrow. The periphery has a closely adherent capsule which is identical with the periosteum of bone.

Osteoma spongiosum has the structure of spongy bone, and the Haversian canals are expanded to form marrow spaces and loose interlacing meshwork of osseous structure, the interior of the spaces being occupied by cell structure identical with red marrow. The blood vessels are more numerous than in the preceding variety.

Osteoma medullosum is composed principally of marrow and has fewer bone spicules than the osteoma spongiosum. The capsule in the last two varieties is well developed.

Combinations.—Osteoma frequently combines with other neoplasms as osteofibroma, osteochondroma, and especially osteosarcoma.

Degeneration.—Secondary degenerative changes, softening, and necrosis are not infrequent in the spongy and medullary varieties.

Nature.—Osteoma is a benign neoplasm, nonmetastatic, and encapsulated. Though usually small, as in the dense variety, the spongy variety may reach the size of a football. Osteoma may be single but more often it is multiple. When in combination with sarcoma it becomes malignant and gives metastasis.

ODONTOMA

Odontoma is the name applied to excrescences on teeth. They are of bonelike hardness, congenital in origin, and composed of dentine, enamel, and pulp tissue. All these tissues are in variable proportion. Simple odontoma affects a single tooth and is met with in cows and horses. It usually surrounds the crown, or more rarely the root of a tooth. It is usually hard, rounded in shape, about the size of a walnut, but has been known to reach the size of an orange.

The mixed odontoma is soft, composed to a large extent of fibrous tissue, numerous blood vessels, odontoblasts, tooth-papilla structure, and rudimentary masses of dentine and enamel mixed in the interior and found also as a thin, peripheral crust. The mixed odontoma may

surround a single tooth, but more often involves a number of teeth. It may occur as a group of cysts completely surrounded by a fibro-gelatinous dental sac and an alveolar bone capsule. It is sometimes described as odontostoma.

Bland-Sutton (3) has given a most complete description of seven different varieties of odontomas in man; but, as such varieties are not recognized in the domestic animals, no further reference will be made here.

MYELOMA

Definition.—Myelomas are neoplasms which are formed from red bone marrow. They vary in color from grayish to yellow, but may be pink and often are deep red. Myelomas occur as primary multiple growths in the cancellated portion of the sternum, ribs, and skull, and according to some authorities less frequently in the long bones except in the tibia, where it is admitted to be not infrequent. They are benign and slow growing.

Structure.—The structure suggests a hyperplasia of the red marrow. During growth they induce active absorption of the bone and an invasion of the soft tissues. Microscopically these neoplasms consist of myelocytes, lymphocytes, erythrocytes, and a scanty amount of interstitial connective tissue. Often giant cells are present. The presence of giant cells was responsible for some pathologists' classifying the myelomas as myelosarcomas. They are frequently very vascular and rather liable to show hemorrhages. The naked-eye appearance and the microscopic appearance therefore suggest malignancy, though these neoplasms are invariably benign in nature and do not metastasize. There is a tendency of the hemorrhagic forms to become cystic.

MYOMA

Definition.—Myoma is a neoplasm composed of striated or non-striated muscle fibers and a variable amount of connective tissue. According to the variety of muscle, myomas are divided into leiomyoma, composed of involuntary or nonstriated muscle, and rhabdomyoma, composed of voluntary or striated muscle. Of these two varieties leiomyoma is more common and occurs where involuntary muscle is normally present, as in the digestive tract, the reproductive organs, and the urinary system, whereas rhabdomyoma frequently occurs in places where voluntary muscle does not exist normally and is therefore considered to be of congenital origin.

Appearance.—Myomas are firm, pale, globular, rounded, nodular, or diffuse structures which more rarely become pedunculated. They vary in size from a pinhead to a man's head and even larger. They are so similar to fibromas, with which they frequently combine, that a differentiation can be made only by microscopic examination. This is especially true of myomas in the uterus. In this location they are often called fibroids until a microscopic examination proves them to be myomas.

Myomas are surrounded by a connective-tissue capsule. They are slow growing, sometimes single, but more often multiple.

Seats.—The most frequent seats are the muscle walls of the uterus and vagina in cows and hogs, and sometimes in dogs. The less

frequent locations are the esophagus, stomach, and intestines in horses and cows, the urinary bladder in dogs, and the serous membranes. The rarest place in domestic animals, but not in man, is the skin. Here myomas originate from the erector piliform muscles of the skin, from the ducts of the sweat glands, from the nipples, or from blood vessels.

Structure.—Microscopically, myoma consists of spindle-shaped cells with rod-shaped or cylindrical nuclei. The cells are arranged in compact bundles which interlace with one another at various angles. The individual cells are held together by a small quantity of cement substance which is collagenous in nature. At times myoglia fibrils have been seen lying alongside of the cells. It is very important to distinguish the spindle-shaped cells of involuntary muscle of leiomyoma from the spindle-shaped cells of soft fibroma and the spindle-shaped cells of spindle-cell sarcoma, as the last two varieties often enter into combination with the leiomyoma and it is not easy to distinguish them. The muscle cells of leiomyoma are usually long, slender and sharply outlined, terminating in a pointed extremity. Their nuclei are long, rod shaped, with rounded ends, and lie within the cell body. Sometimes the muscle cells, as in blood vessels, are short and plump.

The fibroblasts of the cellular fibroma, although spindle shaped, are shorter, and in those places where they form strands or bundles the very character of fibrous tissue is apparent. The principal distinction, however, lies in the fact that the nucleus of the cellular fibroma is short and oval and is peripherally situated. The small-sized neoplasms are much more likely to be pure myomas, while with the increase in size the fibromatous elements predominate in proportion to the diminution in the amount of involuntary muscle. It is for this reason that many of the uterine neoplasms which in reality are fibromyomas are commonly called fibroids. Leiomyoma may be distinguished from spindle-cell sarcoma by greater regularity in the direction of the cells, but particularly by the oblong rod-shaped outline of the nucleus, which is characteristic of leiomyoma.

Combinations.—Myomas frequently combine with other neoplasms, the most frequent combinations being fibromyomas, myxomyomas, myosarcomas, and adenomyomas.

Degeneration.—Calcification is the most common change. Myxomatous change may occur in myomas, which have a preponderance of fibrous connective tissue. Very rarely telangiectasis may be present in the peripheral parts of certain myomas, while the central part of the large neoplasms may be so poorly nourished that hyaline and later necrotic change may set in and result in cystlike softening.

Nature.—Myomas are slow growing, encapsulated, benign, non-metastatic neoplasms. In combination with sarcoma they become malignant, produce metastases, and grow fairly rapidly.

RHABDOMYOMA

Description.—Rhabdomyoma is a rare neoplasm in both man and domestic animals. The characteristic tissue from which it derives its name is striated or voluntary muscle, which is always subordinate to other tissues, especially fibrous connective tissue and cells resem-

bling sarcoma. The greater part of the neoplasm may not contain any striated muscle fibers. Only here and there isolated fibers, or groups of striated fibers, may be present. Rhabdomyoma usually occurs in places where striated muscle is not normally present, except in the heart.

Seats.—The most common seat by far is the kidney, then the testicle, heart, vagina, uterus, bladder, and parotid gland. A case was reported found in the lung of a young sheep. The presence of this neoplasm in places where no voluntary muscle normally exists is an indication of congenital origin. In the kidney rhabdomyoma reaches the largest size, appearing as a rounded or irregular mass, which may lead to a total destruction of the organ. Rhabdomyomas of the testicle are not so large as those of the kidney and are less destructive. The rhabdomyomas of the heart are frequently pedunculated.

Structure.—On microscopic examination the striated fibers in rhabdomyomas are smaller than normal muscle fibers, more irregular, and often spindle shaped, or even club shaped. The sarcolemma is generally present and often droplets of glycogen can be demonstrated. The striation of the muscle fibers is faint and in places may be entirely absent. Fibrillar connective tissue and spindle-shaped, sarcomalike cells, some of which are suggestive of embryonal muscle cells, predominate.

Nature.—Rhabdomyomas are malignant in proportion to the amount of sarcomalike element which they contain. Adenomatous elements may be present, in which case the neoplasm is practically benign.

NEUROMA

Definition.—Neuromas are neoplasms composed of newly formed nerve tissue. The term is indiscriminately applied to any new formation occurring in the course of nerves. A distinction therefore should be made between the neoplasms consisting of nerve fibers, ganglion cells, or both combined, which are the true neuromas, and neoplasms without any increase in nerve fibers or ganglion cells. The latter are composed merely of a fibroconnective tissue enlargement or overgrowth on a nerve trunk, and are false neuromas, commonly called neurofibromas or fibroneuromas. The true neuromas are rather rare in man and almost unknown in domestic animals, whereas the false neuromas are comparatively common in man as well as in animals. Following neurectomy there are terminal thickenings on the nerve stumps, and although they are called amputation neuromas they are simply the regeneration process of the resected nerve trunk, but not neoplasms.

Appearance.—Neurofibromas develop as corded, cylindrical, fusiform, or even nodular thickening of nerve trunks. The perineurium undergoes a marked proliferation, forming a grayish structure which extends along many of the nerve funiculi in a nerve plexus and giving rise to an intertwining plexiform growth.

Seats.—Ostertag (14), Kitt (11), Morot (13), and others have observed these plexiform neurofibromas in the brachial plexus of cattle, and the dorsal, intercostal, and sternal nerves as nodular

thickenings. Thirteen hundred and fifteen such nodules in one old cow were recorded by Morot. Neurofibromas have also been reported in horses and pigs.

Among the rarer forms of neuromas and neurofibromas in man may be mentioned the painful subcutaneous tubercle, ganglion neuromas, and the multiple molluscum fibrosum, a nodular elevation of the skin.

GLIOMA

Definition.—Gliomas are neoplasms which grow from the cells of the neuroglia or glia, the supporting tissue of the central nervous system. Several authenticated cases have been recorded by Kitt (11) in dogs and also in other domestic animals. In man it is the most common neoplasm of the brain.

Appearance.—Glioma is usually a solitary neoplasm, rounded or oval, but difficult to distinguish from the normal brain. It is usually about the size of a cherry but may become as big as an apple. It is either soft or moderately firm and usually grayish white, but at times is dark red, when it appears sharply defined from the brain substance. In the last case it is traversed by numerous blood vessels and may contain hemorrhagic areas.

Seats.—Gliomas occur most frequently in the brain, less frequently in the spinal cord, and rather rarely in the retina. Gliomas of the brain and cord do not metastasize to other organs, but they may invade or disseminate in the tissue where they originally started. In their pure state gliomas are benign except for their situation; they may become dangerous by causing intercranial pressure or producing paralysis by pressure on a motor center, or may cause sudden death by hemorrhage. The retinal glioma is an extremely malignant and more rapidly growing neoplasm. Another rapidly growing glioma occurs in the adrenals, and is rarely found in the nervous system proper. The adrenal gliomas have a tendency to metastasize to the lymph glands and the liver. In the retroperitoneal region there is also a benign form of glioma originating from the sympathetic nervous system which from a predominance of large ganglion cells is called ganglioneuroma.

Structure.—Under the microscope neuroma consists mainly of small, round cells which are larger than ordinary glia cells, with prominent round or oval nuclei and numerous delicate branching processes. Some of the cells may possess a large amount of cytoplasm and several nuclei. The interstitial glia or neuroglia framework may consist of such delicate fibrils that the structure is as cellular in appearance as a sarcoma, and for that reason gliomas are often spoken of as the sarcomas of the brain. It must be borne in mind that the glia elements are of ectodermal and not entodermal origin. The gliomas starting in the retina are very cellular in structure. Some gliomas may have an abundance but never a predominance of neuroglia fibers, while the glioma of the sympathetic system has a considerable number of large ganglion cells, from which it receives the name ganglion-cell neuroma. In some gliomas groups of ependyma cells form rosettes around the blood vessels, resembling the tubules of adenoma. These neoplasms are called gliosarcomas by some pathologists.

Degeneration.—Degenerative changes are frequently found in the gliomas and lead to fatty degeneration, followed by softening, and often result in the formation of cysts.

ANGIOMA

Definition.—Angiomas are neoplasms composed of vascular tissue. If formed of blood vessels they are called "hemangiomas," when formed of lymph vessels they are called "lymphangiomas." They have a relatively small amount of supporting tissue. In either case there must be new formation or proliferation of the vessels. The distention alone of preexisting vessels, without proliferation, does not constitute angioma, any more than the alteration in the blood pressure of a local venous obstruction. Neither do capillary telangiectases, which can take place in local areas of the liver by a partial obstruction of a branch of the hepatic vein; nor do hemorrhoids, which are instances of compensatory dilatation of vessels, constitute angiomas.

Hemangiomas or angiomas proper are usually composed of proliferating and dilated vessels, arteries, veins, or capillaries and are classified as capillary angioma or angioma telangiectaticum. If the blood spaces are large, irregular, and intercommunicating they are designated as the cavernous type. Usually there may be gradations of these two types where the vascular channels are larger than capillaries but not large enough to be called venous spaces.

Seats.—In man there is found a superficial form of skin angioma that is rarely seen in domestic animals. This is probably due to the larger amount of pigment and the thickness of the skin in animals. However, the finding of this type of angioma at the root of the tail in dogs and horses has been reported. A comparatively common form of angioma, which is congenital, is the angioma simplex or the capillary form of angioma found in the skin of man about the face and known as birthmarks.

Structure.—Angiomas consist of capillaries with preformed, imperfect, thin-walled vessels resembling veins. The presence of these vessels conveys a bright-red color to the skin, but its surface is not raised. Rarely the walls of the vessels are thickened and tortuous in their course, superficially situated, forming palpitating groups of vessels in the scalp, which suggest in appearance a bunch of creeping earthworms. This form is described by some writers as angioma plexiform, angioma racemosum, or circoid aneurism.

Cavernous angioma.—Cavernous angioma consists of vascular channels which are dilated to the extent of large, communicating spaces lined with endothelial cells. The spaces are supported by interstitial connective tissue. These spaces are venous channels and suggest the structure of the corpus cavernosum. When situated in the skin they appear as dark red to almost bluish, extensive blotches that are commonly known as "port-wine stains," vascular nevi, or blue warts. Cavernous angiomas, like the angioma simplex or telangiectaticum, occur in the skin and also in internal organs, of which the liver is the most frequent seat in man. It is also very common in the liver of cattle and hogs, but may also be found in other domestic animals. Less frequently angioma is found in the kidney, spleen, intestine, bladder, muscles, bone marrow, brain, dura mater, and very rarely in the spinal cord.

LYMPHANGIOMA

Lymphangiomas are neoplasms consisting of dilated lymph vessels or lymph spaces. They are either acquired or more often congenital in man. In domestic animals they are unimportant and rarely found. Several cases of lymphangioma have been reported in the pleura, pericardium, and heart in horses and as superficial skin changes about the nipples in cats. It is often difficult to separate dilations of lymphatic channels due to obstruction from hyperplastic processes. The dilated lymph vessels usually preserve the original channels, as in lymphangioma simplex, or the number of the lymph vessels may be increased and their spaces enlarged, as in lymphangioma cavernosum; or the lymph spaces may form cystic dilations, as in the cystoid lymphangiomas.

Among the congenital lymphangiomas of man may be mentioned macroglossia, a congenital enlargement of the tongue, macrocheilia, the enlargement of the lips, and nevus lymphaticus of the skin.

Dilated lymph channels are accompanied by stasis of the lymph caused by the presence of a parasite, *Filaria sanguinis*, which produces a hyperplastic process in the skin that is known as elephantiasis or diffuse fibromatosis. This condition is sometimes found in horses and should not be taken for a neoplasm.

LYMPHOMA

Definition.—The name "lymphoma" designates a progressive proliferation of lymphadenoid tissue. The enlargement of lymph glands constitutes a debated subject in pathology. Formerly the name of lymphoma was used indiscriminately for all enlargements of lymphatic tissues independently of their cause.

Seats.—Lymphomas start in any of the lymphoid tissues, which are so widely distributed in the animal economy. They frequently have their genesis in the lymph follicles or nodes found in mucous membranes, and in the compound lymphadenoid structures, as the lymph glands. They are found in the course of lymph vessels, or in the spleen, the red bone marrow, and thymus glands. These lymphoid tissues are regarded as the parent source of leucocytes and lymphocytes, and are therefore affected by disturbances of the circulation and blood disorders. Lymphatic tissue reacts most readily to infective agents in all diseases of a septic and infectious nature. Any irritant that is responsible for an acute or chronic disease produces enlargement of the lymphadenoid tissues.

Conditions resembling lymphoma.—Inflammatory enlargements of the lymphoid tissues are not true neoplasms. It is often very difficult to differentiate between them.

Acute inflammation of the lymph glands which is manifested in the hyperplastic or in the exudative form is common in man and very common in domestic animals. The chronic form is as common in man as in the lower animals. The lesions may occur in a single node, but are more frequently found in several nodes of the same group, or in groups situated in different parts of the body. Tuberculous lymphadenitis is the most frequent of these lymph-gland enlargements in domestic animals, especially in cattle and hogs. The lymph glands are enlarged, often contain hemorrhagic areas, may

show caseation and calcification in the later stages, and upon microscopic examination show the presence of tubercle bacilli. In cattle there may be a tendency to excessive hyperplasia of the lymphoid structures without the presence of recognizable tubercle bacilli. The name of paratuberculous lymphadenitis has been applied to this condition by some observers.

Enlargements of lymph glands in hog cholera should not be overlooked, but the lesions in the skin, kidneys, and digestive tract make possible a differentiation of these gland enlargements from tuberculous lymphadenitis.

Simple or typical lymphoma, described by some writers as hyperplasia of the lymph nodes, constitutes another form of lymph-gland enlargement, the etiology of which is still in doubt. The thymus gland in calves, hogs, and dogs may be greatly enlarged and become confluent. Either a single gland or a group may be affected, and the enlarged gland may remain for a considerable time without any change. The capsule of the gland becomes thickened. On microscopic examination the general anatomical division of a normal lymphoid node is preserved. The germinal centers are often increased in size and show hyperplasia. The lymphocytes, although morphologically normal, are less densely arranged between the stouter connective-tissue trabeculæ.

LEUKEMIC LYMPHOMA

Leukemic lymphomas may be acute or chronic in character. The acute forms occur at a younger age, whereas the chronic form is invariably found later in life. Microscopically, real lymphatoid overgrowth is shown by the overdevelopment of lymphocytes, reticulum, and sinuses. An excess of lymphocytes appears in the circulating blood. This latter condition facilitates the diagnosis of leukemic lymphoma from the other forms of lymphoma.

PSEUDOLEUKEMIC LYMPHOMA

Pseudoleukemic lymphoma or pseudoleukemia in animals, or Hodgkin's disease in man, is another type of lymphatic hyperplasia, with diffuse widespread enlargement of the lymph nodes but without the increase of leucocytes in the circulating blood. Large numbers of lymph nodes may be affected in various regions. The spleen is invariably involved, but the bone marrow is not altered, as a rule. Later in the disease the liver undergoes enlargement and the kidney may also become affected. Histologically the enlarged lymph gland shows no infiltration. The hyperplasia is due essentially to the overgrowth of the connective-tissue reticulum, marked prominence of the endothelial cells, and an actual reduction of the lymphocytes and the cells of the germ centers. There may be an abundance of eosinophiles. Increase of connective tissue in the capsule, trabeculæ, and reticulum of the pulp becomes the marked feature, particularly in the spleen.

SARCOMA

Definition.—Sarcomas are richly cellular, malignant neoplasms of connective-tissue origin. The cells are imperfectly differentiated or embryonic in type, with a scanty amount of intercellular substance

between them. Sarcomas occur frequently in man and in all domestic animals.

Appearance.—Sarcomas are variable in size, shape, color, and consistence. They may be circumscribed or nodular, but more frequently they are diffuse and infiltrate the surrounding tissue. When growing near the surface they may finally protrude from the surface as red, granular masses resembling exuberant granulation tissue of healing wounds. This appearance, resembling flesh, led the older observers to name such neoplasms sarcomas, from the Greek word "sarko," fleshlike. The consistence of sarcomas depends partly on the shape of the cells and partly on the presence of the intercellular substance. This is particularly true when fibrous tissue, cartilage, and bone enter into combination with the neoplasm. The compactness or closeness of the cell arrangement and the vascularity influence not only the softness and the density but have a direct bearing on the color found in different types of sarcomas, which will be described later. The dark-brown to black color of certain sarcomas is due to the presence of melanin, which is a pigment derived from cell metabolism. With the exception of the giant-cell sarcomas, which are partly encapsulated, primary sarcomas, as a rule, are not encapsulated. Secondary sarcomas are more circumscribed and frequently show at least an attempt to form a capsule around the secondary nodule.

Seats.—Sarcomas always start from preexisting connective tissue of the body. The skin and the subcutaneous tissue, also the intermuscular tissue, fascias, the sheaths of tendons, the periosteum of bones, the perichondrium of cartilage, and the bone marrow, are among the most common seats for their growth. Less frequently sarcomas are found in the subcutaneous connective tissue of the respiratory system and of the reproductive and urinary organs, also in the serous membranes of the pleural and peritoneal cavities, in the membranes and the nerve tissue proper of the brain and cord or in the supporting tissue, or in the adventitia of the blood vessels of the choroid plexus. In the liver, pancreas, lung, and heart, they may appear, but usually by metastasis.

Structure.—Sarcomas retain the cellular structure and undifferentiated type throughout their growth. The cells of sarcomas vary in shape, being round, spindle shaped, or polymorphous in form. There is usually a scanty amount of intercellular substance. Their nuclei are large, leaving but little cytoplasm around the periphery. In rapidly growing forms the nuclei are hyperchromatic, stain well with nuclear dyes, and appear granulated or vacuolated, but they stain poorly after degenerative changes have set in. With proper fixation karyokinetic figures may be seen in spite of the small size of the cells. In most sarcomas the intercellular substance is scarcely appreciable, but it may become sufficiently pronounced in some varieties to form well-defined bands of the stroma, which separate the cells into groups or columns, forming an alveolar appearance.

Sarcomas have a different blood supply from other neoplasms. The walls of their blood vessels are imperfectly formed and consist of scarcely more than a single layer of endothelial cells, and in some instances of mere clefts in the sarcomatous tissue through which the blood flows. The thin walls in sarcomas favor frequent hemorrhages and the detachment of sarcoma cells into the blood current to form

finally metastatic deposits. Sarcomas have no lymphatics or nerves, according to most authorities. This is the reason that metastases of sarcomas take place by the blood vessels rather than the lymph channels, except in lymphosarcoma.

Combinations.—Sarcomas may combine with many other neoplasms. The combination with fibromas is very common in all domestic animals. All gradations of fibrous tissue, from a mere trace to a decided excess, may take place. The development of fibrous tissue in a sarcoma has a tendency to make the sarcoma less malignant. In naming these combinations, the name of sarcoma is invariably used last, as in fibrosarcoma, chondrosarcoma, osteosarcoma, myxosarcoma, etc.

Degeneration.—Nearly every form of degeneration may affect sarcomas, especially the more rapidly growing varieties. Fatty degeneration, liquefaction, necrosis leading to the formation of cysts, and ulceration are more common than mucoid degeneration, hyaline degeneration, caseation pigmentation, or amyloid degeneration. It is also customary to speak of angiomatous change, cavernous change, telangiectatic change, fibrous change, etc. These terms denote no special change of degeneration, but are used simply to express the combination of the sarcoma with the other tissue by a different name. Sarcomatosis is a condition characterized by the formation of multiple sarcoma deposits in the skin or in the internal organs. Sarcomatosis in fowls is somewhat common.

SPINDLE-CELL SARCOMA

Spindle-cell sarcoma is a very common neoplasm in man and in the domestic animals. The neoplasms vary in size, usually growing slowly as a single mass, but may be multiple when they grow more rapidly. The cells are either small or large, spindle shaped, elongated, tapering toward the ends. The cells of the small spindle-cell sarcoma are from 10 to 20 microns in length, or approximately one and one-fourth to three times as long as the diameter of a red blood corpuscle (human). The cells resemble fibroblasts. Dense connective tissue in the skin, the fascias, perichondrium, and periosteum are some of the places in which spindle-cell sarcomas most frequently grow. These neoplasms may be very cellular, or may have so much fibrous tissue as to simulate a fibrosarcoma. Such neoplasms are frequently called intermediate types.

The cells in the small spindle-cell sarcoma are usually uniform in size, compactly arranged in interlacing bundles or fasciculi, with very little intercellular substance between them. The nuclei are oblong, not so long as the nuclei of involuntary muscle, but longer than those in fibroblasts. In sections the interlacing bundles of spindle cells are cut at various angles to the axis of the cells, giving the impression that spindle-shaped cells, oval cells, and round cells are intermingled. It is important not to consider this appearance as a mixed type of spindle-cell and round-cell variety of sarcoma. The cells take the nuclear stains well unless degenerative changes are present. These neoplasms are grayish white in color, moderately firm, and not very vascular. They grow very slowly, but may become very large. Small spindle-cell sarcomas, as a rule, are less malignant and less prone to give metastasis than other varieties of

sarcoma which are softer and more vascular. The less malignant spindle-cell fibrosarcoma may be encapsulated, and when subcutaneously situated and multiple they are sometimes called "recurrent fibroids."

The large spindle-cell sarcoma differs from the small spindle-cell sarcoma in the size of the cells, which range from 50 to 80 microns, or from four to six times the size of the small spindle-cell variety. The cells are less uniform in size, and often show all gradations in the size of the cells. The nuclei are large, usually oval, sometimes granular, and often vascular. The bundles of cells are less interlacing and are more nearly parallel in disposition. Large spindle-cell sarcomas are not so compact, owing to a large amount of intercellular substance. Large spindle-cell sarcomas occur less frequently than the small spindle-cell variety.

ROUND-CELL SARCOMA

Round-cell sarcomas are found as commonly in domestic animals as in man. They are the most common variety of sarcoma in man, and according to some observers are even more frequent in domestic animals than spindle-cell sarcomas. The cells may be small or large.

Small round-cell sarcomas are the most malignant form of sarcoma. Their malignancy is due to infiltration and destructive properties, as well as the readiness with which they form metastatic deposits in internal organs. Small round-cell sarcomas are soft to the touch, pinkish-red or fleshlike in color, very vascular, and often so hemorrhagic as to justify the name of "telangiectatic" or "bleeding sarcoma." The cells of the small round-cell sarcoma are about the size of lymphocytes, and their nuclei occupy practically the entire cell, leaving very little cytoplasm around the granular, well-staining nuclei. There is very little intercellular substance between the small globular cells, which enables the loosely clumped cells to metastasize more easily than the overlapping and compactly arranged cells of the spindle-cell sarcoma. Small round-cell sarcomas may occur in any part of the body wherever connective tissue exists. They grow rapidly, infiltrate the surrounding tissues, and recur after removal. Because of their rich blood supply and the thinness of the walls of their vessels, they give metastatic deposits to all internal organs, but especially to the lung, liver, spleen, and kidney.

The large, round-cell sarcoma consists of cells that are often larger than the mononuclear leucocytes. The cells are more variable in size and less regular in shape than the cells of the small, round-cell variety. The nuclei are relatively smaller, with a generous quantity of cytoplasm around them, which gives them the appearance of cells of the epithelial type. The cells stain less deeply than in the small, round-cell variety, and appear more loosely arranged, on account of the abundance of the interstitial substance. Large, round-cell sarcoma occurs less frequently than the small, round-cell sarcoma, and is not so malignant. Several cases in the mammary gland, the ovary, and the testicle have been described, but the neoplasm may be found in other locations.

LYMPHOSARCOMA

Lymphosarcoma or malignant lymphoma is a variety of round-cell sarcoma which produces more cell reaction than a simple hyperplasia of a lymphatic structure. The principal characteristic of lymphosarcoma is that it infiltrates and perforates rather than metastasizes. These neoplasms are often found in the mediastinum and may involve any structure of the thoracic cavity. They grow rapidly, following the connective tissue of the mediastinum, and envelop the trachea and bronchi, following the interlobular connective tissue to the root of the lung. They may also extend along the aorta and larger vessels, invade the pericardium, and infiltrate the heart muscle. The infiltration may also extend along the esophagus, or along the course of the vagi or the phrenic nerves, as well as the sheaths of muscles of the diaphragm.

Lymphosarcoma in domestic animals occurs also in the abdominal cavity, producing marked thickening of the intestinal walls and the stomach. It is also frequent in the kidney, spleen, liver, and reproductive organs.

Microscopically lymphosarcoma consists of small, round cells identical in appearance with lymphocytes. The cells are fairly uniform in size and have a large nucleus slightly displaced to one side, leaving very little cytoplasm around the periphery and staining well with nuclear dyes.

Although the infiltrating property of lymphosarcoma follows the course of lymph vessels which is not the course of ordinary sarcoma, the infiltration from one lymph follicle to another follows, forming finally a fused mass, but does not become generalized as in leukemia. Such extensive local invasion by continuity of structure is referred to by some writers as lymphosarcomatosis. Metastasis by the blood vessels is very uncommon, and secondary deposits in other organs are rarely found.

ALVEOLAR SARCOMA

Alveolar sarcoma is not a separate variety of sarcoma so far as the appearance of the cells is concerned. Alveolar sarcomas are usually a subvariety of round-cell sarcoma, but may be also of the spindle-cell type, with the cells varying in size. It is probably more common in domestic animals than in man and is considered very malignant. The chief characteristic of alveolar sarcoma is the arrangement of cells in groups or nests simulating somewhat the lobules of a gland. These groups or islands of cells are separated from one another by bands or septæ of interstitial connective tissue. In rare instances the alveolar effect may be produced by an arrangement of spindle-shaped sarcomatous cells, but in the type most frequently encountered the alveoli are rendered more prominent by the connective-tissue trabeculae separating the groups of cells, and this form is much coarser than the lymphadenoid reticulum found in the lymphosarcoma. The connective-tissue trabeculae support the blood vessels, which may be very abundant. Alveolar sarcoma is highly malignant and grows where any sarcomas are found, but shows marked preference for the skin and serous membranes, notably the pleura and peritoneum. Alveolar large round-cell sarcoma may be mistaken for carcinoma if the character of the cells is not taken into consideration.

GIANT-CELL OR MYELOID SARCOMA

Giant-cell sarcomas are neoplasms characterized by the presence of multinuclear or giant cells, which are identical with myeloplaxes of bone marrow and are intermingled usually with the cells of spindle-cell sarcoma and sometimes with the cells of round-cell sarcoma. Giant-cell sarcoma, unlike other forms of sarcoma, is encapsulated, practically nonmalignant and not known to metastasize or to recur after removal. The giant cells of sarcoma are irregularly jagged in outline, often large, and may be from 10 to 30 times the size of leucocytes. They often have vacuoles and fat drops. The nuclei may be few in number or very numerous, since as many as 100 have been observed in a single giant cell. The nuclei in giant-cell sarcomas are scattered in the interior and all through the cytoplasm of the cell, and not at the periphery, as is the case in the degenerative type of giant cells found in tuberculosis or around foreign bodies. Giant-cell sarcoma has an extensive supply of capillary vessels from which blood extravasations may often take place. These extravasations give the neoplasm a brownish-red color. Giant-cell sarcoma is moderately firm, slow of development, and often even hard to the touch. In those starting from the bone marrow the hemorrhagic condition may be so abundant as to be mistaken for blood clots resembling currant jelly. Besides the ordinary type of giant-cell sarcoma originating from the periosteum of the jaw or the long bones, there is one variety that occurs in the gum and is known clinically as epulis. It is not uncommon in man, but is rarely found in domestic animals.

OSTEOSARCOMA

Osteosarcoma is sarcoma containing osseous tissue. During the early stages of its growth spindle-shaped sarcoma cells are intermingled with a variable quantity of immature bone and often with a few giant cells. Osteosarcoma is rapid in growth and malignant in nature. It is not uncommon in domestic animals especially in the maxillary bones. The neoplasm infiltrates into the epiphyses of long bones and extends also into the shaft of the bone, replacing the bone structure by imperfect osseous material. During the growth absorption of the bone from the periphery takes place. The tissue absorbed is replaced by an osteoplastic process, which must have been the initial condition responsible for the growth of the neoplasm. Different portions of the growth show microscopically various cells, such as sarcomatous spindle cells intermingled with cartilage cells, imperfect bone lamellæ, and atypical bone cells without branching, which indicate rudimentary bone formation.

Some forms of sarcoma of periosteal origin become intensely malignant. This type has a strong tendency toward calcification but not for true ossification. Metastases to serous membranes and the lung are not common. Some writers describe this type by the name of osteoid sarcoma.

MELANOTIC SARCOMA

Melanotic sarcoma is a pigmented, malignant neoplasm. The names "melanoma" and "melanosarcoma" are synonymous. These neoplasms are common in man but even more frequent in domestic

animals, especially in gray and light-haired horses. The most frequent places to find melanotic sarcomas are the skin and the choroid coat of the eye, where pigment normally exists. The skin at the root of the tail and the external genitals in horses are especially common seats, and the neoplasms occur less frequently in the adrenal glands and in the meninges of the brain. As secondary metastatic deposits melanotic sarcomas may be found in every organ, especially in the liver.

The dark color of melanotic sarcoma is due to the presence of melanin, a brown or black pigment elaborated by the connective cells as the result of metabolism. It was formerly supposed that melanin was of hematogenous origin, but chemical analysis has proved the absence of iron in melanin, whereas hematogenous pigments contain iron. Melanin consists of brownish-black granules found in the cells as well as between the cells. There may be present also a certain amount of diffuse melanin. The granules, which are variable in size, may be sparsely or densely distributed not only in different neoplasms but also in different parts of the same neoplasms. Any variety of sarcoma may become pigmented, especially the alveolar sarcomas.

The consistence varies with the shape of the cells and the amount of vascularity. The spindle-cell type is usually harder to the touch and generally less pigmented than the round-cell variety, which is not only softer but may be very vascular and almost black in color.

Melanotic sarcoma originating in the choroid coat of the eye is common in man and is very malignant, but is seldom found in domestic animals, and when found in them the liver is always involved.

COMBINATIONS OF SARCOMAS

The combinations, intermediate or mixed types, of sarcoma comprise all the atypical neoplasms in which sarcoma combines with benign connective tissue or with epithelial growths and converts them into malignant neoplasms. The most common forms of these mixed types are fibrosarcoma, chondrosarcoma, osteosarcoma, osteochondrosarcoma, myxosarcoma, liposarcoma, neurosarcoma, angiosarcoma, lymphangiosarcoma, gliosarcoma, rhabdomyosarcoma, and adenosarcoma. In all these neoplasms the original tissue indicates so plainly the type of the tissue that a variable amount of sarcoma cells does not prevent recognition by microscopic examination. A detailed description of these neoplasms would be only a repetition of the previously described structures.

ENDOTHELIOMA

Definition.—Endotheliomas are neoplasms which are composed of connective-tissue cells that have originated from the endothelial surface or lining of blood vessels or lymph vessels. When the new growth arises from serous membranes, such as dura mater, pia mater, peritoneum, pleura, or tunica vaginalis the name of mesothelioma is used by some writers. When arising from the endothelium of the perivascular lymphatics and the adventitia of blood vessels, it is known as perithelioma.

Nature and structure.—In origin and malignancy endotheliomas resemble sarcomas, but are less malignant and not so metastatic. In

structure and cell grouping they may resemble carcinoma very closely. Endotheliomas are rich in cells which are arranged in clusters or nests that suggest the acini of glands; hence these neoplasms are sometimes spoken of as endothelial cancers. This arrangement bears also close resemblance to alveolar sarcoma. The endothelial cells in the acini are often cylindrical in shape, forming cords or hollow tubes. The cylindrical cords may undergo hyaline degeneration and appear as homogeneous or hyaline masses, when the neoplasms are called cylindroma. Some endotheliomas originating in the dura mater or the pia mater may have a scanty stroma and numerous cell nests, in the interior of some of which globular clusters of lime salts are deposited. These deposits when found in the brain are known as psammoma or brain sand. Endotheliomas originating from the choroid plexus always contain a considerable amount of cholesterol in deposits and are therefore called "cholesteatomas."

Endotheliomas are rather slow-growing neoplasms and are only slightly malignant, hardly ever giving metastasis. They are not common in man or in animals, though several cases of endothelioma and psammoma from the spinal dura mater, the choroid plexus, and the anterior part of the brain have been reported in cattle. Cholesteatoma in the ventricles of the brain in horses has been described by several pathologists. Endotheliomas on serous surfaces are by no means rare in domestic animals.

EPITHELIAL NEOPLASMS

A brief consideration of the normal relation or grouping of epithelium in the adjacent structures aids in a proper understanding of epithelial neoplasms. Epithelium in the animal economy depends on connective tissue for support, as in the skin and in all mucous membranes, or for the grouping, as in the formation of glands (secretory) or in the compound glandular organs (liver, kidney, etc.). In other words, wherever epithelium is present it is intimately related with connective tissue, which participates during the growth of the neoplasms.

PAPILLOMA

Definition.—Papillomas are benign fibroepithelial neoplasms resulting as outgrowths from surfaces covered by epithelium. The neoplasm originating from a surface covered by stratified squamous epithelium is called hard papilloma, whereas the neoplasm starting from a mucous membrane lined by columnar epithelium is known as soft papilloma.

In its simplest form papilloma constitutes the common wart, which is simply a conical or rounded elevation of the derm covered by the epiderm, a thick, stratified layer of epithelium. Warts usually occur singly but may be multiple. Usually they are not painful, but when irritated they may ulcerate and bleed. They have been known to appear suddenly and sometimes disappear spontaneously. When persistent they may become large and may be readily mistaken for malignant growths. The connective-tissue elevation or core may become expanded at the apex and have secondary plications be-

tween which the epithelium sinks in, leaving an uneven surface not unlike the outside of a mulberry. At times the elevation of the core branches out, forming secondary plications, when the neoplasm assumes a grapelike or cauliflower formation. When the elevations are long and narrow the papilloma is known as villous papilloma. The weight of a downward-growing papilloma may stretch the core and form a pedunculated growth.

Seats.—Papillomas occur in the shape of warts, grapelike or cauliflowerlike clumps, or as pedunculated growths, common in man and domestic animals. The skin about the head and neck and also the udders of cows and about the legs of horses are common places. Such superficially located papillomas are readily exposed to traumatism, which renders them susceptible to infections, resulting in ill-smelling discharges. Frequently papillomas are found on mucous surfaces including the lips, mouth, tongue, larynx, esophagus, stomach, intestines, kidney, bladder, and endometrium, and rarest of all on the choroid plexus in the cerebral ventricles.

Structure.—On microscopic examination papillomas vary according to their shape, complexity of structure, and location. In the hard papilloma there is a connective-tissue stalk or core composed of fibrous-tissue bundles which are interlaced and contain a fair number of cells and a moderate amount of blood vessels. Stratified, squamous epithelium covers the stalk. The outermost cells are usually keratoid or horny. Papillomas growing on mucous membranes lined by columnar epithelium are softer on account of the more loosely arranged bundles, which are also fewer in number. The villous soft papillomas are found in the larynx, urinary bladder, and mucous surface of the esophagus, as well as in the kidney, ovary, and uterus. Unlike other benign neoplasms, papillomas are not encapsulated, because of their outward growth from surfaces. Serous degeneration or dropsical conditions are frequently present in the polypoid type of papilloma. Mucous or myxomatous degeneration is not infrequent in this type. Suppuration and ulceration are sometimes present.

ADENOMA

Definition.—Adenomas are usually benign epithelial neoplasms resembling the structure of a tubular or alveolar gland. They are usually single, slow-growing neoplasms, differing in shape in their attempts to reproduce the many types of glands from which they have originated.

Structure.—Adenomas, like their ancestors the glands, consist of epithelium, which corresponds to the parenchyma or functional part of the secreting gland, and the stroma forming the interstitial supporting tissue.

As there are many varieties of glands, such as the sweat and sebaceous glands of the skin, the uterine, mammary, and salivary glands, the liver, renal, and seminal glands, so there may be many kinds of adenoma differing in the shape and size of the acini and in the character of the lining cells, which may be shorter or longer than those from which they originated. In the earlier stages adenomas resemble glandular hypertrophies so closely that it is difficult to distinguish them from each other. With the growth of the neoplasm there is an increase in the complexity of structure resulting

from a process of budding of the preexisting tubules or saccules of the gland. Adenomas have no ducts, and any secretion that may be formed in the neoplasm remains in the acini, distending the alveoli, and forming cystlike dilatations. The neoplasm then is known as cyst adenoma. The retained secretion is of a degenerative character. In simple adenomas the epithelium rests on the basement membrane, as in a normal gland.

Destructive adenoma.—When the cell proliferation is so active that the epithelium has been desquamated, the neoplasm assumes a malignant tendency and is known as destructive adenoma, often found in uterine neoplasms, or as adenocarcinoma, which is frequently present in mammary and rectal neoplasms.

CARCINOMA

Definition.—Carcinoma or cancer is the type of a malignant epithelial neoplasm. The name "cancer" is universally used by the laity to designate a dreadful affliction in man and a hopeless condition in animals. This conclusion is derived from the fact that the number of deaths in man annually amounts to tens of thousands. No other neoplasm has received from scientists more attention, study, painstaking investigation, and special research to ascertain the true cause, the mode of propagation and spreading, and means of eradication and control.

Carcinomalike adenomas are epithelial neoplasms of glandular origin. Although the individual gland compartments in adenoma are tubular or alveolar in structure, with the acini lined by a single layer of cells and a lumen in the center of the acini, the epithelial cells of carcinoma are heaped up in irregular clumps, nests, or cylinders, which are continuous with one another. These clusters of epithelial cells penetrate the surrounding tissues by budding or by an extension of branching processes that have been compared to the roots of a tree or the legs of a crab. From this resemblance the name "cancer" originated.

The epithelial cells in cancers are the most conspicuous structures. The cells are in different stages of development and vary greatly in shape and size. Therefore, the statement sometimes found in print that "a typical cancer cell," found in a certain preparation or present in a certain neoplasm is diagnostic of cancer, is an erroneous and misleading impression. It is not the size, shape, structure, or variety of a cell that determines whether it is a cancer cell, but the relation of the parenchyma to the stroma that determines whether the epithelial cell and fibrous-tissue combination should be called carcinoma, adenoma, or papilloma.

A single cell isolated from a cancer can not be told with certainty from a normal epithelial cell. The epithelium in the cancer is the more conspicuous or basic structure, but the interstitial tissue, which may be either scanty or excessive, is of great importance in the development of cancers. According to Ribbert, (17) "cancers always start from chronically inflamed tissue."

Chronic inflammation of connective tissue brings about cell proliferation. The accumulated connective-tissue cells multiply and separate the epithelial cells by destroying the intercellular cement. The liberated epithelial cells then begin to multiply, acting collectively as

a foreign body, and as such attract leucocytes by their positive chemotactic property. The leucocytes are deposited around this area of multiplying epithelium. The epithelial multiplication continues to the extent of forming buds or roots which penetrate the newly formed hyperplasia constituting the stroma. The penetration takes place in the direction of the least resistance, which is along the course of the lymph vessels, and these therefore become the principal avenue for the extension of the cancer roots as well as the leading channels for the transmission of secondary cancer deposits.

The lymph glands that are interposed in the course of the lymph vessels act as temporary detention places or sieves for the retention of any particles which may be carried in the lymphatic stream. This is the reason that secondary carcinomatous deposits are transmitted by the lymph vessels and are generally multiple and numerous.

Appearance.—Carcinomas differ considerably in various parts of the body and may grow on free surfaces, where they are known as epitheliomas, or in the interior of organs, where when soft they are known as medullary cancers. Epitheliomas that start from the Malpighian layer of the skin and are composed of flat epithelial cells are known as squamous epitheliomas. The epitheliomas starting from mucous membranes lined by cylindrical cells are called cylindrical or columnar epitheliomas. The medullary cancers usually have an abundance of parenchyma and a scanty amount of stroma; when they are soft they are known as encephaloid or soft cancers. A preponderance of the supporting stroma conveys rigidity or hardness to the touch, and the carcinoma is known as scirrhus or hard cancer.

SQUAMOUS EPITHELIOMA

Definition.—Squamous epitheliomas are malignant epithelial carcinomas occurring in the skin and mucous membranes lined with stratified squamous epithelium. Epitheliomas are common in man and are even more frequent in domestic animals. The malignancy of epitheliomas is expressed by proliferation of the epithelial cells, the subsequent infiltration and destruction of the affected tissue leading to inflammation, suppuration, and ulceration.

Appearance.—Squamous epitheliomas differ somewhat in appearance, depending on the location and the structure of the affected part. When in the skin they appear as nodular elevations which are very prone to ulcerate. In the beginning the elevation hardly rises above the surface, but in the later stages epithelioma often assumes a dendritic shape. It then resembles a papilloma, differing, however, from the latter by its growth, which is only outward in the papilloma but both inward and outward in the squamous epithelioma.

Seats.—Squamous epithelioma is often found at the junction of the skin with a mucous membrane. This is the vulnerable point, beyond which the cornification of the skin does not extend into the mucous membrane, as at the conjunctival margin of the external auditory meatus, the external nares, lips, and muzzle. Less frequently it is found in the larynx, tongue, esophagus, cervix uteri, vagina (which is very often affected in women but seldom in animals), the penis in horses and dogs and also around the anus. Squamous epithelioma is rarely found in the bladder, scrotum, and pelvis of the kidney.

Structure.—Microscopic sections of squamous epithelioma show a perverted state of epithelial hyperplasia. In neoplasms from the skin the epithelium of the stratum Malpighii proliferates, forming cylindrical cords which extend inward and penetrate and invade the underlying connective tissue. These branching cords, though extending in different directions, are continuous with one another in sections and may show the epithelium in cylindrical groups or nests. The outer cells of these cords, which are in contact with the stroma, are cuboid or cylindrical, resembling the cells of the stratum germinativum. The cells in the interior of the cords are polyhedral, often larger in size than the cells found normally in the skin and resembling prickly cells. The inner cells, which are the oldest, are flattened, cornified, and homogeneous in appearance. They form concentric or lamellar groups that are known as "pearly bodies," which constitute the definite characteristic of squamous epithelioma in sections.

In man a special form of squamous epithelioma of the face about the eyes and nose has been described by some pathologists under the name of "basocellular cancer." This neoplasm is almost benign and shows no tendency to infiltrate the surrounding tissues. This form of epitheliomas has not been described in domestic animals.

The epithelial cords of squamous epithelium are separated by a variable amount of interstitial connective-tissue stroma. The stroma may be abundant or scanty, and is the tissue which contains the blood vessels and lymphatics. The stroma may consist of loose fibrous tissue or may be composed of tissue rich in cells. When ulceration affects the epithelial portion, the stroma becomes the seat of inflammatory cell infiltration.

CYLINDRICAL EPITHELIOMA

Definition.—Cylindrical epithelioma is a form of carcinoma which originates on surfaces lined by columnar epithelium or from glands of the columnar-cell variety.

Seats.—Cylindrical epitheliomas are found most frequently in the mucous membrane of the gastrointestinal tract and of the uterus, at the pyloric end of the stomach, at the ileocecal valve, and in the rectum, at the junction of the columnar epithelium with the squamous epithelium. The location last mentioned is considered the typical seat for the occurrence of cylindrical epithelioma. Less frequently is this neoplasm found in the mammary gland, the respiratory tract, kidney, and liver.

Nature and structure.—Cylindrical epitheliomas are soft to the touch, grow rapidly, are often papillary, and frequently ulcerate in the interior. They readily undergo degeneration, especially mucoid change, which makes them more malignant. On microscopic examination cylindrical epithelioma is seen to consist of columns resembling tubular glands. A lumen may be present between the rows of cells. When the columnar cells proliferate the tubular structure may consist of several rows of cells, the outer row retaining the columnar shape while the inner cells may be irregular, but the cylindrical epithelioma retains the tubular shape. When the lumen becomes distended the appearance is not unlike that of an adenoma.

The stroma of the cylindrical epithelioma is more loosely arranged and is more cellular than the stroma of squamous epithelioma. The looseness is due to the anatomical differences in the structure of the submucosa in which cylindrical epithelioma develops, from the denser and more compact derm of the skin which gives rise to the stroma of squamous epithelioma. Cylindrical epithelioma metastasizes slowly, and the secondary metastatic nodules in internal organs reproduce the columnar type of the parent structure. In malignancy and metastasis the cylindrical epithelioma resembles more closely the glandular carcinoma than the squamous epithelioma.

GLANDULAR CARCINOMA

Definition.—Glandular or medullary cancers are malignant, metastatic, epithelial neoplasms which resemble racemose glands in arrangement. They are the most malignant and most widely distributed variety of cancers in humans and in domestic animals. Statistics show cancer to be on the increase, not only in man, but also in domestic animals.

Nature and structure.—Medullary cancers, like surface carcinomas, consist of an epithelial parenchyma and a connective-tissue stroma or matrix. The parenchyma of glandular cancers forms continuous branching cylindrical masses of proliferating epithelial cells which extend in various planes. These masses in sections appear as alveolar spaces filled with epithelium obliterating the lumen, proliferating into the surrounding tissue. The cells in cancers differ in shape, size, and structure, depending on the kind of gland from which they originated, the pressure exerted by the stroma, and the amount of nutrition which the cells receive. These structural differences are sufficient reason why a single cell isolated from a cancer does not convey characteristics enough to identify it as a cancer cell. In fact that cell could have come from a papilloma, an adenoma, or a normal racemose gland.

The alveolar walls are composed of connective tissue which supports the blood vessels and lymph vessels to supply the nutrition to the neoplasms. The fibrous-tissue stroma may be scanty or abundant. When the stroma is scanty the parenchyma forms large cancer nests; the neoplasm is soft to the touch and is generally known as encephaloid, medullary, or soft cancer. If the stroma is abundant and the connective tissue densely arranged the cancer is hard to the touch and is known as scirrhus or hard cancer. The cancer nests in the hard cancer are small, indicating that the epithelial cell proliferation is very inactive. Soft cancer develops in well-nourished subjects, whereas hard cancer grows in emaciated subjects.

The rapidity of the growth of cancers appears to be influenced by the state of nutrition which governs the specific "tissue reaction." Soft cancers grow more rapidly, as the tissue reaction is diminished in consequence of a smaller amount of connective-tissue stroma present, when less resistance is offered to the epithelial-cell proliferation. Hard cancer, on the other hand, grows very slowly, as the tissue reaction appears to be increased in the emaciated subject where the

excessive connective-tissue development increases the resistance by retarding at the same time the epithelial-cell proliferation.

Besides the variation in the amount of connective tissue in the stroma of cancers, ranging from a mere scantiness to a conspicuous abundance of fibrous tissue, the stroma may undergo hyaline or myxomatous degeneration and become gelatinous in appearance. The stroma at times is very cellular, when the cancer is known as sarcomatous carcinoma, which is not a good term.

Appearance.—For a time a cancer is limited to the gland from which it has originated and is known as primary cancer. Cancers do not remain long in an inactive state. They are not encapsulated and the epithelial cells proliferate and penetrate into the surrounding tissues in the direction of least resistance, which is the course of the lymph vessels. It is not possible, on macroscopic inspection, to define the limits of the cancer from the surrounding tissues. Microscopic examination alone can determine the exact limits of the cancer invasion. When the cancer has existed for some time the nodular condition becomes more apparent. On section a whitish milklike seroalbuminous fluid exudes, which is generally called cancer juice. The ill-defined limits of cancer invasion necessitate total extirpation of the neoplasm and a generous amount of the adjacent and apparently unaffected tissue to avoid recurrence of the growth.

Secondary metastatic deposits in internal organs and tissues are sharply circumscribed nodes which stand out in great contrast from the affected part. The nodes are generally multiple, have a tendency to reach to the periphery, and often become umbilicated in the center. This is particularly the case with cancer nodes in the liver, spleen, and lungs. In the kidneys the nodules may be so numerous and so extensive as to convert the entire organ into a shapeless mass which has been known to weigh as much as 15 kilograms.

Clinical observations have shown that metastases may be extensive or limited. The extensive metastatic invasions are found in cases of soft cancer, which always grows rapidly, but in cases of hard cancer the metastasizing property is limited in extent and slow to start. The lymph vessels are the principal channels for the transmission of secondary metastatic deposits in cancer, while in sarcoma metastasis takes place essentially by the blood vessels. As in sarcoma (lymph sarcoma), metastasis may take place by a different route, the lymph vessels, so in carcinoma, when the neoplasm occurs in the stomach or the intestine the cell proliferation may be so close to a blood vessel as to admit some of the epithelial cells into the blood current to be carried to other tissues.

Seats.—The common seats for medullary cancers are the pyloric ends of the stomach, the mammary gland, uterus, intestine, liver, pancreas, kidneys, lung, ovaries, and testicles. As secondary metastatic deposits carcinoma may be found in lymph glands, and when the emboli gain entrance into the circulation the cancer may develop in any tissue where the emboli become lodged.

Though the usual way of cancer transmission is by the lymph vessels, less frequently by the blood vessels, it may very rarely be transferred by an eruption on a peritoneal surface. These infections result from peritoneal rupture and separation of detached cells in cancers of the uterus and of the gall bladder. The lesion results

either in miliary carcinomatosis of the peritoneal cavity or a generalized deposit of cancer nodules, which are more of the nature of plastic masses and frequently become confluent.

Age as a diagnostic factor.—In human cases the age of the subject has considerable diagnostic value, as it has been found that cancer usually occurs after middle age, and that malignant neoplasms in the young are almost invariably sarcoma. These facts are of great interest, as they have some bearing on the frequency of cancers in domestic animals. Statistics show that medullary cancers are fairly frequent in the glands of aged dogs and mares, whereas in bovines, most of which are usually killed at an early age, medullary cancer is rare, while sarcomas are more common. Carcinomas are probably as frequently found in aged cattle and sheep as in horses.

COMBINATIONS OF CARCINOMA

Combinations.—Carcinoma frequently combines with adenoma to form adenocarcinoma. This is the most common combination. Opinions differ as to whether these neoplasms were originally adenomas which in the course of growth had proliferation and in which detachment of the lining cells led to the accumulation of these cells in the interior of the acini, resulting in the formation of cancer nests, or whether they started as glandular cancer, with a limited number of rows of cells, and as a result of degeneration and accumulation of serous fluid the rows of cells separated, resulting in a structure resembling disorganized acini of glands.

Vascular changes in carcinomas are frequent, when the neoplasms are known as angiocarcinomas or telangiectatic carcinomas.

Degeneration.—Colloid cancer is often described as a special form of cancer. It is more appropriate to call this alteration a gelatinous change, as in most cases the entire structure, stroma as well as parenchyma, is changed into a substance resembling jelly, which is in reality a retrogressive mucous degeneration. Very rarely a true colloid degeneration affects the epithelial parenchyma; when such change does occur it is usually in neoplasms of the thyroid gland. Cancers of the stomach, mammary gland, and intestines are affected more often by mucous degeneration than by colloid.

Suppuration is very common in all forms of cancer, especially when they are exposed to infections of pathogenic microorganisms inducing a septic condition in the body. The products of septic microorganisms are toxins which are absorbed into the blood stream, producing a general disturbance known as cancerous cachexia.

Infection.—Clinical observations show that cancers of the mammary glands are invariably sterile unless surface ulceration has set in, which sometimes occurs in advanced stages. Some of the cancers, as those of the lip, tongue, esophagus, and especially those of the uterus, intestine, and rectum, harbor excessive numbers of microorganisms. Such cancers are usually called infectious cancers. It is therefore important to bear in mind that long-protracted, chronic cases of cancer may terminate in death by terminal infection, which may result in uremia, pneumonia, meningitis, or peritonitis, and is due to the toxins formed by the multiplication of microorganisms that infect the cancer. Infectious cancers often resemble chronic

inflammation of the lymph vessels and glands so closely that it requires a microscopic examination to tell them apart.

DISTINCTION BETWEEN CARCINOMA AND SARCOMA

According to the histogenetic classification of neoplasms, a sharp line of distinction exists between sarcomas, which are mesoblastic or of connective-tissue origin, and carcinomas, which are of epiblastic or epithelial origin. As a matter of fact, however, certain neoplasms which are classed as sarcomas (alveolar) show a histological structure which resembles carcinoma so closely that in a single slide and without the history it is difficult to distinguish one from the other.

Transplantation experiments of carcinoma in mice have shown that carcinomas become changed into sarcomas after 12 or 14 successive generations of transplantation.

Some of the textbooks on pathology have tables of the diagnostic features of sarcoma and carcinoma. The following points may be helpful in distinguishing between sarcoma and carcinoma:

SARCOMA	CARCINOMA
1. <i>Origin</i> .—Mesoblast (connective tissue).	Epiblast or hypoblast and mesoblast (both epithelium and connective tissue).
2. <i>Cells</i> .—Embryonal connective-tissue cells.	Epithelial cells contained in alveoli, varying in shape and size.
3. <i>Intercellular substance</i> .—May be present.	Absent, or merely fluid.
4. <i>Stroma</i> .—Intercellular stroma rarely forms alveoli.	Connective tissue forms communicating alveoli in the course of lymphatics.
5. <i>Blood supply</i> .—Vessels are embryonic, often mere channels in contact with the cells. No muscle in the walls.	Vessels well developed, contained within and supported by the walls of the alveoli. Seldom in contact with the cells. Have distinct muscle walls.
6. <i>Metastasis</i> .—Ordinarily by blood vessels, exceptionally by lymph vessels.	Usually by lymph vessels, but in later stages also by blood vessels.
7. <i>Malignancy</i> .—Marked.	Very marked.
8. <i>Usual seats</i> .—Primary sarcoma is generally found in connective tissues, as corium, fasciæ, periosteum, brain, ovary, rarely in liver, lung, and uterus. Occurs primarily in lymph glands but not by metastasis.	Primary cancers occur on epithelial surfaces and in glands, especially on the lips, in mammary gland, stomach, intestines, uterus, vagina, and penis. Can be carried to any tissue by metastasis. Does not occur primarily in lymph glands but is usually present secondarily.
9. <i>Sensitiveness</i> .—Usually not painful.	Always painful.
10. <i>Age</i> .—Occurs usually in the young.	Generally occurs in middle life or later.
11. <i>Growth</i> .—Often interrupted.	Continuous, often rapid.
12. <i>Shape</i> .—Often rounded, flesh-like masses.	Nodular, tubular, dendritic, often ulcerating on surface.
13. <i>Hereditiy</i> .—Rarely hereditary.	Often hereditary.
14. <i>Secondary changes</i> .—Myxomatous degeneration common. Calcification and pigmentation very common. Ossification and condroid not so common. No fat within the neoplasm.	Fatty degeneration very common, almost from the start. Mucocolloid frequent. Pigmentation rare. Cystic change rare. Fat may be present within the cancer tissue.

TERATOID NEOPLASMS (TERATOMA)

Teratomas comprise a group of neoplasms containing heterogeneous tissue elements of one or several mature tissues or organs, and seem to be derived from all three layers of the embryo. They are always of congenital origin and are usually cystic in nature. Dermal structures are the prominent feature comprising skin, muscle, cartilage, bone, teeth, hair, also nerve tissue, and even certain of the viscera. The dermal tissues invariably predominate; hence the name dermoid is generally used, and as the process is always accompanied by cystic change, the name dermoid cyst is used. When the cystic change is lacking and reproduction of the viscera and other peripheral structures resemble fetal parts the growth is termed congenital malformation or monstrosity. Some pathologists include in this group the so-called mixed neoplasms of congenital origin which have been previously mentioned as combinations of neoplasms.

Dermoid cysts occur in man and are not uncommon in domestic animals.

DERMOID CYST

Small dermoid cysts occur frequently in dogs, horses, and cattle, in the order named. Not infrequently they are found in sheep and hogs. It is interesting to note that the hair fibers in the dermoid cysts in sheep resemble wool, whereas the fibers in the dermoid cysts of hogs resemble bristles, and the dermoids in birds frequently contain feathers. In humans (children) small dermal nodes occurring on the face are described by the name mandibular tubercles. In many mammals, especially dogs, similar mandibular tubercles or cutaneous nodes have been recorded.

The most common place for dermoid cysts is the ovary. Some writers describe them by the name cystic embryomas. Less frequently are dermoid cysts found in the testicle. They are also found in the thoracic cavity, in the abdominal cavity, starting behind the peritoneum, involving the kidney, in the mesentery, and in the omentum. Dermoid cysts are occasionally found in the mammary gland, in the parotid gland, about the eyeball, on the head at the junction of the cranial bones, on the face, and on the neck.

Dermoid cysts in the ovary, like those occurring elsewhere, are lined with epithelium. They generally contain hair, teeth, or other dermal tissues, and are filled with fluid, which may be clear or cloudy. The cyst contents may also be gelatinous, mucous, fatty, or sebaceous in nature. Microscopic sections show the structure of skin, hair follicles with hair, sebaceous and sweat glands, developing and adult teeth, pharyngeal mucous membrane, intestine, and thyroid gland. Wilms reports finding traces of nerve tissue in ovarian cysts.

Most dermoid cysts are benign and grow slowly, but some of them are malignant and grow as rapidly as any malignant neoplasm, give metastasis, and recur after removal.

Some cysts in the ovary are not congenital, and are described as simple cysts or cystadenomas. They are covered by a connective-tissue capsule and are lined by columnar epithelium. Such cysts are variable in size, may become very large, and contain a thin, watery

fluid, or the fluid may be thick and viscid. Neither the walls nor the interior contain any dermal structure.

CYSTS

Cysts (not dermoid) are circumscribed, encapsulated, or walled-in cavities containing an abnormal accumulation of fluid or semi-fluid substance and not provided with an outlet. The term is often very loosely used by some writers. Cysts are generally classed with neoplasms, but this is more for convenience and not by reason of structural or etiological similarity, as cysts stand midway between neoplasms and dermoid cysts. Cysts are described as simple or unilocular when the cyst wall is passive, serving only to retain the contents. When several cysts occur together and are identical in structure, arising from the same cause, they are called multiple cysts, or when the cysts spring from the inside wall of a cyst they are spoken of as multilocular cysts.

According to the method of formation, cysts may be classified as retention cysts, exudation cysts, extravasation cysts, softening cysts, and parasitic cysts.

Retention cysts arise from the accumulation of secretion when the duct of a gland has been occluded, preventing the escape of the secretion. The most common cysts are the sebaceous cysts of the skin, called wens, the mucous salivary gland cysts of the tongue, called ranula, the pancreatic cysts, the galactoceles (milk cysts) in the mammary glands, etc. The cyst contents are derived from the functional activity of the glands and are eventually altered by absorption of some of the fluid and by the subsequent degenerative changes that affect the fluid as well as the lining and the walls of the cyst. These degenerative changes may bring about an irritation that gives rise to inflammation.

Exudation or distention cysts resemble so closely the retention cysts that many writers make no distinction between them. They are cysts which occur in closed cavities not supplied by an excretory duct, as in hydrocele that may be found in the tunica vaginalis testis, or cysts in the ovaries. The distention of enlarged bursæ occurring in the elbow and the hock in horses as pouchlike dilations and the cysts found in the course of tendons are retention cysts and are known as windgalls. The dilated spaces forming cysts in the thyroid gland and the pituitary gland may be classed with the retention or with the exudation cysts.

Extravasation or hemorrhagic cysts are the result of blood escaped from a vessel into a tissue or an organ. They are known as hematocoele or sanguineous cysts. They become eventually surrounded by a capsule, which varies in thickness in different organs. Such cysts are common in domestic animals and are generally the result of traumatism, or they may result from rupture due to disease in the walls of a blood vessel.

Softening cysts are pathological cavities which result from disintegration of solid tissues by retrograde changes and liquefaction necrosis. Such cysts may be found in rapidly growing neoplasms, especially in sarcomas and carcinomas in which myxomatous degeneration has taken place. Colloid and mucoid degeneration finally terminates in the formation of softening cysts. Some writers also

class the hemorrhagic cysts, especially those occurring in the brain, among the softening cysts. It must be remembered that some hemorrhagic cysts may undergo regeneration instead of softening.

SYNCYTIOMA

Syncytioma (chorion carcinoma, chorioepithelioma, deciduoma, placentoma) is a malignant neoplasm, soft, friable, and spongy in structure, dark in color, generally containing blood clots. The neoplasm resembles placental tissue in appearance and structure. It originates during or after pregnancy and sometimes follows abortion. Recent observations have shown that it may be the result of teratomatous or embryomatous growth, as it has been found as testicular teratoma or embryoma, also as a mediastinal and cranial teratoma. The neoplasm is most malignant and generally gives metastasis to the external genitalia and less frequently to the liver, kidney, spleen, or other organs.

Syncytioma has not been described in domestic animals.

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UNITED STATES DEPARTMENT OF AGRICULTURE



DEPARTMENT BULLETIN No. 1453



Washington, D. C.



January, 1927

THE CHEESE SKIPPER AS A PEST IN CURED MEATS

By

PEREZ SIMMONS, Associate Entomologist, Stored-Product Insect Investigations
Bureau of Entomology

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INTRODUCTION

These cheese skipper, *Piophilæ casei* (L.), has been mentioned in literature as a domestic pest since the middle of the sixteenth century and is one of the longest-known economic insects. A reference to this species can be recognized in the writings of Olaus Magnus (46, p. 812),² in 1567—a “kind of grub which infests cheese, leaping in the shape of a bow in fat cheese, and which no cold destroys” (“Vermis deniq; alius caseorum, salinis instar arcus in pinguibus caseis, qui nullo frigore interimitur”). It is thus very certain that it was established in Europe before commerce with the Western Hemisphere had become extensive, and it seems improbable that the insect was introduced into Europe from the New World. Other pre-Linnean writers who were familiar with the cheese skipper include Redi (58), Goedaert (27), Frisch (25), and Merian (50). Redi's account is of especial interest because he used experiments with this fly to strengthen the evidence opposing the theory of spontaneous generation.

For a half century after Linné (41 p. 597) described it, in 1758, the cheese skipper was referred to in literature as a pest of cheese

¹ This bulletin represents a portion of the results of an investigation of the insect enemies of cured meats. The writer gratefully acknowledges the assistance of George W. Ellington, junior entomologist, who aided materially in obtaining much of the information in this report.

² Reference is made by number in italics to “Literature cited,” p. 51.

but of no other stored food product. The fondness of the larvæ for ham was originally noted in the English edition of *Systema Nature* (43, p. 610) in 1806, and the first detailed account of injury to cured meats was given in France by Dufour (19) in 1844. In 1918 (67) it received considerable official attention in Europe, this time as a pest of brine-cured fish in Astrachan, on the Caspian Sea, where very serious damage was done for several years through various causes incident to the war.

The record of the cheese skipper in the United States curiously parallels its European history, but the first mention of injury to hams appeared many years later. In 1841 Harris (30, p. 417), who seems to have been the first outside of Europe to write of the insect, made no mention of infestation of cured meats. In 1870 Riley (59) gave cheese as the sole material in which oviposition took place; but in 1874 (61, p. 100) he reported that hams had been injured at St. Louis, in 1871, by "certain blowflies" which, he stated later (62), included flies which were identical with the adults of the cheese skipper. In 1880 (62) Riley reported further injury to meat products, one firm at Peoria, Ill., having lost over \$2,000 worth of smoked hams from this pest. Serious injury at Kansas City in 1891 was reported by Kellogg (37, pp. 114-115); in a week as much as \$1,500 worth of spoiled hams and bacon were returned by consignees.

In 1870 Willard (80) reported that "Immense losses are sustained every year on account of skipper cheese. Sometimes thousands of pounds * * * are tainted in this way * * *." According to Murtfeldt (53, p. 171), however, the situation had changed by the year 1893, when she asserted that the insect had within recent years become a far more serious pest of meats than of cheese, causing thousands of dollars' annual property loss and in addition "other thousands in labor and mechanical contrivances to keep it in check."

At the present time there are no indications that the American cheese industry suffers severe losses from the skipper, although this insect is still the principal cheese pest. Extensive losses occur, however, both to the meat trade and to farmers who cure small quantities of meat for home use. According to Howard (35, p. 5), Federal meat inspectors annually condemn over \$1,000,000 worth of meat of all kinds on account of injury by insects, of which the skipper "is probably the most serious."

Piophilila casei is without question the principal insect species attacking cured meats in the United States, and the value of meat actually destroyed in commerce, on farms, and at small abattoirs where there is no official inspection, plus the prorated cost of such preventive measures as screening and wrapping, added to injury to commercial reputations and loss of good will, undoubtedly make a total of large proportions.

SYSTEMATIC POSITION AND SYNONYMY

Piophilila casei (Linné), type species of the genus *Piophilila* of Fallén and dominant economic member of the acalyptrate muscoid family Piophililidae, was described in 1758 (41, p. 597) as *Musca putris casei*.

In 1775 Fabricius (21, p. 780) referred the species to the genus *Musca*, later, in 1805 (22, p. 323), assigning it to the genus *Tephritis*, in both instances under the specific name *putris*. The genus *Piophilila* was erected on this species by Fallén in 1820 (23), but in 1822 Kirby and Spence (39, p. 229) referred it to the genus *Tyrophaga*; Curtis (16, p. 126) used the same nomenclature four years later. In 1855 Schiner (68) reviewed the synonymy of the species and concluded that *Piophilila casei* Fallén (23, p. 9), *P. atrata* Meigen (48, p. 396), and *P. petasionis* Dufour (19) were one and the same. Rondani (65, p. 249), in 1874, stated that the *casei* of Linné (41), Fallén (23, p. 9), Meigen (48, p. 395), Macquart (45, p. 541), Zetterstedt (83, p. 2510; 82, p. 772), etc., was the same insect as the *atrata* of Fabricius (22), Meigen (48, p. 396), Macquart (45, p. 542), and Zetterstedt (83, p. 2511; 82, p. 772); the *vulgaris* (in part) of Fallén (23, p. 9); the *petasionis* of Dufour (19), and the *putris* (in part) of Linné (41) and Scopoli (69, p. 337). The species *affinis*, treated by Zetterstedt (83), and *melanocera*, referred to by Rondani (65), are questionably synonymous in the opinion of Melander and Spuler (49, pp. 69-70), recent reviewers of the sepsid and piophilid flies. These writers listed and described 17 species of *Piophilila* from North America, and erected the family Piophililidae.

The generic name has been misspelled in literature as follows: By Riley (60) in 1870 as *Peophila*, by Mégnin (47, p. 47) as *Pyophila*; and again by Riley (63, p. 226) as *Piophilus*. Much of the confusion in the nomenclature seems to have been due to the variation in size of larvæ and adults, to the variety of food materials, and to certain color variations.

COMMON NAMES

The earliest writers used the term "cheese worm," "cheese maggot," or "cheese mite," the context, in the case of the last, leaving no doubt as to the pest designated. Swammerdam, in his extensive treatise on this insect (73, pp. 63-75), used the title "Acarus or mite," at the same time explaining that the true mite of cheese is an entirely different pest. Unless accompanied by some descriptive matter, early references to "mites" of cheese in nonscientific literature may refer either to the cheese skipper or to the acarids which infest cheese.

The following list includes the common names which appear in the literature of *P. casei*, the first being that recommended for exclusive use by the American Association of Economic Entomologists (6, p. 524):

cheese skipper	ham skipper
cheese-skipper	ham fly
cheese mite	ham worm
cheese-fly	meat skipper
cheese-maggot	skipper-fly
cheese skipper fly	skipper
cheese and meat skipper	jumper
cheese-maggot fly	hopper
cheese and bacon hopper	hopper maggot
cheese worm	mite-fly
cheese feeding fly	bacon and cheese hopper-fly
cheese and bacon fly	

DISTRIBUTION

In common with many other domestic species, the cheese skipper has become widely distributed through commerce. There are records of its occurrence in nearly all countries of continental Europe, in England, India, the West Indies, Greenland, Alaska, and many localities in this country. In its capacity as a scavenger it is capable of perpetuating itself in carrion, and this is an excellent reason for believing that it has become established in many other parts of the world.

The records of cheese-skipper damage in the files of the Federal Bureau of Entomology include the District of Columbia and localities in the following States: Alabama, California, Illinois, Maryland, Massachusetts, New York, North Carolina, Pennsylvania, Tennessee, and Virginia. Melander and Spuler have specimens from Idaho, Kansas, Louisiana, South Dakota, Texas, and Washington.

MATERIALS INFESTED

It was generally believed that the older, softer, and richer cheeses were most subject to attack, the accuracy of which opinion is evident from laboratory experiments in which the infestation of old dry cheese was observed to be a slow process. In the time of Redi (1688) (58) the epicures boasted that they knew how to grow worms in cheese to please the palate. Swammerdam (73, p. 63) stated that the worms were "generally held in detestation, though some eat them voluptuously with the rest of the cheese, from a vulgar notion, that they are formed out of the best parts of it * * *," Linné (42, p. 456) gave the habitat of this species as cheese; Scopoli (69) defined its food as soft, buttery, moist cheese; whereas Fabricius (21, p. 780) listed "dung-hills, cheese and other fats."

The first mention of attacks on ham and bacon appeared, as already noted, in 1806. Bouché (13, p. 99) stated that the larvæ are found in human excrement, in the summer and fall; rotten fungus was given as a host food by Zetterstedt (83, p. 2510). John Curtis (16, p. 126) received larvæ from powdered rhubarb, and Germar (26) was given a sample of cooking salt infested with the larvæ, both occurrences probably being explainable by larval migration to these substances for pupation.

The occurrence of cheese-skipper larvæ in human cadavers was first recorded by Rondani (65, p. 249) in 1874. Large numbers of the larvæ were found infesting an exposed human cadaver at Paris in December, 1888, the account of which forms a part of Mégnin's treatise (47, p. 170) on the significance of the insect fauna of corpses in determining the date of death. The point in the entomological sequence in such cases chosen by Piophilæ, he stated, is that at which decomposition has reached the stage where fatty acids and caseous products are present, or from the third to the sixth month.

The findings of Mégnin were criticized and compared with their own observations by Johnston and Villeneuve (36). These investigators reported the examination of exposed cadavers in Canada, one in May and one in August, infested with the cheese skipper, which, they concluded, appears only after the saponification of the fat is well marked.

The only considerable work on the occurrence of this pest in human graves was done by Motter (52), at Washington, D. C., and reported in 1898. Doctor Motter found remains of this insect in at least 10 of the 150 graves examined, these 10 graves being from 3 to 10 years old and from 3 to 6 feet deep. These data not only invite speculation as to the avenue of invasion of graves by the species, but oppose the theory advanced by some writers that darkness is a condition repellent to the insect.

Murtfeldt (53, p. 174) was unable to obtain oviposition on fresh meat of any kind and she found that *P. casei* did not seem to be able to develop on salted but unsmoked meat. She reported that smoked beef is also attacked but not so severely as smoked pork. In the discussion following the reading of her article before the American Association of Economic Entomologists it was brought out that in England and continental Europe the custom exists "of placing cheese under the tap of a beer keg so that the drip would encourage the development of the insect."

Ormerod (54, p. 9) included salted beef in the list of food media of the cheese skipper, and stated that there is no doubt about the failure of the insect to oviposit in fresh meat.

According to the investigations of Howard (33 p. 589) the adult is attracted to human excreta.

Krausse (40) reported that sheep-milk cheese, an extremely salty product, swarmed with the maggots during the summer on the island of Sardinia.

A single record, not duplicated since, of infested oleomargarine was noted by Banks (10, p. 35).

Mote (51, pp. 314-315) found that both lean and fat beefsteak having a slightly putrid odor was apparently the most attractive food material to adults, exceeding in this respect lean and fat ham, lean and fat bacon, and Schweitzer cheese. He observed that "the adult flies lived longer, and the larvæ fed and matured more readily, on the beefsteak than on the other substances."

In his popular account of the cheese skipper, published in Italy, Berlese (11, pp. 118-121) made no mention of other food media than cheese.

Among the packing houses of the Middle West, Bishopp (12, p. 271) found skippers plentiful, especially among inedible materials in storage. Hoofs, horns, and particularly dried bones produced the insect in large numbers. Further observations under the same conditions were recorded by Laake in Pierce's work on Sanitary Entomology (57, p. 455). This investigator found skippers, often accompanied by hide beetles, swarming by millions in bone-storage houses. Improperly dried stocks of bones and hog hair are often infested with skippers and the larvæ of blowflies.

Bachmann (9) could not get the larvæ to thrive in fat ham or in bacon. After feeding on cheese, and in one case after feeding first on ham and then on cheese, larvæ were given common salt for a time, after which, he reported, pupation occurred. He also recorded having seen the larvæ living in water glass (sodium silicate).

The most extensive and graphic account of damage by the cheese skipper is that of Sakharov (67), a translation of whose interesting publication on the insect pests of cured fish in Astrachan has been

obtained. Although dealing with conditions not found in the United States, the following paragraph, an abstract of pertinent parts of his report, is of interest because it emphasizes the power of increase and destruction inherent in the cheese skipper in the presence of an unlimited food supply resulting from careless sanitation:

Very large quantities of fish are smoked at the Astruchan fisheries, but on account of the ability of the cheese skipper to infest this product the smoking is discontinued in summer. Fish packed in barrels and covered with brine has been very severely attacked by the insect, which is the chief pest and the only dipterous enemy of fish preserved in this way. Because of the use, during the Great War, of imperfectly seasoned lumber to make the barrels, cracks appeared in the latter as they dried, allowing the brine to leak out. The eggs of *P. casei* were laid in the moist cracks thus formed and the young larvae entered the barrels, often reducing the contents to a formless mass of flesh and skeletons. On account of the war, also, the ice supply in the storage houses was below normal and this condition promoted increase of the pest. At one plant the puparia among and under the barrels of fish could be gathered by the shovelful; in another ice house the floor was so covered with puparia that it resembled the floor of a grain elevator.

Sakharov also stated that the insect attacks green sealskins.

A list of the food materials of the larvæ and adults which are reported in the literature of *Piophilæ casei* includes cheese, bacon, ham, human excrement, rotten fungus, human corpses (both buried and exposed), oleomargarine, smoked beef (also known as dried beef or beef hams), putrid beefsteak, salted beef, hoofs, horns, dried bones, moist hog hair, smoked fish, fish in brine, and green sealskins. Verbal reports to the writer state that infestations have been known to occur in marrow bones and in lard. Common salt and water glass are recorded as larval foods, but these records are open to question. It should be noted, also, that flies of other species of *Piophilæ* (immature forms unknown), closely resembling *P. casei*, occur out of doors; consequently some recorded observations may have been incorrectly assumed to relate to the cheese skipper. Furthermore, larvæ of certain flies of the families Ortalidæ and Drosophilidæ and of the genus *Lonchæa* also possess the ability to skip, according to C. T. Greene, of the Bureau of Entomology.

The writer has not succeeded in rearing skippers in the circum-muscular fat of ham, and in general it appears that the generic name *Piophilæ* (derived from the Greek *πικρον*, fat, and *φιλος*, loving) is not strictly appropriate. The fat parts of cured ham are not nearly so attractive for oviposition or feeding purposes as are the lean portions and the connective tissue—points which will receive further attention in this discussion. Both smoked herring and salted herring supported the life cycle in the laboratory. Semi-liquid putrid beef, Bologna sausage, several varieties of cheese, the marrow of ham bones, and lean ham have proved suitable media. An attempt to rear the insect on decomposing mushrooms was unsuccessful, no progress was made by larvæ in lard substitute, and a number of trials with ham fat showed that it was entirely unfavorable as a food, although this may have been due partly to suffocation of the larvæ by the melted fat.

A flask containing several thousand puparia, many of them in a fermenting condition because of metabolic moisture confined in the stoppered container, was observed to be infested with the mag-

gots of the skipper, some adults having been able to emerge and produce eggs. A number of the larvæ were able to pupate under these adverse conditions. The attribute of resistance of the cheese skipper to unfavorable conditions is referred to on succeeding pages. Infestations in bacon, salt pork (unsmoked), and dried cooked bones have been observed by the writer.

By far the greatest damage to edible products in this country is done to hams and shoulders which have been cured and smoked. In the writer's experience the fresher these are the more rapid the progress of the infestation. Old pieces of meat which have become hard and dry, sometimes covered by a coating of blue mold and by a salvelike layer of fat, seem to be relatively immune from attack.

THE CHEESE SKIPPER AND DISEASE

Were it not for the fact that stored food products such as ham and bacon are usually cooked before being eaten, the possibilities for the adult fly to bring infection to human beings through the medium of polluted food might be considerable. The sources from which the flies may come include some which are extremely filthy. Aside from differences in size and abundance, adults of *P. casei* might be viewed with much the same concern as are now those of the house fly (*Musca domestica* L.). Visits of the adults to cheese, which is usually eaten uncooked, might result in the spread of enteric diseases and other maladies. Although no experimental evidence is at hand to indict this species, its haunts and habits do not absolve it from suspicion as a possible vector of disease.

The custom of consuming infested cheese has sometimes caused much discomfort to those who have indulged themselves in it. Thébault (76) concluded that larvæ can pass through the intestines of man without dying, and that serious intestinal lesions are caused by them. Similar conclusions have been reached by Alessandrini (4, 5), and this investigator found that the same is true of dogs, in which intestinal lesions are always caused when they are fed with the maggots. Austen (8, pp. 13-14), Banks (10, p. 35), Pavloski (56), and Colombe and Foulkes (14) also reported cases of intestinal myiasis. This is the insect most often found in the intestines of man, according to the publication of the Office of the Secretary of Agriculture on the insects of military camps (77, p. 8). It has even been known to pupate in the human intestine and there to develop into adults, causing intense colic (71). The case of a woman who suffered from larvæ of *P. casei* in the nose was reported by Bond (2). Austen (8) stated that in Italy the larvæ "have been expectorated by a patient suffering from an infection of the chest." According to Riley and Johannsen (64, pp. 137-138), Portschinsky found several dead larvæ of this species in the appendix of a dog.

From the foregoing compilation of cases it is evident that to swallow the larvæ of this insect, equipped as it is with sharp oral hooks or claws, and with extraordinary powers of resistance, may result in much discomfort. The utter inconsistency of people who eat these maggots has been pointed out by Berlese (11, pp. 118-121), who argued that those who prefer skippered cheeses would turn in disgust from food polluted by an adult fly of the same species.

NATURE OF INJURY TO CURED MEATS

The injury to cured meats which results from cheese-skipper infestation is usually deep-seated. This is in contrast to the work of other ham pests such as the red-legged ham beetle (*Necrobia rufipes* DeGeer), which usually burrows near the surface in the soft fat or just beneath the hide, and the larder beetle (*Dermestes lardarius* L.), which is also typically a surface feeder. The favorite starting place for skipper infestation is at the butt end of newly smoked hams and shoulders. Here, where the soft muscles and the connective tissue are exposed in cross section, are ideal feeding areas, the muscles often being somewhat separated, a condition which encourages penetration by the maggots. In hams entrance is effected frequently

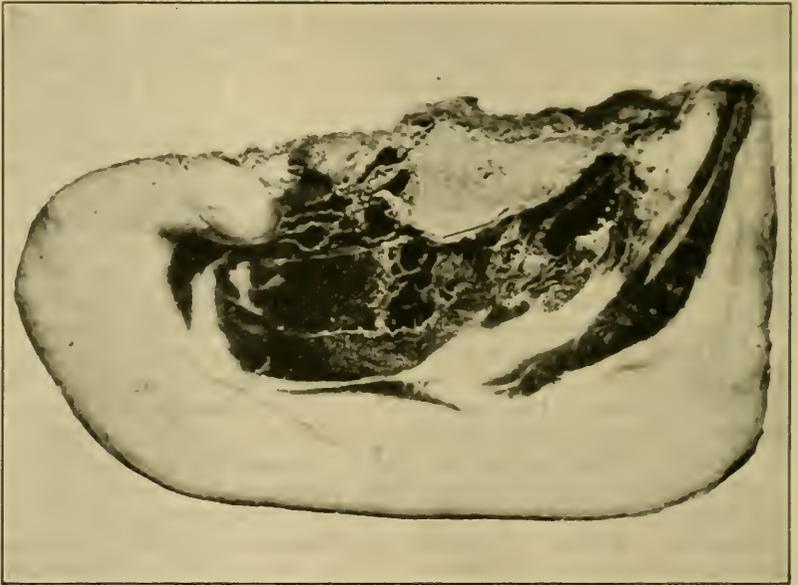


FIG. 1.—Cross section through middle of a dry-cured ham badly injured by feeding of larvæ of *Piophilæ casei*. The outer layer of fat at the upper left has collapsed over the eaten-out cavities. Much reduced

around the exposed bone on the inside, and less often at the hock end where the string passes through, in the small but deep holes left by the inspector's trier, and in small cuts. In the usual well-advanced infestation the insects are found at the center of the meat, in the vicinity of the joint of the bones.

In cured meat, putridity does not usually become marked until the infestation is rather old and consequently fouled by larval excreta. New colonies of the larvæ, even though extensive, have little offensive odor, but the cavities of hams infested for some time give off a strong moldy-sour odor similar to that of old brood comb.

Murtfeldt (53, p. 172) noted the lack of putrefaction in infested hams, but Sakharov (67) has given data to show that in infested fish the skipper maggots have a symbiotic relationship with an undetermined putrefactive organism.



A



B

FIG. A.—*Piophilta casti*: Adult male. $\times 13$
FIG. B.—*Piophilta casti*: Adult female. $\times 13$

An advanced case of cheese skipper infestation in ham is shown in Figure 1. The history of this infestation is given herewith to bring out several points of interest, particularly the fact that large numbers of the insects may develop in one piece of meat.

This dry-cured ham weighed 21 pounds and 4 ounces when removed from the smoke on May 14, 1920. On August 15 it was found to be infested, discarded as inedible, wrapped in paper, and placed in a cotton sack. On May 10, 1921, after being stored during the winter in a cold building, there were found to be 14,819 puparia, nearly all empty, among the folds of the paper and on the surface of the meat. Apparently none of the adults were able to escape, but large numbers of dead ones were present. From May 13 until July 15, 1921, on which latter date the ham ceased to produce skippers, probably because of the presence of the predacious ham beetle *Necrobium rufipes*, 37,808 full-grown larvæ migrated from the interior of the meat, making the total recorded production of skippers 52,627. On October 31, 1921, this ham weighed 15 pounds, thus showing a loss in weight, due to evaporation, the feeding of the skippers, and (toward the end of the observations) to some feeding by ham beetles, of 6 pounds and 4 ounces in 18 months. The daily migration of mature larvæ from the ham is recorded in Table 1.

TABLE 1.—Daily migration of larvæ of *Piophilæ casei* from an infested ham from May 13 to July 15, 1921, at Washington, D. C.

Date	No.	Date	No.	Date	No.	Date	No.	Date	No.
May 13.....	75	May 27.....	308	June 10.....	648	June 21.....	988	July 8.....	266
14.....	64	28.....	342	11.....	754	25.....	1,150	9.....	254
15.....	152	29.....	333	12.....	758	26.....	920	10.....	171
16.....	310	30.....	610	13.....	1,173	27.....	989	11.....	97
17.....	417	31.....	799	14.....	1,265	28.....	887	12.....	66
18.....	303	June 1.....	772	15.....	1,250	29.....	731	13.....	28
19.....	280	2.....	813	16.....	1,230	30.....	667	14.....	38
20.....	249	3.....	879	17.....	1,226	July 1.....	591	15.....	30
21.....	337	4.....	753	18.....	992	2.....	546		
22.....	556	5.....	741	19.....	957	3.....	410		37,808
23.....	437	6.....	837	20.....	878	4.....	328		+14,819
24.....	763	7.....	721	21.....	949	5.....	340		
25.....	444	8.....	689	22.....	990	6.....	332	Total...	52,627
26.....	266	9.....	606	23.....	769	7.....	274		

¹ Migrated before May 13.

THE ADULT INSECT

TECHNICAL DESCRIPTION

Head black above, the front sericeous except for the large ocellar triangle, toward the antennæ narrowly yellow; occiput finely roughened, polished, the lower occipital orbits narrowly pruinose; face, cheeks, mouth parts and antennæ yellow, the cheeks greatly broadened behind, vibrissæ prominent, oral hairs weak or absent; third joint of the antennæ short, oval, the arista brown. Notum black, with faint genescent tinge, not smoothly polished but minutely roughened, bearing three rows of fine setulæ in lieu of the irregularly scattered hairs of the other species of *Piophilæ*; mesopleuræ with scattered minute hairs, propluræ pollinose, the bristle evident; scutellum convex. Abdomen more oblong than usual, the black pubescence conspicuously long. Legs largely black and hairy, coxæ, trochanters, knees, and posterior tarsi more or less yellow. Wings hyaline, veins pale, anterior crossvein shorter than usual but variable, located beyond the middle of the widened discal cell, basal cells indefinitely wider than usual, anal vein evanescent some distance before the margin.

Length 2.5 to 4 mm.

The foregoing description has been taken from Melander and Spuler (49, p. 69).

GENERAL DESCRIPTION

The flies (Pl. 1, A, B),³ as Redi (58, p. 74) described them, are "small flies resembling winged ants, which immediately after birth skipped about with incredible sprightliness and vivacity so that they seemed to be the embodiment of perpetual motion." Superficially this species appears shining black, with reddish-brown eyes,



FIG. 2.—Skipper flies and three specimens of the common house fly, showing comparative sizes. $\times 2$

and wings held flat over the dorsum when at rest. The females are usually larger than the males, and the largest ones are about three-fifths as long as an average-sized house fly and more slender. The comparative sizes of skipper flies and house flies are shown in Figure 2. When feeding and courting the flies are feverishly active, run-

³ Sibly Swegman MacDonald, insect delineator with the Bureau of Entomology, prepared the drawings shown as Figures 2, 3, 8, and 9, and J. G. Pratt, scientific photographer of the bureau, made the photographs.

ning, making short jumping flights, cleaning themselves, and engaging in brief, vigorous sparring matches with other flies. In these bouts the forelegs are used the most and are employed to seize and shake the opponent. When not feeding, mating, or ovipositing the flies may be found at rest, usually on a vertical surface. They may be easily captured in a vial or killed with the hand.

The ovipositor of the female is a three-jointed telescopic organ, hyaline, with a black, slightly hairy, chitinized tactile tip. Some chitinous reinforcing lines are present, these lines on the proximal joint being sparsely hairy. The proximal joint of the extended ovipositor is twice as long as the other two combined, and the opening of the tube is between the second joint and the tip or distal joint. The abdomen of the female is pointed, that of the male blunt.

The external reproductive organs of the male consist of a basal knob bearing the copulatory claspers and a coiled filiform penis nearly equal in length to the entire insect and coiled out of sight beneath the right hand of the two dorsal asymmetrical scales which protect the terminal segment of the insect. The penis is reinforced with a hirsute black line of chitin, which chitinization, having a permanent tendency to coil, seems to be the means whereby the insect is enabled to return the organ to its serpentine position beneath the dorsal scale.

The mouth parts of the adult are similar in structure to those of the house fly, the distal end of the proboscis being provided with a perforated pad, of gridiron pattern, which functions as a strainer.

MATING

Before the newly emerged female has assumed the adult form and color, and often when she is but a soft transparent sac with wrinkled wing pads, she is beset by the male flies. The act of mating, which is consummated with great vigor, continues for a length of time which is controlled by the temperature. Several records are given to illustrate this: In a number of trials at 65° F. pairs remained in copula as follows: Two pairs 9½ minutes, 1 pair 10 minutes, 1 pair 11 minutes, 1 pair 19 minutes. At 75° F. 2 pairs remained in copula 5½ minutes and other pairs, respectively, 6, 6, and 8 minutes. At times, with room temperatures in the neighborhood of 90° F., the mating impulse was markedly decreased.

Mating takes place more than once in the case of pairs confined in vials. Ovipositing females are not molested by the males, and are sometimes observed in groups, apart from any males, depositing eggs in masses. The act of mating is terminated by vigorous efforts of the female, but in the case of old flies, with body fluids and strength depleted, the separation often can not be made and in the laboratory considerable numbers of confined flies die in copula. Of 1,353 flies which died when confined without water, 60 pairs and 3 trios (9.5 per cent) met death in this condition. Microscopic examination of the trios showed that in each case two males were actually in copula with a single female. It is not probable that death in copula often precedes oviposition, but the writer has observed its occurrence.

FEEDING OF THE ADULT

Suitable moist food is a prerequisite to normal oviposition. The adults lack the power to soften desiccated food, and because of the structure of the mouth parts can not do more than "lap" and suck semiliquid or liquid materials. Oviposition does not occur, or takes place infrequently, when the supply of proper food is insufficient. Flies given water alone do not lay eggs. Water is frequently sought by the adults, which were often found in the laboratory about dripping faucets.

Murtfeldt (53, p. 174), one of the few who have considered the matter of adult feeding, stated that "It will sip a little at sweets, * * * while the odor of smoked meats speedily summons it." She reported that the flies were first noticed in the packing houses around vats of yellow wash—a mixture of glue, rye flour, coloring matter, and water. Mote (51, pp. 314-315), as previously stated (p. 5), found that the adults live longer on putrid beefsteak than on ham, bacon, or cheese. Lodge (44, p. 486-487) stated that peptone, both moistened with water and mixed with bread, and sometimes containing maggots, attracted many adults of *P. casei*. She found a casein bait effective. Sakharov (67) reported that these flies can feed on many substances, even the nectar of flowers.

Although adults live without food for several days in warm weather, as shown elsewhere (Table 8), nourishment prolongs the life of both sexes, especially of the males. This appears to be due to the fact that fed females oviposit and the consequent drain upon their vitality results in earlier death. In one trial about 200 unfed and unwatered adults were given thin slices of juicy ham; this was immediately covered with the flies, lapping at the surface with rapid, shifting pecks, like chickens eating scattered grain. Water-soaked cotton was then introduced, but failed to lure more than a few flies from the meat. Fresh pieces of cheddar cheese were eagerly attacked by them, but once the surface of these foods became lapped dry no more nourishment could be obtained.

Water-soaked cotton attracted many flies when offered to a large number of them which were thirsty. Some were observed to draw drops of water away from the main supply and then to suck it up from the glass; others inserted their proboscides through the surface film of the main supply. In one experiment newly emerged adults which were fed upon fresh cheese, and were thereby enabled to reproduce, soon became unable to obtain food on account of the hardening of the cheese, but began feeding again a few days later, after their progeny, with ability to soften the cheese, had reduced it to a paste.

Bachmann (9) stated that the adults regurgitate droplets of liquid food, after the manner of house flies, but the writer has not been able to observe this.

The odor of putrid meat is attractive to cheese-skipper adults. Cultures of larvæ in putrid ham unfailingly attract most of the adults in the room, and the same is true of strong-smelling cheese, decaying beef, and freshly cured ham. Adults confined with semiliquid, putrid beef gorged themselves with it until they were noticeably distended, and oviposition was observed to be profuse.

PREOVIPOSITION PERIOD

At summer temperatures and in the presence of a moist food medium, the laying of fertile eggs usually begins in about 24 hours after newly-emerged adults have been mated. With less favorable conditions the preoviposition period is lengthened, the determining factors being temperature and food supply. Table 4 shows typical preoviposition periods. One female 24 hours old laid eggs 3 hours after mating, but these did not hatch. Fertile eggs have been secured 10½ hours after the mating of newly emerged flies.

OVIPOSITION

The process of egg laying is accomplished in a rapid manner, eggs being deposited every three or four seconds or at longer intervals. The female runs about over the meat in nervous haste with her ovipositor extended and its tip, held downward at an angle with the ovipositor, touching the surface. As she goes actively about she feels the surface with the tactile extremity of the ovipositor moving from side to side and exploring crevices in the meat. No sooner has an egg been deposited than another appears in the translucent basal segment of the ovipositor, whence it is rapidly ejected at the will of the fly. As the egg passes through the opening in the ovipositor the latter often bends sharply for an instant, whereupon the egg is wiped off by contact with the meat. The eggs are laid singly or in groups on the surface of the meat or, where many flies are present, are packed by thousands into crevices where the membranous connective tissue seems to fill the requirements of the females for an ideal location. The laying of eggs in masses favors the development of the progeny, as indicated later. In vials where the meat was placed on cardboard, eggs were often laid between the meat and paper, arranged in groups like the pleats of an open fan.

In the time of Redi (1688) the process of oviposition had evidently not been observed. Most people believed in the spontaneous generation of low forms of life, particularly those found in filth. An interesting theory, mentioned also by Redi (58, p. 73), was that of Gassendi, who believed that the skipper flies deposited their eggs on grass, which was eaten by cows, sheep, and goats and thereby introduced into milk and cheese.

A female fly in the act of thrusting her ovipositor through the meshes of a linen bag covering a ham was observed by Dufour (19).

The observations of Kellogg (37, pp. 114-115) in infested packing houses at Kansas City showed that the adults were literally swarming in the smoky sacking rooms where hams were being wrapped and in the smoke-filled shaft where the meats were smoked. The eggs were laid upon the hams even while the meat was in the wrappers' hands, with the result that the wrapped hams were infested before being shipped.

Murtfeldt (53, p. 173), however, found that the eggs were deposited on the wrapper, preferably among the folds or in spots where the fat had penetrated and loosened the yellow wash. Sakharov (67) asserted that eggs are not deposited on a dry medium, but the writer has observed eggs upon the dry muslin cover of a jar of strong-smelling cheese. It is evident that actual contact with the proposed

larval food is usually but not always necessary for the deposition of eggs. According to the writer's observations, eggs laid on a dry surface (that is, one that is neither damp nor greasy) do not hatch.

FECONDITY

Swammerdam (73, p. 74) dissected an adult female and found that the ovaries contained 256 eggs. In 1861 Taylor (75, p. 609) reported that nearly 300 eggs were laid, but more recently published data show much smaller numbers. The average number of eggs laid by females in Murtfeldt's experiments (53, p. 173) was 30, and several dissections made by Sakharov (67) gave an average of 64 eggs, a maximum of 84, and a minimum of 44.

Sakharov computed the probable increase of the cheese skipper in Astrachan, basing his computations on an average of 60 eggs per female and assuming the resulting progeny equally divided as to sex. Starting with a pair of flies in April, he estimated that the total progeny of five generations (the minimum number during the Astrachan summer) amounted to 50,279,860.

With two generations a month at Washington during the summer, and at least double the average individual reproduction figures used by Sakharov, it is apparent that the cheese skipper is potentially extremely prolific in climates like that of the District of Columbia. The limited food list of this species, together with the care which is usually taken to guard edibles and dispose of carrion, prevents the enormous increase of which the species is capable.

Table 2 details some of the oviposition records made in 1921 on several foods at Washington, D. C.

TABLE 2.—Oviposition records of *Piophilta casci* on various food materials at Washington, D. C., in 1921

Date emerged	Date mated	Day after mating and number of eggs laid							Longevity		Total eggs	Remarks
		1st	2d	3d	4th	5th	6th	7th	Male	Female		
									Days	Days		
June	1	June	1	57	0	91	3	4	178	On lean ham.
	1		1	0	99	3	4	99	Do.
	1		1	55	7	4	55	Do.
	6		6	3	5	0	On dried beef. ¹
	6		6	5	6	0	Do.
	18		18	95	80	7	3	175	On lean ham.
	18		18	43	4	2	43	Do.
	18		18	85	1	6	2	86	Do.
	18		18	78	87	5	11	22	6	5	203	Do.
	18		18	93	0	66	7	4	159	Do.
	28		28	30	31	3	3	61	Do.
	28		28	128	6	4	128	Do.
	28		28	68	61	3	2	129	Do.
July	7	July	7	3	2	0	On lean Smithfield ham.
	7		7	8	3	0	Do.
	7		7	4	2	0	On Smithfield ham fat.
	8		8	5	2	0	Do.
	8		8	5	2	0	Do.
	13		13	65	7	6	65	On lean Smithfield ham.
	13		13	8	2	0	Do.
	13		13	85	14	7	85	Do.
	13		13	7	3	0	Do.
	13		13	8	3	0	Do.

¹ Dried beef and Smithfield ham are unsuitable as food for adults and larvæ because they contain comparatively little water.

TABLE 2.—Oviposition records of *Piophilæ casei* on various food materials at Washington, D. C., in 1921—Continued

Date emerged	Date mated	Day after mating and number of eggs laid							Longevity		Total eggs	Remarks
		1st	2d	3d	4th	5th	6th	7th	Male	Female		
July 19	July 20	58	51	0	22				8	8	131	On lean ham.
20	20	70	0	27	0	44	0	41	11	11	182	Do.
22	22	0	19						2	5	19	Do.
Sept. 1	Sept. 1	73	63						10	3	136	Do.
1	1	66	63						26	4	129	Do.
1	1	73	65	0	0	14			8	6	152	Do.
1	1	66	0	36					5	4	102	Do.
1	1	45	14						9	2	59	Do.
1	1	36	60						11	5	96	Do.
8	8	54	0	0	23				11	13	77	Do.
8	8	0	54	0	31				10	4	85	Do.
8	8	60	0	24					18	5	84	Do.
8	8	49							5	5	49	Do.
8	8	0	44						14	5	44	Do.
8	8	60	0	0	16				3	4	76	Do.
7	8	0	37	0	0	19			12	6	56	Do.
7	8	63							6	5	63	Do.
15	15	37	0	31					3	3	68	Do.
15	15	66	33						6	3	99	Do.
30	Oct. 1								39	31	0	On lean ham in refrigerator.
30	1	73	78						7	7	151	On lean ham.
30	1	101	83						17	7	184	Do.
30	1	0	85						13	9	85	Do.

Table 3 gives the daily mean temperatures in the laboratory during the time the records shown in Table 2 were being made.

TABLE 3.—Daily mean temperatures in the laboratory at Washington, D. C., in 1921, during the period when the experiments on *Piophilæ casei* shown in Table 2 were made

[Based on daily average of thermograph readings taken at two-hour intervals]

Date	Temperature	Date	Temperature	Date	Temperature	Date	Temperature	Date	Temperature
May 19	74	June 24	89	July 30	82	Sept. 4	84	Oct. 10	69
20	74	25	89	31	85	5	82	11	75
21	76	26	89	Aug. 1	78	6	81	12	74
22	80	27	87	2	78	7	79	13	71
23	82	28	86	3	80	8	79	14	70
24	72	29	86	4	83	9	79	15	71
25	67	30	85	5	82	10	79	16	68
26	71	July 1	82	6	84	11	80	17	69
27	69	2	83	7	78	12	80	18	72
28	74	3	86	8	78	13	79	19	73
29	76	4	88	9	79	14	76	20	74
30	76	5	88	10	75	15	78	21	70
31	74	6	83	11	74	16	77	22	72
June 1	76	7	84	12	75	17	79	23	69
2	75	8	88	13	78	18	82	24	71
3	74	9	88	14	82	19	75	25	68
4	78	10	87	15	75	20	73	26	67
5	74	11	84	16	73	21	75	27	70
6	73	12	81	17	72	22	76	28	73
7	72	13	82	18	79	23	75	29	74
8	72	14	83	19	79	24	73	30	68
9	74	15	82	20	80	25	75	31	73
10	76	16	78	21	81	26	71	Nov. 1	73
11	80	17	80	22	74	27	69	2	70
12	82	18	80	23	73	28	74	3	69
13	84	19	83	24	73	29	78	4	69
14	82	20	84	25	73	30	76	5	68
15	78	21	81	26	72	Oct. 1	68	6	59
16	78	22	79	27	72	2	67	7	63
17	82	23	79	28	73	3	68	8	69
18	80	24	81	29	80	4	66	9	69
19	79	25	85	30	84	5	67	10	69
20	78	26	84	31	85	6	69	11	57
21	81	27	86	Sept. 1	85	7	70	12	64
22	85	28	86	2	85	8	73	13	64
23	88	29	83	3	85	9	61		56

Further oviposition experiments, in which lean ham was used as food for adults and larva, are given in Table 4. The temperatures affecting them are given in Table 5.

TABLE 4.—Oviposition of *Piophilus cusei* on lean ham at Washington, D. C., in 1922

Date emerged	Date mated	Day after mating and number of eggs laid														Total eggs	Longevity of female		
		1st	2d	3d	4th	5th	6th	7th	8th	9th	10th	11th	12th	13th	14th				
																		<i>Days</i>	
Aug. 28.	Aug. 28.	0	52															52	5
28.	28.	0	65	66	75													206	6
28.	28.	0	111	0	2													113	6
28.	28.																	0	2
28.	28.	0	97	56	0	19												172	6
28.	28.	0	106															106	5
28.	28.	0	130	0	0	5												135	5
28.	28.	0	140	0	93	0	89	0	37									359	9
28.	28.																	0	2
28.	28.	0	0	0	45													45	5
29.	29.	40																40	3
29.	29.	75	63															138	3
29.	29.	0	145															145	5
29.	29.	0	78	0	27													105	5
29.	29.	67																67	7
29.	29.	0	13	51														64	5
29.	29.	0	10	72														82	3
29.	29.	0	45	67	21													133	7
29.	29.	0	70	62	0	0	20											152	7
29.	29.	0	32	79														111	5
30.	30.	82	46															128	5
30.	30.	70	72	0	48	0	0	0	0	26								216	12
30.	30.	79	87	0	6													172	7
30.	30.																	0	1
30.	30.	38	35															73	3
31.	31.	55	0	72	82													209	6
31.	31.	81																51	3
31.	31.	39	22															61	4
31.	31.	0	50															50	4
31.	31.																	0	2
Sept. 4.	Sept. 4.	0	86	25														111	3
4.	4.	52																52	4
4.	4.	70	38															108	5
4.	4.	54																54	3
4.	4.	0	30															30	4
4.	4.	0	80															80	3
4.	4.	110	0	31														141	4
4.	4.	27	87															114	3
27.	27.	0	63	70														133	6
27.	27.	0	75	0	0	0	66	0	0	117	0	29						287	12
27.	27.	0	147	0	0	0	0	0	73	96	0	52						368	12
27.	27.	0	57	0	109	0	0	0	0	0	43	0	29	42				280	17
27.	27.	0	97	0	95	0	0	0	0	40	73	0	0	52				357	18
27.	27.	0	87	0	89	0	0	0	74	60	4	61						375	17
27.	27.	0	89	0	0	0	0	0	89	0	55	0	0	0	41			277	19
27.	27.	0	89	0	73	0	0	0	0	90	92	83	53					480	12
27.	27.	0	88	21	5	0	0	8	0	0	65	13						300	11
27.	27.																	0	10
27.	27.	0	0	110	0	0	27	0	4									141	11
27.	27.	0	0	0	0	0	72	0	56									128	9
27.	27.	0	151															151	3
27.	27.	90	101	0	73	0	24	0	38	28								354	9
27.	27.	0	159	78	0	0	43											280	6
27.	27.	0	117	0	0	0	31	127	0	73	77							425	12
27.	27.	0	0	0	0	0	87	36	48	0	0	30						201	12
Oct. 4.	Oct. 4.	81	63	0	53	0	0	12	0	47	0	0	0	12				268	16
4.	4.	70	86	0	0	0	0	57	0	0	0	0	0	0	60			273	22
4.	4.	92																92	6
4.	4.	16	62															78	5
4.	4.	79	63	31	48	0	0	0	61									282	10
4.	4.	71	72															146	6
4.	4.	54	83	0	49	0	0	39										225	12
4.	4.	0	79															79	2
4.	4.	39	89	0	0	86	0	47	0	0	0	0	72					333	17
4.	4.	89	58	0	55													202	13
4.	4.	74	71															145	6
4.	4.	49	72															121	6

¹ In incubator at 80 to 85° F.

TABLE 4.—Oviposition of *Piophilæ casci* on lean ham at Washington, D. C., in 1922—Continued

Date emerged	Date mated	Day after mating and number of eggs laid														Total eggs	Longevity of female	
		1st	2d	3d	4th	5th	6th	7th	8th	9th	10th	11th	12th	13th	14th			
Oct.	15.	0	0	87	0	0	0	0	130	0	0	0	0	0	0	224	Days 26	
	15.	16.	0	0	57	0	61	0	0	61	0	0	0	0	41	220		24
	15.	16.	0	0	60	0	0	0	0	0	64	0	0	0	0	124		26
	15.	16.	0	0	40	0	15	0	0	0	0	0	0	0	0	55		29
	15.	16.	0	13	2	0	0	0	21	96	0	0	0	0	0	135		15
	15.	16.	0	62	0	0	0	0	123	0	0	0	0	0	0	185		10
	15.	16.	0	35	0	0	19	17	0	27	23	0	0	0	13	134		22
	15.	16.	0	54	0	57	0	0	81	0	41	0	0	0	0	236		13
	23.	23.	0	0	0	0	71	0	0	0	0	0	0	0	0	74		16
	23.	23.	0	81	0	25	42	0	0	0	0	0	0	0	0	148		16
	23.	23.	0	8	70	0	0	0	0	0	0	0	0	0	0	78		12
	23.	23.	0	0	0	0	0	0	0	0	89	0	0	0	0	89		11
	23.	23.	0	0	35	0	0	0	0	0	0	0	0	0	0	35		16
	23.	23.	0	81	0	0	33	0	0	0	0	0	0	0	0	117		21
	23.	23.	0	91	0	0	65	0	0	0	0	0	0	0	0	156		16
	23.	23.	0	0	0	0	18	0	0	0	0	0	0	0	0	18		7
	23.	23.	0	0	85	0	0	0	0	0	0	0	0	0	0	85		3
	23.	23.	0	0	81	0	0	0	0	0	0	0	0	0	0	84		16
	23.	23.	0	0	55	0	0	0	0	0	0	0	0	0	0	55		21
	23.	23.	0	0	54	0	0	0	0	0	0	0	0	0	0	54		3
	23.	23.	0	0	64	0	0	0	0	0	0	0	0	0	0	64		12
	23.	23.	0	0	73	0	0	0	0	63	0	0	0	0	0	136		21
	23.	23.	0	0	68	0	0	0	0	0	0	0	0	0	0	68		10
	23.	23.	0	0	0	0	0	0	0	65	0	0	0	0	0	65		12
	23.	23.	73	0	68	0	0	19	0	48	0	0	0	0	0	208		12
	23.	23.	72	67	0	0	0	0	0	0	0	0	0	0	0	139		7
	23.	23.	79	69	0	0	0	0	0	26	0	0	0	0	0	174		11
	23.	23.	76	77	0	0	37	0	0	0	0	0	0	0	0	190		5
	23.	23.	74	0	70	0	0	33	0	0	0	0	0	0	0	177		7
	23.	23.	80	92	0	0	0	36	0	0	51	0	0	0	0	259		11
	23.	23.	101	0	92	0	40	35	0	0	50	0	0	0	0	318		14
	23.	23.	87	70	0	0	0	0	0	0	0	0	0	0	0	157		2
	23.	23.	67	56	0	0	0	0	0	65	0	0	25	0	0	213		11
23.	23.	0	53	0	0	59	0	0	0	0	0	0	0	0	112	14		
23.	23.	63	0	60	0	21	39	0	0	32	0	0	0	0	215	14		
23.	23.	89	0	73	0	0	0	0	0	0	0	0	0	0	162	5		
23.	23.	98	0	60	0	0	0	0	0	0	0	0	0	0	158	5		
Nov.	1.	0	0	18	0	0	51	0	0	0	0	0	0	0	0	69	12	
	1.	0	0	26	0	46	0	0	0	0	0	0	0	0	0	72	7	
	1.	0	72	0	0	61	0	0	0	0	0	0	0	0	0	133	19	
	1.	0	0	0	0	0	68	0	0	0	0	0	0	0	0	68	9	
	1.	0	55	0	0	55	0	0	0	0	0	0	0	0	0	110	24	
	1.	0	0	0	0	0	75	0	0	0	0	0	0	0	0	75	8	
	1.	0	44	0	0	78	0	0	0	0	0	0	0	0	0	110	7	
	1.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	75	12	
	1.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	122	10	
	12.	13.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5
	12.	13.	0	0	40	60	0	0	0	0	0	17	0	0	0	117	15	
	12.	13.	0	0	64	53	0	0	38	0	0	0	0	0	0	155	11	
	12.	13.	0	41	0	24	0	0	0	0	0	27	0	0	0	92	11	
	12.	13.	56	0	0	47	0	0	0	0	0	0	0	0	0	103	5	
	12.	13.	0	57	46	0	0	0	0	0	0	0	0	0	0	103	8	
	12.	13.	0	0	0	0	75	0	0	0	0	0	0	0	0	75	16	
	12.	13.	83	65	0	49	37	0	0	0	0	25	0	0	0	259	11	
	12.	13.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	16	
	18.	18.	0	0	86	0	40	0	0	0	0	0	0	0	0	126	10	
	18.	18.	47	60	0	0	0	0	0	0	0	0	0	0	0	107	2	
	18.	18.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	10	
	18.	18.	42	0	0	0	0	0	0	0	0	0	0	0	0	42	5	
	18.	18.	0	55	0	0	0	0	0	0	0	0	0	0	0	55	5	
18.	18.	51	28	0	0	0	0	0	0	0	0	0	0	0	79	5		

Total eggs laid by flies..... 17,669
 Total females..... 128
 Average eggs per female (including those which did not oviposit)..... 138

¹In incubator at 80 to 85° F.

²Including 7 eggs laid on nineteenth day. No eggs were laid from the ninth day to the eighteenth day, inclusive.

TABLE 5.—Daily mean temperatures in 1922 in laboratory at Washington, D. C., where the experiments on *Piophilu casei* shown in Table 4 were made.

[Based on daily average of thermograph readings taken at two hour intervals]

Date	°F.	Date	°F.	Date	°F.	Date	°F.	Date	°F.
Aug. 29.....	75	Sept. 18....	62	Oct. 8.....	75	Oct. 28.....	67	Nov. 17....	67
30.....	74	19.....	68	9.....	71	29.....	62	18.....	67
31.....	76	20.....	69	10.....	73	30.....	60	19.....	64
Sept. 1.....	76	21.....	72	11.....	67	31.....	64	20.....	64
2.....	75	22.....	69	12.....	64	Nov. 1.....	68	21.....	65
3.....	75	23.....	70	13.....	65	2.....	68	22.....	63
4.....	79	24.....	73	14.....	68	3.....	68	23.....	66
5.....	80	25.....	67	15.....	68	4.....	68	24.....	66
6.....	80	26.....	62	16.....	69	5.....	69	25.....	66
7.....	80	27.....	65	17.....	70	6.....	68	26.....	64
8.....	76	28.....	68	18.....	68	7.....	69	27.....	64
9.....	77	29.....	70	19.....	67	8.....	66	28.....	65
10.....	78	30.....	70	20.....	68	9.....	67	29.....	67
11.....	79	Oct. 1.....	69	21.....	66	10.....	66	30.....	60
12.....	77	2.....	69	22.....	60	11.....	67	Dec. 1.....	66
13.....	73	3.....	70	23.....	65	12.....	62	2.....	68
14.....	74	4.....	73	24.....	68	13.....	67	3.....	59
15.....	77	5.....	74	25.....	66	14.....	67		
16.....	78	6.....	74	26.....	67	15.....	70		
17.....	70	7.....	73	27.....	65	16.....	67		

A general impression gained from the experiments reported in Tables 2 and 4, in which temperature was the only apparent variable of importance, is that very hot weather is not optimum for the oviposition of *P. casei*. That the mating instinct wanes during extremely hot weather has been previously noted, and the rapidity of expenditure of energy under such conditions shortens life. Larval growth, however, is most rapid during the hottest weather, as is also the process of metamorphosis within the puparium.

In Table 4 the pairs which were mated September 27 were superior in fecundity to all other groups, although the temperatures which they experienced were not unusually high. Table 6 presents a comparison of data relating to the first nine pairs mated September 27 with those of the group immediately preceding, which emerged and were mated September 4. Not enough insects are involved in this comparison to justify the drawing of conclusions, but the indications are of interest.

TABLE 6.—Comparison of conditions influencing the fecundity of certain females of *Piophilu casei* recorded in Table 4

	Pairs mated Sept. 4	Pairs mated Sept. 27
Number of pairs used in comparison.....	8	9
Average longevity of females, in days.....	3.6	13.8
Minimum longevity of females, in days.....	3	6
Maximum longevity of females, in days.....	5	19
Average number of eggs laid.....	86	306
Minimum number of eggs laid.....	30	135
Maximum number of eggs laid.....	141	480
Average daily mean temperature (°F.).....	79	69.4
Minimum daily temperature (°F.).....	73	59
Maximum daily temperature (°F.).....	85	79

In the records in Table 6 the two average longevities are to each other as 1 is to 3.8+ and the two oviposition averages are to each

other as 1 is to 3.6; in other words, fecundity is here very nearly in direct proportion to longevity.

During hot weather the usual reproductive period is brief. Weather sufficiently cool to delay the beginning of oviposition to the second day after mating seems to be advantageous to fecundity, since it enables more feeding prior to egg laying; and this delayed egg laying, and the lessened general activity in cool weather, apparently prolong life. In the case of the group of females mated on September 27, 1922, the cool weather continued and the temperature was such as to allow the females to have the advantage of a recuperative period after their first heavy egg laying and to develop a second series of eggs. Females which laid 200 or more eggs typically show comparatively long egg records, the eggs laid being divided more or less definitely into two groups, but hot weather usually results in the exhaustion of the vitality of the females after five or six days.

Parthenogenesis has not been observed. Virgin females seem to lay about as well as mated females but all of their eggs fail to hatch. Table 7 gives oviposition records of unmated females.

TABLE 7.—Oviposition of virgin females¹ of *Piophilha casci* at Washington, D. C., in 1922

Female No.	Date emerged	Number of eggs laid on—								Length of life	Total eggs	
		Oct. 2	Oct. 3	Oct. 4	Oct. 5	Oct. 6	Oct. 7	Oct. 8	Oct. 9			
1.....	Nov. 1	77	71	31	0	0	94	-----	-----	Days	6	273
2.....	1	0	0	0	81	25	-----	-----	-----		13	106
3.....	1	61	50	-----	-----	-----	-----	-----	-----	6	111	
4.....	1	80	36	0	33	0	0	0	41	20	190	
5.....	1	-----	-----	-----	-----	-----	-----	-----	-----	19	0	
6.....	1	5	53	0	0	52	0	32	-----	16	142	
7.....	1	0	25	0	0	0	19	-----	-----	21	44	
8.....	1	0	57	-----	-----	-----	-----	-----	-----	16	57	
9.....	1	0	74	0	79	-----	-----	-----	-----	7	153	
Total.....	-----	223	366	31	193	77	113	32	41	-----	-----	-----
Average.....	-----	-----	-----	-----	-----	-----	-----	-----	-----	13.8	-----	119.5

¹ These females were given fresh ham on November 1 and were kept at laboratory temperatures. Relative humidities in the room had little reference to the humidities in the vials, which contained moist meat. During the oviposition the daily mean temperatures were all about 70° F. None of the eggs laid by unfertilized females hatched.

Several experiments were made to determine the approximate maximum temperature at which reproduction takes place. Pairs incubated at a constant temperature of 104° F. did not reproduce, whereas those in a temperature of 102.2° F. reproduced abundantly. The indications of all trials are that the maximum temperature for reproduction lies between 102.2 and 104° F.

OVIPOSITION PERIOD AND POSTOVIPOSITION PERIOD

As is shown by the data in Tables 2 and 4, eggs are frequently laid within the first 24-hour period after mating. This is especially true of the records in Table 2 which includes records obtained in an abnormally hot summer. The first batch of eggs is as a rule larger than subsequent ones. Eggs are usually laid on three or four different days and during the oviposition period, the time from first

oviposition to the laying of the last eggs, a few days are often interspersed on which no eggs are laid. The oviposition period varies in length with the temperature, as does the postoviposition interval, but in cool weather the latter is proportionately longer than the oviposition period.

LONGEVITY OF ADULTS

The length of life of mated and fed adults was from 1 to 39 days, as shown in Tables 2 and 4. None of the unfed flies kept in a refrigerator at 48 to 50° F. lived as long as 30 days, the longest life of a fed fly in the refrigerator. The data in Table 2 show that the males usually live longer than the females.

Unmated adults kept without food or water lived as shown in Table 8. Until June 10 the weather was cool or warm, but on June 11 the daily average temperature passed above 80° F. and thereafter remained high. For this reason two divisions of the longevity records are made. The temperatures experienced by the flies included in Table 8 are given in Table 3.

TABLE 8.—*Longevity of unmated adults of Piophilæ casci confined without food or water at Washington, D. C., in 1921*

Died on—	Flies emerged May 19 to June 10	Flies emerged June 11 to June 22	Died on—	Flies emerged May 19 to June 10	Flies emerged June 11 to June 22
First day.....	3	5	Sixth day.....	39	0
Second day.....	4	95	Seventh day.....	6	0
Third day.....	103	150	Eighth day.....	1	0
Fourth day.....	222	65			
Fifth day.....	163	8	Total.....	541	323

The average longevity of the flies in the first group (Table 8) was 4.3 days and in the later group slightly less than 3 days. The average of the daily mean temperatures experienced by the flies of the first group was 74° F. and by those of the second group 81° F., the difference of 7° in the averages of the daily means being apparently responsible for the difference of over 1 day in the average lives of the insects. Temperature was the only apparent important variable.

The females used in the experiment lived longer than the males; the average female life was 4 days and the average male life 3.5 days. When pairs are mated and fed, oviposition usually results and the longevity relation of the two sexes is reversed. A summary of the longevity records of 46 such pairs (Table 2) shows that the males lived an average of 8.5 days and the females 5.1 days.

SEX RATIOS

Previous to the work included in this bulletin, the only records of the relative abundance of the sexes were published by Bachmann (9), who believed the males to be in the minority, and by Sakharov (67), who found that of 1,077 flies, 625 were females and 452 were males. The writer has observed little difference in the numbers of the sexes, but has always found a small plurality of males. Of the 864

flies shown in Table 8, 463 were males and 401 were females. Of 2,112 other flies observed (Table 9), 1,074 were males and 1,038 were females. These flies composed the entire progeny of females which laid eggs on ham in vials, each day's eggs of each individual being kept separate.

DEVELOPMENTAL PERIODS OF THE SEXES

Emergence records consistently show that the females take longer to develop than the males. Data to support this conclusion are detailed in Table 14 and also in Table 9 which follows:

TABLE 9.—Comparative rate of emergence of the sexes of *Piophilæ casei*¹ at Washington, D. C., in 1921

Sex	Number emerged on—															Total
	1st day	2d day	3d day	4th day	5th day	6th day	7th day	8th day	9th day	10th day	11th day	12th day	13th day	14th day	15th day	
Male.....	258	437	127	69	65	36	23	19	22	8	7	2	0	1	0	1,074
Female ..	18	233	351	145	82	84	38	22	25	17	12	9	1	0	1	1,038

¹ Emergence of adults resulting from daily batches of eggs laid by isolated females. Each batch of eggs was allowed to develop in a separate vial. The flies which emerged first in each vial are recorded under "1st day," the entire series being consolidated as though the beginning of emergence in all the vials had been simultaneous.

The rather long developmental periods of some of the insects recorded in Table 9 are explained by the condition of the food supply. These records were made in warm weather, when the first and last emergence of adults from a given day's eggs would have extended over only four or five days, if the larvæ had invariably had access to a plentiful supply of moist food.

BEHAVIOR OF ADULTS

The adult flies are usually eager, when confined in small glass containers, to move upward and toward the light—responses which facilitate handling them. These two responses are not particularly strong in flies which are flying freely in a room, however, and the flies are not strongly attracted to the windows, as might be expected. Unconfined flies respond principally to the stimulus of food odors. Jars containing cheese or meat, especially if these are infested with the maggots and have a decided odor, are foci for the free adult skippers in the room. Females may sometimes be observed running about over the muslin covers of the jars, feeling for apertures with their ovipositors. By placing an inverted cone in the opening of jars containing cultures of the larvæ in ham, it has been possible in the laboratory to trap numbers of the flies.

Newly emerged adults are especially attracted by odors of their foods, and it was found difficult to remove adults from a large ham riddled with galleries of the larvæ. Rather than take flight the flies preferred to dodge down into the dark interior of the meat. At another time it was found almost impossible to remove adults from a paper can, which contained thousands of puparia, both normal and empty. The attraction of the dark interior of this can was almost irresistible to the flies which had emerged in it.

In a storage room containing cured meat, flies of both sexes were always found upon the screen covering the only window, but there were more flies on the meat, even in dark corners of the room, than on the window. A few flies have been observed in the smoke chamber of an abattoir after the smoke was dissipated. The darkness of any storage room seems to be ineffective as a repellent in the presence of the overwhelmingly attractive food odors.

Mated females confined in shell vials in an incubator oviposited profusely on ham; the fact that the interior of the incubator was absolutely dark did not hinder reproduction in the least. Murtfeldt (53, p. 174) stated that the flies are not active at night but are able to work in partially darkened places; Kellogg (37, pp. 114-115) recorded flies swarming in smoky compartments; and Sakharov (67) believed that fish may be infested during the smoking.

In discussing the behavior of adults of *Piophilu casei* it is appropriate to refer again to the interesting habit of combat between adults. This was observed by Rühl (66), who could find nothing similar recorded. Combat does not always appear to arise from the frenzied impulse of the males to mate; adults often spar and maul one another, apparently purely as a means of discharging their superabundant energy.

Bachmann (9) has given an extended account of his observations on the behavior of the flies in their fighting and mating. He observed severe fighting in which combatants were injured and even killed. Fights do not occur, he stated, in a group of flies containing only females, and the writer has made the same observation.

It is a rather common occurrence to observe adults, confined in a vial, sham death for a few seconds when the container is jarred.

THE EGG

The egg is opaquely white, very smooth and shiny, slightly curved and roundly pointed at the ends. The length is usually about 0.6 millimeter. The appearance of freshly laid eggs upon lean ham is shown at A in Figure 3.

INCUBATION PERIOD

A few observations have been made by other writers on the duration of the egg stage. Kellogg (37, pp. 114-115) found that eggs hatched after 4 days; Murtfeldt (53, p. 173), after 1½ days; Mote (51, p. 310) recorded incubation periods of from 23 to 54 hours; whereas Sakharov (67) gave the duration of the egg stage as 2 days. The writer has observed periods as short as about 23 hours, and during the hot months hatching may usually be expected after about 1 day.

HATCHING

When the egg hatches, the larva slowly works its way out of the eggshell through a small longitudinal slit in the anterior end of the egg. The empty shells collapse and are opaque, white, and conspicuous in contrast with the red color of ham.

THE LARVA

The larval stage is the most destructive and most resistant stage of the insect. It is the stage which has engaged the attention of a

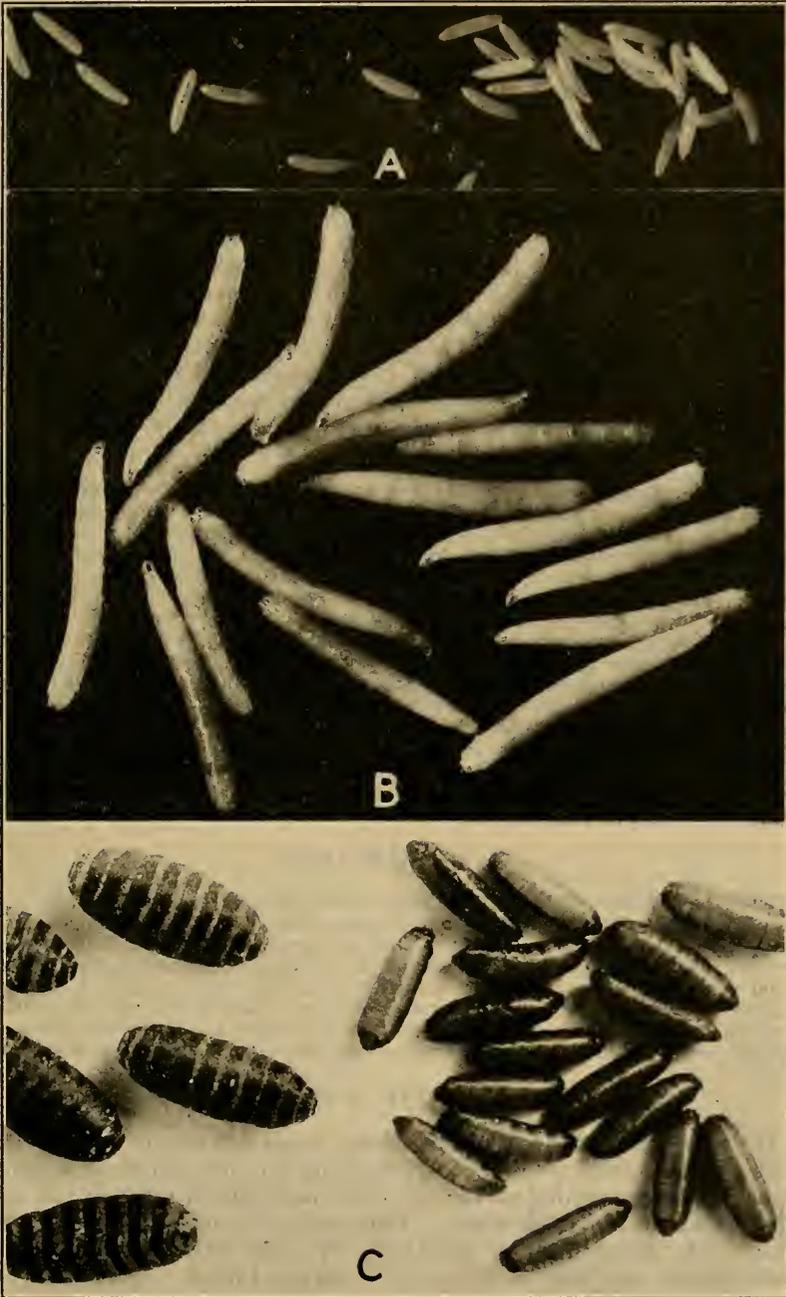


FIG. 3.—A, Eggs of *Piophilidae* on lean ham; B, Migrant larvæ of *Piophilidae*; C, Puparia of *Piophilidae* compared with puparia (on left) of *Lucilia sericata*, one of the common blowflies sometimes found infesting cured meats

number of the early writers, principally on account of the remarkable saltatorial ability displayed by the maggot. The jump of the full-grown larva has given the species its common name. The writer concludes that there are three larval instars; these have been identified by Sakharov (67) and by Wille (81).

FIRST-STAGE LARVA

The first-stage larva appears as a diminutive mass of translucent jelly. When it leaves the collapsed, flat eggshell behind, its progress is marked by a groove in the grease on the meat. Shortly after the hatching begins all the larvæ are free and soon seek the crevices of the meat, where they feed en masse. The clustering habit of these maggots is marked throughout the larval life. Larvæ transferred from one piece of meat and scattered about on another may be found the next day gathered in one or two groups. The effect of group feeding is advantageous to the individual because of the decided softening effect produced on the food. All stages of the larvæ exhibit strong negative phototropism.

As with muscoid larvæ in general, the principal taxonomic characters of the present species are the deeply pigmented oral hooks and cephalopharyngeal framework and the spiracles. A minute set of oral hooks and a very small supporting skeleton are visible in the first-stage larva, but no anterior spiracles are present; the tracheæ in the anterior region end in fine branches within the tissues. Otherwise the tracheal system is very similar to that of subsequent instars. The posterior spiracles are conspicuous.

Observation of first-stage larvæ in a shallow drop of water on dark cardboard can be made under the binocular. The principal concern of the insect under these conditions is to keep the spiracles above water, and to this end the caudal extremity of the body is kept elevated, and whenever possible the spiracles penetrate the surface film. The excrescences on which the spiracles are situated are movable at the will of the larva, which feels about with them in attempts to locate a supply of air. The writer has observed first-stage larvæ to hold the two spiracular openings in close contact with one another, evidently for the purpose of effecting a more complete closure of the respiratory system.

SECOND-STAGE LARVA

The larva of the second stage is provided with a rather slender, black cephalopharyngeal framework and slender mouth hooks. The anterior spiracles are present and consist of a pair of flat, yellow, fan-shaped processes arising between the second and third segments. Their distal edges are digitate. When closed these spiracles are withdrawn beneath the anterior margin of the third segment. The posterior pair of spiracles is very evidently the pair most used; larvæ in moist meat arrange themselves so that these breathing apertures are exposed, whereas the anterior spiracles are not usually in free contact with the air.

LARVAL SKINS

The cast skins of the first and second stage larvæ may be separated from a meat culture by vigorously dousing the infested meat in water, allowing the suspended matter to settle, pouring off most of the clear liquid, and adding fresh water. This process results in concentrating larvæ and cast skins in a small dish of clear water. In collections made in this way only two sizes of skins are found.

Skins of the first-stage larva are 1.5 to 1.8 millimeters in length, with a dorsal split at the anterior end and typically with several of the posterior segments invaginated. This infolding apparently results from the pull occasioned by the friction between the forward-moving body of the molting insect

and the posterior part of the sloughing-off linings of the tracheæ and the posterior spiracular structures. The same in-pulled condition is typical of second-stage skins.

To the anterior extremity of first-stage skins a flagellum-like appendage usually adheres. This probably consists of the gut lining, and appears to inclose the cephalopharyngeal skeleton. The anterior end of the first-stage skin also bears a pair of two-jointed, fleshy antennæ and a pair of minute, indistinct areas bearing four or five dark spots which the writer assumes to be structures functioning as eyes.

The second-stage larval skin, about 4 millimeters in length, lacks the whip-like appendage of the first-stage skin, but has a pair of prominent, slender mouth hooks and a delicate cephalopharyngeal skeleton. The antennæ and eye spots are present in all stages.

THIRD-STAGE LARVA

The third-stage larva, when full-grown and ready to migrate from its food in search of a pupation place, is about 6 to 8 millimeters long, the ultimate size depending on food and environment. There are 12 segments, including the head. This stage has a robust cephalopharyngeal framework and strong mouth hooks, and is whiter and more opaque than the preceding stages.

The tracheal system is clearly visible in specimens immersed in a liquid, the confined air giving it the appearance of being filled with mercury. Both pairs of spiracles are yellow; the posterior ones are provided with conspicuous yellow, bulbous bases or stigmatic chambers. The ends of the spiracles are very small and the pattern of the openings (three oval apertures) is not easily seen. The tracheal system of the full-grown larva, seen from the side, is shown in Figure 4. The two halves of the tracheal system are joined dorsally by commissures, of which the first and last are of greatest diameter.

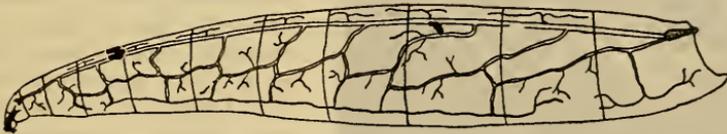


FIG. 4.—Tracheal system of migrant larva of *Piophilidae casei*. Left-hand half of system shown. The dorsal tracheal trunks are joined by commissures; these are not visible from the side. $\times 10$

The modes of progression of the mature larva are two: Skipping, and creeping along by peristaltic movements of the body wall, aided by transverse rows of ambulatory teeth on the ventral surface of the last seven intersegmental lines and at the anus. The microscopic ambulatory teeth are triangular in shape, are directed posteriorly, and are arranged in triple rows, except at the anal region where only a few teeth are present.

The skip frequently propels the maggot 10 inches horizontally or 6 inches vertically. As Swammerdam (*73*, pp. 63-64) tersely expressed it, "the worm leaps with a surprising violence," and it is "surprisingly strong, and has a most vigorous constitution." In skipping, the insect bends its body in the shape of a ring and hooks its oral claws over the sharp angle formed by the ventral edge of the posterior beveled truncation. The larva then pulls hard, so hard that the two halves of the body are brought together by the strain, and the hold is suddenly released, the resulting snap throwing the insect into the air. The act is comparable to the behavior of a strip of whalebone when the two ends, which have been held together, are released. The process of adjusting the hooks is deliberate, the larva using considerable care in placing them before the strain is brought to bear. Although the skip is useful when the larva is alarmed and

is also employed in the course of undisturbed migration, the most usual and reliable method of locomotion is by creeping. This always brings the insect to a dark spot, if obstructions do not prevent, whereas the leap is haphazard and is as likely to throw the insect toward the light as toward the shadow.

Wille (81) has made a study of the modes of larval progression. He stated that locomotion by springing occurs in third-stage larvæ only, and is most pronounced within one day of pupation.

A photograph of larvæ of *Piophilta casei* is reproduced in *b* of Figure 3. In Figure 5 is a comparison of the appearance of skippers and the larvæ of *Lucilia sericata* Meig., one of the common blowflies.

INSINUATING ABILITY OF THE MAGGOTS

An outstanding attribute of the larva is its remarkable insinuating ability. Being pointed anteriorly, slender, and very strong, it is able to enter exceedingly small crevices and therefore is difficult to confine.



FIG. 5.—Larvæ of *Piophilta casei* (a), compared with larvæ of *Lucilia sericata* (b), one of the common blowflies. Slightly enlarged

Petri dishes and jars closed with muslin secured by tight rubber bands do not confine the larvæ. When masses of larvæ crowded together have moistened the muslin covers of the jar containing them, some are able to force their way through the close weave of a good grade of cloth. Six layers of cheesecloth have failed to prevent the escape of the maggots from glass containers. The most effective container is a paper can, which absorbs the moisture from the surface of the larvæ, making it impossible for them to mount the sides. In glass vessels the efforts of hundreds of larvæ to escape soon coat the surface with a thin oily film, which enables the maggots to cling to the glass.

The penetrating power of the larva is useful to it in forcing its way among the layers of connective tissue between the muscles, and accounts for the depth at which maggots are found in recently infested meat. The ability of the newly hatched larva to enter a small aperture may at times lead to infestation of wrapped meat in cases where eggs are laid on greasy spots on the outside of the wrapper.

FACTORS RETARDING GROWTH OF LARVÆ

Normally the two principal influences which inhibit larval development are low temperature and starvation. The former is discussed in some detail later in this bulletin under "Control measures," and the influences of both are referred to in the consideration of the life cycle (pp. 30-34). Starvation results ordinarily from the desiccation

of food; seldom because of its exhaustion. The usual clustering habit is exhibited on dry food, but in the case of dry meat the food resists the agency which enables the maggots to soften cheese, and the larvæ become quiescent and develop alate margins on account of impoverishment. Under such adverse conditions, however, their hold-on life is extremely tenacious, and even in midsummer they are able to resist starvation for weeks, and when moistened with a few drops of water become active at once.

It is worth while to note that masses of well-grown larvæ, which often congregate in the lower part of culture dishes, give rise to heat. In one case the bottom of a glass dish containing several thousand maggots clustered in a moist mass was found to be 13° warmer than the room temperature of 69° F.

The entire larval stage requires, under optimum conditions, but five days for completion. Unfavorable food and temperature conditions lengthen this period; in one case a starved larva lived for over six months, from October 2 to April 7, after which it pupated and became adult. Pavloski (56) reported that the larvæ have lived confined in a corked test tube without food for eight months, and later pupated.

MIGRATION OF THE MATURE LARVA

It is during migration that the insinuating ability of the skipper and its leaping powers are particularly useful. Like many other dipterous larvæ, the full-fed larva of *Piophilæ casei* is impelled by a strong instinct to leave the food and gain a dry, dark, close location. Of these three specifications, closeness is least important and darkness comes next, whereas dryness and freedom from grease are nearly always matters of necessity. When darkness and dryness are provided, closeness in the form of a tight crevice is sought for in addition. According to the writer's observations, puparia are formed somewhat more readily in darkness than in the light, but in hot weather, even when light was provided without interruption, the rapidity of pupation of both illuminated larvæ and those in darkness was such that the difference between them was negligible.

The behavior of full-grown larvæ which are prevented from leaving the greasy medium in which they developed is of much interest. This situation retards pupation or, if the grease is abundant, prevents it and the larvæ become quiescent. There follows a prolonged period of rest during which the insect literally has nothing to do with the exception, perhaps, of restoring slight metabolic losses by occasional feeding. Cold likewise retards or prevents pupation. At 45° to 50° F. pupation does occur, but slowly and irregularly, and many larvæ do not pupate for weeks. When hundreds of migrant larvæ are placed together in a dry container at room temperatures, the mass of maggots keeps in constant motion from the futile efforts of each individual to skip or crawl away, and this condition likewise retards pupation. When larvæ which are held in greasy or cold locations are removed to favorable surroundings, pupation takes place promptly.

In the case of a certain culture reared by the writer, a number of mature larvæ were confined with their greasy food beyond the normal time for migration. Upon their removal the pupation process was so precipitate that in 35 cases the usual prepupal contraction was

forested by the thickening and hardening of the skins of the larvæ. From these vermiform puparia only one adult emerged. The same circumstances, in which the migrant larva is overtaken by the phenomenon of pupation before it has reached a suitable location, probably account for the occasional puparia which are found in somewhat greasy situations upon pieces of infested meat.

MIGRATION-PUPATION PERIOD

The time which elapses between the end of the feeding period and pupation is very short, often in warm weather only two or three hours. In Table 10 it will be seen that 90 per cent of the migrant larvæ pupated within 48 hours. These larvæ were confined for periods up to 24 hours within a greasy paper wrapper inclosing the meat in which they developed.

TABLE 10.—*Migration-pupation records of mature larvæ of Piophilæ casei at Washington, D. C., in 1921*

Number of days after cessation of feeding	Number of larvæ pupated	Number of days after cessation of feeding	Number of larvæ pupated
1 and 2.....	34,314	10.....	1
3.....	3,053	11.....	2
4.....	129	15.....	1
5.....	40	16.....	1
6.....	17	20.....	1
7.....	9		
8.....	5	Total.....	137,579
9.....	6		

¹ In addition to the 37,579 larvæ which pupated, 229 died without pupating, making a total of 37,808 larvæ used in the experiment. The migration records of these larvæ are given in Table 1.

The numbers of the puparia in Table 10 were estimated by means of a chemical balance, it having been determined by averaging a number of weighed lots that well-nourished larvæ form puparia 230 of which weigh 1 gram. Death without pupation occurred with 0.6 per cent of the larvæ.

MATAMORPHOSIS

PUPATION

Pupation occurs readily in such situations as dry earth, sawdust, cotton, dust in floor cracks, and under boxes and sheets of paper. Frequently migrant larvæ partly or wholly enter empty skipper puparia, where they transform.

Having found a suitable place for pupation the larva contracts in length, principally at each end, and increases slightly in girth, and the skin rapidly changes from waxy white through buff and pink to a rich coppery red. At first the head retains its mobility. Just at this stage the larva, if disturbed, is able to relax and again become active, but in a very short time a point is reached beyond which there is no possibility of reversal of the pupation process.

After the hardening of the skin of the last active stage of the larva, which process forms the puparium, the insect becomes for a brief period a prepupal larva. This is a sac-like transition stage.

THE PUPARIUM

The puparia of *Piophilha casei* vary considerably in size, the largest ones of normal shape measuring about 5 by 1.5 mm. The color of puparia formed by well-nourished larvæ is coppery red, whereas larvæ from dried beef, dry cheese, or old ham form puparia which are smaller and golden yellow. Puparia examined ranged from 2.5 by 0.5 mm. to 6 by 1.25 mm. A gram of puparia from an old ham culture contained 482—more than twice as many as a gram of puparia formed by well-nourished maggots. Bachmann (9) measured the lengths of a number of puparia and arranged the results in a frequency table. The most common length was 5 mm.

The puparia are shown in *c* of Figure 3, at right. They are deeply wrinkled at either end, with fine circumferential lines marking the surface between the intersegmental constrictions. In some puparia the latter are deeply incised, whereas flattened puparia and specimens with alate margins are not uncommon. Puparia formed by larvæ which became wedged between threads of cotton were sometimes so deeply constricted by a tight strand as to be nearly severed—a condition which of course made emergence impossible.

Puparia frequently are attached to the surface upon which they rest by a minute globule, secreted at the larval anus and attaining a resinous appearance by the time the puparium is completely hardened. Threads of cotton (Fig. 6) become glued into this globule, making the disentanglement of puparia from cotton somewhat tedious. In warm, moist weather the brittle consistency of this spot disappears and it may soften enough to stretch into a short thread capable of suspending puparia beneath the point of attachment. With the puparium secured in place by means of the globule, the adult insect is probably materially aided in the struggle to emerge.

THE PUPA

The pupa is inclosed in a thin, white membrane, the skin of the prepupal larva, which lines the horny puparium. The first pigment appears in the eyes, which become pink. As the time for emergence approaches the insect assumes a smoky-gray color. A pupa with part of the puparium is shown in Figure 6.

PUPAL PERIOD

At temperatures of 80 to 90° F., the pupal period occupies a minimum of 5 days. From May 10 to June 7, 1921, no pupal period less than 7 days in length was recorded in the laboratory, most of the adults emerging on the eighth day. On June 8 the first 6-day period was recorded and on the twentieth of that month the first 5-day period. Of 1,923 puparia observed from May 10 to June 19, 250, or 13 per cent, failed to produce adults. Table 11 is a consolidation of data on the pupal period. Temperatures relative to the dates of emergence from May 19 to July 16 are recorded in Table 3.



FIG. 6.—Pupa of *Piophilha casei* with part of the puparium dissected away. $\times 10$. Threads of cotton are shown glued into the resinous globule secreted at the larval anus during the process of puparium formation.

TABLE 11.—Pupal period of *Piophilha casei* at Washington, D. C., in 1921

	Number of days in pupal period								
	5	6	7	8	9	10	11	12	13
Number of flies which emerged from May 10 to June 19, 1921.....	166	543	350	455	145	11	1	1	1
Number of flies which emerged from June 20 to July 16, 1921.....	166	360	29	2	-----	-----	-----	-----	-----

Table 11 shows to what extent hot weather shortens the metamorphosis. The first group, including flies which emerged from May 10 to June 19, experienced moderately warm temperatures, whereas the group of flies which emerged from June 20 to July 16 were exposed to hot weather during their pupal stage. Table 12 includes other pupation data.



FIG. 7.—Adult of *Piophilid caspi* showing appearance during the act of emergence. $\times 10$. Part of the puparium has been removed. The ptilinum is here shown at nearly maximum expansion and the pressure of the body fluids has temporarily greatly increased the size of the head.

EMERGENCE OF ADULT

By vigorous use of the balloonlike ptilinum the insect forces off the dorsal half of the anterior tip of the puparium. This sometimes falls away, but more frequently opens as on a hinge and returns to its normal position after the escape of the fly. Often the dorsal and ventral halves of the anterior end of the puparium are both broken off during the fly's struggle for liberty.

The emerging fly, shown in Figure 7, rapidly becomes darker as its exoskeleton hardens. The use of the ptilinum may be observed when newly emerged flies are trying to escape from a vial plugged with cotton. The organ is greatly expanded, the force of the expanding fluid being such as to affect the whole head, displacing the eyes laterally until their inner margins are separated by an interval greater than the width of the thorax. The insect then uses its legs to push the thorax against its head, in a supreme effort to escape, the process being comparable to the driving of a wedge.

LIFE CYCLE

Table 12 summarizes available information from literature in regard to certain aspects of the biology of the cheese skipper, including facts brought out in this bulletin.

TABLE 12.—Summary of known data on the life history of *Piophilta casei*

	Number of eggs	Incubation period	Larval period	Pupal period	Life cycle	Adult life	Overwintering stage
Redl, 1088 (58, pp. 72-75)	1 256		3 or 4 days	12 days			Pupa.
Swammerdam, 1738 (73, p. 74)				8 to 10 days			Pupa.
Bouché, 1834 (13, p. 99)	3 300			8 to 10 days			Larva.
Taylor, 1861 (75, p. 609)				7 days	28 to 35 days	8 days	
Taschenberg, 1880 (74, pp. 147-153)				10 days	21 days	6 to 14 days	
Kessler, 1883 (58)		4 days	14 days	1½ to 10 days	18 days	7 days	Adult.
Kellong, 1893 (37, pp. 114-115)	3 30	1½ days	7 to 8 days	1½ to 10 days	50 days		
Murtfeldt, 1893 (55)							
Ormerod, 1900 (54, p. 9)							
Howard, 1901 (34, pp. 179-180)							
Alessandrini, 1909 (5)							
Mote, 1914 (51)		23 to 54 hours	14 days	12 days		4 to 10 days	
Ealand, 1915 (20, pp. 244-245)		1½ days	14 to 15 days	10 days			
Berlese, 1917 (11, pp. 118-121)			8 days	12 days			
Fletcher, 1917 (24, p. 94)					11 days		
Bachmann, 1918 (9)	4 85		5 8	6 2			
Sakharov, 1921 (67)	4 84	2 days	20 days	8 days	30 days		Larva and pupa. Larva and a few newly formed pupae.
De Ong, 1922 (18, pp. 401-403)		30 hours to several weeks	8 days to several months	7 days to 5 weeks		7 to 20 days	
Data in present paper	4 480	23 hours 1	5 days 2	5 days 3	12 days 4	39 days 4	As larvae.

1 In ovary.

2 Nearly that number.

3 Average.

4 Maximum.

5 Minimum.

NOTE: Some of the data by other writers were obtained by rearing the insect in cheese, which is inferior to ham as a food for adults and larvae. Temperatures of course differ greatly with locality and season, and vary from year to year. Strictly speaking, therefore, the data given above are not comparable.

Tables 13 and 14 include life-history information recorded at Washington, D. C., in the hot summer of 1921. The temperatures are listed in Table 3.

TABLE 13.—Results of rearing *Piophilta casti* from eggs laid in vials on july ham at Washington, D. C., in 1921

Date eggs were laid	Number of eggs	Minimum period, egg to pupa	Maximum period, egg to pupa	Total puparia	Minimum period, egg to adult	Maximum period, egg to adult
		Days	Days		Days	Days
June 19	95	7	13	90	12
19	43	8	13	13	13
19	78	6	9	72	12
21	93	7	11	65	12
23	47	7	7	11	12
29	22	8	11	16	13
29	30	7	17	25	12
29	128	6	10	33	12
30	68	6	12	68	11
30	31	6	11	31	11
July 20	61	6	8	54	11
21	17	7	10	16	13
21	44	7	9	44	13
22	70	7	15	68	12
23	51	8	10	40	14
Sept. 2	8	8	8	2	13
2	78	6	7	69	12	13
2	72	7	9	72	13	15
2	33	7	8	33	13	14
2	66	7	9	60	13	16
2	73	6	7	71	12	15
3	63	8	11	50	14	18
3	60	7	8	56	13	17
3	63	8	17	59	15	26
3	14	7	8	14	13	15
4	36	6	9	31	14	17
9	54	9	12	30	15	20
9	60	8	13	56	14	21
9	49	8	9	41	15	17
10	51	8	9	54	14	17
10	44	7	8	40	14	18
10	37	8	12	34	15	20
12	23	9	12	20	17	21
12	31	7	8	31	15	17
12	16	10	11	11	18	19
13	19	9	11	15	17	20
16	93	10	15	87	20	26
18	68	9	23	31	19	32
18	52	10	15	52	20	26
Oct. 2	58	12	1151	15	25	164
2	77	13	1187	41	23	208
2	89	14	1108	72	23	146
2	101	12	1164	83	23	179
3	118	6	20	28	11	16
3	67	14	1145	51	25	163
3	78	15	1163	76	25	178
3	83	14	1145	73	25	163
5	65	17	1161	48	27	184
6	53	16	1142	30	26	160

¹ Approximate duration of period in days. Development of these cultures, on account of cool weather, was slow at first, as indicated by the minimum egg-to-pupa periods, and this resulted in the food's becoming dry before the more backward larvæ had become full fed. Fresh food was provided on November 26, and on January 18 more fresh ham was given to the larvæ hatching from the 17 eggs laid on October 2 and to the larvæ hatching from the 78 eggs laid on October 3. No other attention was given except occasional brief soaking in water to separate the starving larvæ from the cavities in the hard meat. This was necessary in order that the numbers present might be recorded.

Results of the foregoing rearing experiments show that the minimum life cycle of the cheese skipper, when provided with juicy ham as food for adults and larvæ, is 12 days, the term "life cycle" being here understood to include the preoviposition period. This brief life cycle is divided about as follows: Preoviposition period, 1 day; incubation period, 1 day; larval stage, 5 days; pupal stage, 5 days. The majority of the insects which are produced in hot weather take

a day or two longer, and it is safe to say that two generations per month represents the normal rate of summer increase at Washington, D. C.

The method of rearing *P. casei* for life-history data is shown in Figure 8. In this vial one day's batch of eggs laid by one female hatched into larvæ which developed on juicy ham, migrated to the cotton and pupated there. The resulting adults died without reproducing on account of the advanced stage of drying reached by the ham at the time they emerged. This species thrives in close confinement.



FIG. 8.—Vial used in studying the life history of *Piophilta casei*, showing dead adult progeny resulting from one day's eggs laid on ham by one female. Pupation occurred in the cotton plug and emergence took place after the food was too dry to permit further reproduction.

INSECTS FOUND ASSOCIATED WITH THE CHEESE SKIPPER

Sakharov (67) has pointed out that the cheese skipper when infesting brine-cured fish has practically no competitors. The same is also true in the case of its favorite food in this country—juicy, newly cured ham. When cured meat becomes older, drier, and rancid, however, various other sarcophagous insects appear and the changes in the food medium gradually render it unfavorable for skipper development. In general, a succession of species (as suggested by Mégnin (47) and Stefani (71) with respect to cadavers) attacks cured meat as changes take place in its composition. The ham beetle (*Necrobia rufipes* DeG.) prefers meat which has been in storage for some time, and the same preference is shown by the larder beetle (*Dermestes lardarius* L.) and certain tyroglyphid mites. Skipper

larvæ in freshly cured meat are sometimes accompanied by maggots of *Lucilia sericata* Meig. (fig. 5, b), and probably other blowflies.

In stores of bones the skipper is usually present, but in such locations the species may be at a disadvantage both because of the condition of the food supply and because of the abundance of a number of other scavengers, several of which are predacious. Skippers in heaps of bones have been found by the writer and

George W. Ellington in company with the species of insects listed below.⁴

COLEOPTERA

Dermestidae: *Dermestes lardarius* L., *D. talpinus* Mann., *D. vulpinus* Fab.,
Trogoderma sp., *Attagenus piccus* Oliv., *Anthrenus* sp.
 Silphidae: *Necrodes surinamensis* Fab.
 Staphylinidae: *Crocophilus macillosus* L.
 Ptinidae: *Plinus brunneus* Duft.
 Tenebrionidae: *Tribolium ferrugineum* Fab., *Tenebrio molitor* L.
 Cucujidae: *Oryzaephilus surinamensis* L.
 Trogostidae: *Tenebroides mauritanicus* L.
 Cleridae: *Necrobia rufipes* DeG., *N. ruficollis* Fab.

DIPTERA

Lucilia sp.

THYSANURA

Lepisma saccharina L.

HYMENOPTERA

Undetermined ants.

EUPLEOPTERA

Anisolabis annulipes Lucas.

Of the foregoing, the cadelle (*Tenebroides mauritanicus*), the two species of *Necrobia*, and the earwig, *Anisolabis*, are predacious, the last three species feeding freely on live skipper larvæ in the laboratory. *Dermestes vulpinus* has predacious tendencies; a half-grown larva was deprived of other food and given migrant skipper larvæ, some of which pupated, but 10 were killed and eaten either as larvæ or pupæ within four days.

CONTROL MEASURES

There are four phases to the practice of control of *Piophilæ casei* as a pest in cured meat: (1) Preventing adult skippers from entering meat storage rooms, (2) preventing infestation of meats stored in rooms to which the flies have access, (3) killing skippers in infested meat, and (4) killing skippers in storage rooms.

PREVENTING THE FLIES FROM ENTERING STORAGE ROOMS

Screening is the best method for keeping the skipper flies out of storage rooms. A number of entomologists have recommended that wire cloth with 20 or 24 meshes per inch should be used for this purpose. Several trials of these sizes were made during the present investigation, and the writer concludes that wire cloth should be at least 30 meshes per inch in order to prevent passage of the flies. Table 15 gives the results of these experiments, in which puparia were placed in glass containers which were then closed with wire cloth and inclosed in a larger container. Flies which escaped through the wire cloth were counted.

⁴The writer is indebted to E. A. Schwarz and A. N. Caudell, of the Bureau of Entomology, for the determination, respectively, of several of the Coleoptera and of the earwig.

TABLE 15.—Results of experiments in confining adults of *Prophila casei* with various sizes of wire cloth

Size of wire	Number of flies	Number escaped	Per cent escaped	Remarks
20-mesh.....	639	183	28.6	Puparia of average size, from ham.
Do.....	856	263	30.7	Do.
24-mesh.....	1,000	1	.1	Puparia of average size, from Roquefort cheese.
Do.....	1,044	188	8.4	Puparia small; from Roquefort cheese.
Do.....	928	11	.1	Puparia average size; from beef ham.
Do.....	1,353	101	7.4	Puparia small; from old ham culture.
30-mesh.....	1,540	0	0	Do.

¹ Including 20 females.² Male.³ Including 11 females

The presence, in the vicinity of stores of cured meats, of skipper-infested bone refuse is undesirable. F. C. Bishopp, in correspondence with the writer, stated that he has advised packers "of the danger of bringing in infested prairie bones and also of storing bones about their premises, especially in proximity to cured-meat storage departments."

PREVENTING INFESTATION OF MEATS IN ROOMS TO WHICH THE FLIES HAVE ACCESS

Most common among the methods of protecting cured meats from infestation when they are hung in rooms to which the flies have access is careful wrapping of the meat. This is done in several similar ways and the wrapping may be followed, as additional protection, by a coating of whitewash or yellow wash.

As directed by Ashbrook, Anthony, and Lund (7, pp. 25, 26), cured meat may be wrapped in heavy paper, inclosed in a muslin sack, and painted with yellow wash composed of 3 pounds of barium sulphate (barite, barytes, or "heavy spar"), 1 ounce of dry glue, 1¼ ounces of chrome yellow (neutral lead chromate), and 6 ounces of flour, for 100 pounds of hams or bacon.

Half fill a pail with water and mix in the flour, breaking up all lumps thoroughly. Mix the chrome yellow in a quart of water in a separate vessel, add the glue and pour both into the flour-and-water mixture. Bring the whole to a boil and add the barium sulphate slowly, stirring constantly. Make the wash the day before it is required. Stir it frequently while using, and apply with a brush.

Cured meat coated with yellow wash, these writers stated, should be hung up, never stacked in a pile. Before it is wrapped, the original string should be removed from each piece of meat and a new string tied tightly around the outside of the package. This is important, because it is impossible to make an insect-proof package if a string passes from the meat through the wrappings.

Special wrappings are often used to protect smoked meats to be shipped to the Tropics. These are of various colors and ingredients. A favorite protection consists of a tough though flexible coating of a black asphaltic preparation applied while warm to carefully wrapped meats.

Hams are sometimes rubbed with black pepper before wrapping. This is said to aid in preventing skipper damage by its drying action on the surface of the meat.

Borax (sodium tetraborate) is applied to the surface of cured meats by many who prepare these products for local or home consumption. This preservative is said to give protection by harden-

ing the surface of cured meats, but its use in meat products subject to the Federal meat inspection law is prohibited except in the case of shipments destined for certain foreign countries.

One of the preventive measures employed by commercial firms is rapid handling of the product; that is, meats are smoked near the retail markets and as far as possible are distributed to the retail trade promptly after the smoking is completed.

It is probable that a screened closet or cage carefully made with 30-mesh wire cloth would prove adequate and satisfactory for use on farms and in retail stores where cured meat is stored for several weeks or months. Such an inclosure would represent an initial expense only, and on farms would give protection without the necessity of wrapping and dipping meat. Screened closets in retail stores observed by the writer have been ineffective because the wire cloth used in their construction was too coarse.

But both where meats are screened and where they are wrapped the efficiency of the methods depends upon their application to hams, shoulders, and bacon which are not infested. Inspection of suspected pieces of meat can not give the assurance that they are free from eggs or larvæ of *P. casei* because the former are small and hidden in crevices by the female fly and the latter burrow so deeply that it is necessary to cut a ham in half before their favorite feeding spots can be examined.

Curing and smoking meats on farms during cool weather when the adult flies are not active is a good way to make certain that meats will not be infested before they are protected by wrappings or screens.

It has been recommended that smoked meats be wrapped and buried in a grain bin (55) or in sawdust or bran (1).

KILLING *P. CASEI* IN INFESTED MEAT

In the control of *P. casei* it would be desirable to be able to kill all insects and eggs in infested meat so that it can be definitely known, before shipping, wrapping, or screening suspected stocks, that they are free from infestation. This is difficult, because of the deep-seated nature of the infestations, the remarkable resistance of the larvæ, and the necessity for avoiding undesirable changes in the meat treated.

Swammerdam (73, p. 65) appreciated the vitality of the maggots, which when put in rain water lived for six or seven days. Curtis (17) decided that fumigation with sulphur was "a very doubtful remedy," and Murtfeldt (53, p. 175) found that this treatment impaired the appearance of sacked hams coated with yellow wash. Smith (70, p. 368) asserted that fumigation with tobacco or pyrethrum did not kill the maggots, although the adults succumbed. Grinnan (29) removed skippers from infested meat by sunning it, a process which, he maintained, brings the maggots to the surface and kills them.

TREATMENT OF LARVÆ WITH CHEMICALS AND WITH RAYS OF SHORT WAVE LENGTH

Extensive experiments with about 70 reagents as skipper larvicides have been made by Alessandrini (4). Chloroform he found to be instantly fatal, and death was speedily caused by immersion for one minute in carbon disulphide. He suggested the possibility of eradicating the pest in cheese factories by the fumes of chloroform, diluted with water for the sake of economy. In his experiments larvæ survived in spring water for 280 hours (nearly 12 days); in paraffin

for 38 hours, in 95 per cent alcohol for 32 hours, and in xylol for 7 hours. Ultraviolet rays (4) completely stopped development, whereas radium emanations merely arrested development in most cases.

Other trials of a like nature were reported in 1909 by Krausse (40), who used as a check for comparison specimens of an ant, *Messor structor* Ltr. His skipper larvæ were alive after 90 minutes in 96 per cent alcohol, after 301 minutes in spring water, and after 1,030 minutes in glycerine, the ants being apparently dead in each liquid after 4 minutes or less. Krausse also found that chloroform caused instant death.

Sakharov (67) found that infested fish may be freed of the larvæ by immersion for from 3 to 5 days in a strong brine solution, and with these results in mind he suggested that the larvæ may be successfully removed from cured meats in the same way. He tried several liquids as larvicides and found that larvæ remain alive in kerosene for 5 hours and in benzene for 10 minutes.

Trials by the writer with some common reagents agreed with the results of Alessandrini, Krausse, and Sakharov in that they show the remarkable resistance of the maggots when exposed to conditions ordinarily considered fatal to insects. However, chloroform did not give instant death. None of the materials tried gives promise of being useful for killing larvæ in meat. The requirements for this work are that the liquid be inexpensive, that it should quickly kill larvæ deep in the meat, and that it should not affect the taste or keeping qualities of the meat. Prolonged soaking, as recommended by Sakharov, or more rapid dipping would be the method used in applying a liquid for this purpose. The materials used in the experiments recorded in Table 16 are obviously unfitted for either of these purposes but the results are included in this bulletin to emphasize the unique hardihood of the maggots of *P. casei*. Following immersion, the larvæ were dried on a blotter and placed in ventilated pill boxes. The results given show that many formed puparia and that some of the pupæ had sufficient vigor to become adults. In several of the trials the skipping power of the maggots returned soon after their removal from the liquids.

TABLE 16.—Results of immersing migrant larvæ of *Piophilæ casei* in various liquids

Liquid used	Duration of immersion		Total larvæ used	Condition of larvæ 24 hours after removal from liquids to pill boxes			Remarks
	Hrs.	Min.		Dead larvæ	Live larvæ	Pu-paria	
Gasoline.....		30	13	0	12	1	No locomotion; slight movement.
Do.....			14	0	8	6	2 larvæ able to make some progress.
Do.....	1	30	15	1	10	4	6 larvæ able to make some progress.
Do.....	2		14	0	9	5	5 larvæ able to make some progress; 1 larva able to skip.
Do.....	3	15	13	1	11	1	3 larvæ able to make some progress.
Do.....	24		11	11	0	0	
Chloroform.....		1/6	9	2	7	0	
Do.....		1	8	2	4	2	
Carbon disulphide.....		1/2	5	0	5	0	
Do.....		1	12	2	10	0	
Do.....	24		9	9	0	0	
Carbon tetrachloride.....		20	14	5	3	6	
Ether.....		5	11	5	3	3	
Ethyl acetate.....		12	12	2	1	9	
Ammonia (concentrated solution).....		34	15	2	3	10	3 of the larvæ skipping.

TABLE 16.—Results of immersing migrant larvæ of *Piophilæ casei* in various liquids—Continued

Liquid used	Duration of immersion		Conditions found in pill boxes after all emergence had been completed. All insects dead		
			Adults	Puparia	Larvæ
	Hrs.	Min.			
Gasoline.....		30	2	10	1
Do.....	1		8	4	2
Do.....	1	30	9	4	2
Do.....	2		8	4	2
Do.....	3	15	1	4	8
Do.....	24		0	0	11
Chloroform.....		½	5	0	4
Do.....		1	2	2	4
Carbon disulphide.....		½	5	0	0
Do.....		1	1	6	5
Do.....	24		0	0	9
Carbon tetrachloride.....		20	4	3	7
Ether.....		5	5	1	5
Ethyl acetate.....		12	3	4	5
Ammonia (concentrated solution).....		34	6	7	2

The remarkable resistance of these maggots is attributed by Alessandrini (4) to (1) the nature of the cuticle, (2) the closure of the spiracles, (3) the amount of air held in the body and the diminished consumption of oxygen due to the immobility which they usually assume shortly after immersion, (4) the large quantity of reserve food in their bodies. Crawford (15) has furnished an interesting account of similar resistance by the larvæ of the ephydrid fly *Psilopa petrolei* Coq., which inhabit pools of crude petroleum.

LOW-TEMPERATURE EXPERIMENTS

Cold storage of meat is, of course, a reliable preventive of infestation, and the writer's experiments indicate that cold will kill all stages. The results of the low-temperature trials were irregular, but it is certain that speedy killing effects with cold-storage temperatures not well below freezing can not be expected. In the earliest known reference to this species (1567) Olaus Magnus (46, p. 812) referred to the resistance of the larvæ to cold. Murtfeldt (53, p. 174) asserted that "severe and protracted cold" kills all stages, and Sakharov (67) found that activity ceases at 8° C. (46.4° F.) and that the lowest temperature at which reproduction takes place is 13° C. (55.4° F.). The latter reported that larvæ survived -22° C. (-7° F.) for two weeks.

Oviposition trials in the laboratory resulted in the deposition of eggs by flies exposed to artificial temperatures which ranged from 56 to 62° F.

The experiments which follow show the ability of *P. casei* to resist cold.

In an ice refrigerator at 48 to 50° F.—The growth of the larvæ is suspended by temperatures of from 48 to 50° F., but under these conditions some migrant larvæ are able to pupate, and many of these pupæ produce adults and pupation is prolonged by several weeks. Eggs are not laid at these temperatures, and eggs placed in the refrigerator do not hatch. Adults are feebly active. In the case of 15 newly emerged adults placed in the refrigerator deaths began on

the sixteenth day and ended on the thirty-third day. Thirty other adults showed the first mortality on the thirteenth day and the last on the twenty-eighth day. Fifty newly formed puparia kept in the refrigerator at this temperature produced the first of 42 adults on the thirty-eighth day and the last on the forty-fifth day.

Of migrant larvæ placed in a Petri dish in the refrigerator at 48 to 50° F. on September 17, 15 were still alive on February 11, 13 were alive March 15, and 1 was alive April 17 after seven months' refrigeration. Another lot of larvæ was placed on dry sifted earth in a Petri dish October 17. A brief rise in temperature April 9 gave some an opportunity to pupate, but one was still in the larval stage May 8. Two adults emerged after June 13, showing that the insect survived at this temperature for eight months. In another test, begun January 14, in which several hundred larvæ which had been developing in a poor culture for about a month were used, 8 or 10 live adults were observed August 15.

Experiments with migrant larvæ in a refrigerator show that the duration of this stage of the insect may be considerably lengthened by certain manipulations. After such larvæ have been confined for several weeks at about 48° F., their shrunken appearance indicates that they have undergone metabolic losses, and this is further shown by the readiness with which they begin feeding again when placed on juicy ham. In a day or so the maggots again become full fed, whereupon they migrate a second time. If they are then collected at once and replaced in the refrigerator, the process may be continued, probably over a long period if the temperature is always kept low enough to prevent most of them from pupating.

In a sulphur dioxide refrigerating machine at about 32° F.—Mature puparia were exposed in a sulphur dioxide refrigerating machine at 32° F. on March 15, after having been in the ice refrigerator since March 2 at from 48 to 50° F. A sample of these puparia was removed June 3, and emergence resulted after exposure to room temperatures. This pupal period was therefore three months.

About 50 adults were exposed on February 16, having been taken from a temperature of 51° F. One of these survived until after March 15, a period of one month. In another lot of 98 flies, one survived 33 days and one lived 37 days.

Full-grown larvæ at 32° F. do not pupate. After removal to room temperatures, following refrigeration for periods up to nearly three months, puparia were formed which produced adults.

Half-grown larvæ, removed to 32° F. from a temperature of 86°, were all dead after six weeks; in another lot, with the same history, three were alive after six weeks.

Eggs refrigerated at 32° F. for periods up to two weeks hatched with hardly an exception after removal to favorable temperatures. In this test newly emerged and newly mated pairs were allowed to oviposit on ham and then the adults and eggs were placed in refrigeration. Upon removal, after progressively longer periods of exposure to cold, the adults were given favorable food and temperatures. The females which were subjected to this degree of cold for periods up to and including 10 days resumed the deposition of fertile eggs.

Eggs exposed to 32° F. for one month failed to hatch.

In an ammonia refrigerating machine at 0, 5, 10, and 15° F.—Table 17 gives results of a few experiments in an ammonia refrigerating machine at temperatures considerably below freezing. The larvæ which were able to survive the cold for periods of 44 hours or more were less than half grown; all maggots of other sizes were killed. It is interesting to note that these larvæ survived low temperatures for periods greatly in excess of the exposures which killed all stages of a variety of other species of stored-product insects which have been tested with the ammonia machines.

TABLE 17.—Results of exposing adults, pupæ, and mixed sizes of larvæ of *Piophilæ casei* to low temperatures

Stage	0° F.	5° F.	10° F.	15° F.	Results
	Hrs.	Hrs.	Hrs.	Hrs.	
Pupæ.....	16½				All dead.
Larvæ.....		16½	16½		Not all dead.
Pupæ.....		16½	16½		Do.
Adults.....		16½	16½		All dead.
Larvæ.....		24	24		Do.
Pupæ.....		24	24		Not all dead.
Adults.....		24	24		All dead.
Larvæ.....			41		Do.
Do.....		41			Not all dead.
Do.....		44	44		Do. ¹
Do.....		64½		208½	Do. ¹

¹ Of mixed sizes of larvæ subjected to these exposures, only specimens less than half grown survived.

A large number of full-grown larvæ were placed in an outdoor fumigating box on December 16, 1922. On February 27, 1923, several hundred were removed to room temperatures and all of them became active after about 15 minutes, and subsequently developed into adults which laid fertile eggs.

EFFECT OF HIGH TEMPERATURES

Except for the statement of Grinnan (29) that he was accustomed to place infested meat in the sun to kill the skippers in it, and a record by Alessandrini (4) that 55° C. (131° F.) was fatal in two minutes, there is no published mention of the use of heat as a control measure. At a small abattoir near Washington the resmoking of infested meat was tried with some success several years ago, but as this involves considerable labor in handling the meat, the writer attempted to raise the temperature of the meat as it hung in the storage room. The results were negative. After several hours the kerosene heaters, as expected, so exhausted the oxygen of the compartment that they were extinguished, and sufficient ventilation to allow them to burn freely kept the temperature from rapidly reaching the required point. It is possible, however, that under certain conditions steam heat may be used effectively. When the kerosene stoves were used—and their use to produce high temperatures is not safe—the reading of the thermometer at the floor, which was about 68° F. at the start was 98.5° after 15 hours of constantly rising temperature; halfway up to the ceiling it was 115°, and at the ceiling, 132°—a difference of 33.5° between floor and ceiling in a room 7 feet 6 inches high. The floor was of concrete and the walls and

ceiling plastered. Since the meat was suspended at all levels in the room, it would appear necessary to use a fan to obtain a more even distribution of heat.

The rapidity with which heat from heated air penetrates cured meat was the subject of a test in an electric oven. An 8-pound shoulder, old and rather dry, was placed in the oven at 8.35 a. m. Table 18 shows the temperatures during the test. The temperature of the room from which the shoulder was taken was 72° F.

TABLE 18.—Data showing details of results of heating an 8-pound shoulder in an oven

Time	Temperature of oven	Temperature of surface of meat	Temperature of center of meat	Remarks
	° F.	° F.	° F.	
8.35 a. m.	124	-----	-----	
9 a. m.	128	-----	-----	
9.45 a. m.	130	-----	-----	
10.23 a. m.	128	-----	-----	
11 a. m.	130	-----	-----	
12 noon	128	-----	107.6	4 adults of <i>Necrobia rufipes</i> and 2 larvæ active on meat. 2 adults of <i>Necrobia rufipes</i> active on meat.
12.40 p. m.	132	122	110.3	
1.05 p. m.	130	122.9	113.0	
2 p. m.	132	125.6	116.6	
2.40 p. m.	130	125.6	120.2	
3.15 p. m.	130	126.5	121.1	Several dead larvæ of <i>N. rufipes</i> on meat.
3.45 p. m.	130	126.5	123.8	
7 p. m.	136	131	128.3	

High temperature in an incubator.—Experiments with the exposure of adults and larvæ to high temperatures in a water-jacketed electric incubator were not satisfactory. When Petri dishes and cotton-plugged vials were used, the exact temperatures to which the larvæ and adults were subjected were not known, especially in the case of short exposures. The time required for the air in a stoppered 20 by 100 millimeter vial to reach oven temperature was found to be considerable. A vial removed from a room temperature of 78° F. was fitted with a thermometer passing through the tight cotton plug, the bulb being suspended in the center of the vial. This was put in the incubator where the air was 120° and a period of 30 minutes was required for the air in the vial to become heated to 118°.

In general, it is apparent that adults are killed or seriously paralyzed when confined at 120° F. for half an hour. Migrant larvæ were still active after 22 hours' exposure to 110 to 112°; they were able to skip following 69 minutes in a temperature of 120°; others formed puparia after being heated for three hours at 118 to 122°; some recovered after four hours at 122 to 124°; and larvæ became active after 40 minutes at 126 to 128° F. After allowing a liberal margin for slow heat transference, it is evident that migrant larvæ of the cheese skipper are resistant to dry air temperatures up to 124° for exposures of several hours.

Since so little is known as to the shrinkage or possible injury to infested smoked meats heated to temperatures and for lengths of time which would be larvicidal and at the same time practical to use, the writer does not recommend the use of dry heat to kill skippers in smoked meats.

High temperature in hot water.—It is possible to assemble accurate information regarding the resistance of migrant larvæ of *Piophilæ casei* to heat by immersing them in hot water. In experiments of this kind the only apparent variable is the heat, which can be closely regulated and which reaches the larvæ without passing any insulating barrier such as is present when maggots are exposed in vials to hot air. In Figure 9 the results of a number of trials with migrant larvæ are plotted. The position of the dots (fatal immersions) and circles (immersions not fatal 24 hours after removal from the water) defines the approximate location of a mortality curve for this species.

Each test shown in Figure 11 was made by holding about 10 larvæ in a coarse strainer immersed in several gallons of water. Inasmuch as immersion in water of room temperatures has no effect on the

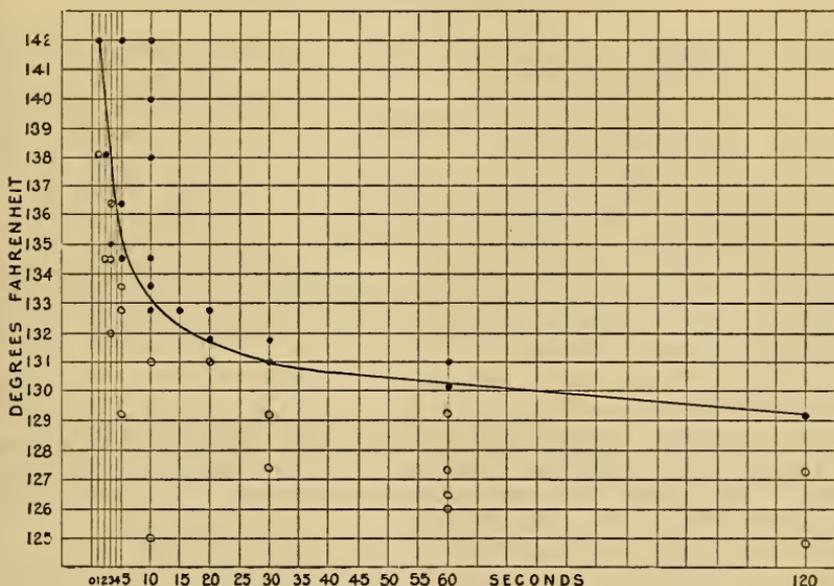


FIG. 9.—Mortality curve for migrant larvæ of *Piophilæ casei* immersed in hot water. The dots represent experiments in which all were dead 24 hours after immersion; the circles indicate trials which resulted in either continued activity or metamorphosis at the end of 16 days; the tests which were not fatal after 24 hours but which showed 100 per cent mortality after 16 days are shown as circles crossed by a diagonal line

larvæ even if continued for two or three hours, the drowning action of the water in the tests is not considered to be the primary cause of death.

Hot water transfers heat to meat more rapidly than does hot air, but in attempting its use as a skipper larvicide two possibilities must be guarded against—leaching the meat and cooking it. The temperature should be high enough to provide for a brief though fatal period of immersion, yet not so high as to produce a noticeable cooking effect.

According to information compiled by the meat inspection division of the Bureau of Animal Industry, commercially cooked hams are not usually boiled but are cooked at temperatures as low as 155° F., a temperature of about 170° being commonly used. It is evident, then, that the maximum useful temperature for killing skippers in

smoked meats which are to be stored uncooked is rather low, probably less than 150°.

Trials by the writer with shoulder butts weighing about 2 pounds each show clearly that the period of hot-water immersion necessary to heat the center of even small pieces of meat to a lethal temperature would be impracticably long, even with water temperatures which would result in some cooking. With protracted hot-water immersion there would not only be danger of leaching the meat but the attention required to keep the temperature nearly constant would be so considerable that the method does not seem to be applicable.

Dipping cured meats in boiling water will not reach maggots buried in the tissues unless immersion continues long enough to cook the surface.

FUMIGATION WITH HYDROCYANIC-ACID GAS

In the summer of 1920, E. A. Back, in charge of stored product insect investigations, Bureau of Entomology, in cooperation with R. H. Kerr, in charge of laboratories, meat inspection division, Bureau of Animal Industry, undertook some experiments with hydrocyanic-acid gas against *P. casei* in cured meats. The unpublished results of the analyses of fumigated meat, made under Kerr's direction, showed that acid taken up by the meat during fumigation was very rapidly dissipated when exposure to the gas was discontinued, and that none of the acid was retained. Following these experiments, the Bureau of Animal Industry authorized the use of hydrocyanic-acid gas for fumigating meats in establishments subject to Federal regulation (78).

Griffin and Back (28) subsequently published analyses of cured meats which had been fumigated with the gas, using a dosage of 1 ounce of sodium cyanide per 100 cubic feet. These results showed that some of the acid was absorbed and that small quantities were retained for several days, but no conclusions were drawn regarding the safety of such fumigated meats for use as human food.

The writer has used this method of treating infested cured meats, usually with dosages of about 2 ounces of sodium cyanide for each 100 cubic feet of space. No ill effects have been experienced from the consumption of meats thus fumigated, which were largely disposed of by sale to employees of the Bureau of Animal Industry in Washington. The safe use of such fumigated meats probably depends upon airing them for several days after exposure to the gas and upon the fact that they are cooked before being consumed.

Hydrocyanic-acid gas, used as stated above, causes very high mortality among skipper maggots, but a dosage of 2 ounces of sodium cyanide per 100 cubic feet is not always to be depended upon to kill all of those which are deep in the tissues of meat. On one occasion about 25 hams and shoulders were examined after having been exposed to the gas from Saturday afternoon to Monday morning. Hundreds of skippers had crawled to the surface of the meat and died there, and small heaps of dead maggots had accumulated on the floor beneath some of the heaviest infestations, but inspection revealed live larvæ in nearly all of the pieces of meat.

Eggs exposed at 70 to 80° F. to a dosage of 1 ounce of sodium cyanide per 100 cubic feet for 24 hours were all killed. Adults,

pupæ, and unprotected larvæ have been killed by exposure to the same dosage for 23 hours, during which period the temperature fell from 65 to 55° F.

Any process used for killing skipper maggots in cured meats should of course be followed by cutting out infested parts.

KILLING *PIOPHILA CASEI* IN INFESTED ROOMS

According to Murtfeldt (53, pp. 174-175) the fumes of burning sulphur or pyrethrum powder kill the adults. One firm with which she corresponded whitewashed infested rooms after fumigation, using carbolic acid in the whitewash. Howard (32, p. 104) suggested that infested places be washed with kerosene emulsion, special attention being given to the cracks. Burning sulphur or pyrethrum on live coals kills the flies if rooms are kept closed for from 8 to 24 hours (Smith, 70, p. 368), but as this does not kill the maggots it should be repeated. Smith also believed that carbon disulphide could be used with good effect.

Surface (72, pp. 21, 24) suggested that badly infested rooms be fumigated with hydrocyanic-acid gas, and Herrick (31, p. 292) directed that such rooms be washed with kerosene oil.

The writer found that strong dosages of pyrethrum powder or of pyrethrum smoke almost completely paralyzed the adults after 10 to 15 minutes, and that death followed in about 2 days. Measurements of the dosages used were not attempted. Migrant larvæ were placed in a mass of pyrethrum powder which was taken from a freshly opened air-tight bottle, and 2 days later 22 of the 29 larvæ had pupated in the powder. Eighteen of these puparia produced adults.

Carbon disulphide, at the rate of 1 pound per 100 cubic feet for 20 hours, was tested as an insecticide for all stages. The temperature was about 75° F. and the relative humidity ranged from 86 to 98 per cent. Some of the larvæ (migrants) were not killed, but there was no emergence from the puparia exposed to the gas. No progeny developed from the eggs, and the adults were all killed.

The vapor of carbon disulphide is inflammable and highly explosive when mixed with air in certain proportions. There must be no fire, or sparks of any kind, where fumigation is being carried on.

Sulphur fumigation has been extensively used in the past for the control of various insects, but it has now been largely superseded by other fumigants, chiefly on account of its strong bleaching and tarnishing action in the presence of moisture and its harmful effects on growing plants and on the germinating power of grain. Records of the use of this fumigant against insects indicate that the method has generally been effective. Although sulphur fumigation tests with *P. casei* were not made in this investigation, it is probable that strong fumes are fatal to this species except when the larvæ are imbedded in the tissues of meat. In tight compartments an effective concentration of the gases from burning sulphur appears to be obtained by the use of about 3 pounds of stick sulphur per 1,000 cubic feet of space, with exposure for 24 hours.

The most reliable method of treating infested rooms is thorough sweeping followed by fumigation for 24 hours with hydrocyanic-

acid gas, using at least 2 ounces of sodium cyanide per 100 cubic feet.

Since hydrocyanic-acid gas is very poisonous to human beings when it is inhaled, its use in occupied buildings or in locations where the gas may leak through into adjoining occupied buildings should not be attempted. Only careful persons thoroughly informed as to the proper methods of procedure should undertake to generate this gas. After fumigation, rooms must be thoroughly ventilated before being entered.

On account of the uncertainty which attends attempts to kill all the maggots that are deep in the tissues of infested meats, it is suggested that infested stocks be removed from storage spaces from which it is desired to eradicate the insect.

NATURAL ENEMIES

Indefinite reference to a parasite of *Piophilæ casei* was made by Swammerdam (73, p. 69), Taylor (75, p. 609), and Fletcher (24, p. 94). In the summer of 1921 the writer reared from pupæ of the cheese skipper numbers of a pteromalid parasite (Hymenoptera), identified by A. B. Gahan of the Bureau of Entomology as *Pachycrepoides dubius* Ashmead. Records of the distribution of this parasite include Illinois, the Philippine Islands, Hawaii (introduced), Canada, and eastern Australia. It is an enemy of a number of Diptera, notably the house fly (*Musca domestica* L.). In Hawaii, where it is also a parasite of the Mediterranean fruit fly (*Ceratitis capitata* Wied.), it has been introduced from the Philippines, propagated, and liberated as a parasite of the horn fly (*Haematobia irritans* L.), and in 1910 it was reared in Canada from a breeding jar containing the puparia of the cabbage root maggot (*Hylemyia brassicae* Bouché). In Australia it parasitizes various sheep-maggot flies. The records do not indicate ability on the part of *P. dubius* to make an important contribution to the control of any of its hosts, and there is small probability that it will ever be of much assistance in the control of the cheese skipper.

In the laboratory in the summer of 1921 a minimum period of 16 days elapsed between the exposure of skipper puparia to oviposition by *P. dubius* and the emergence of adult parasites. As a rule only one parasite developed in each puparium, but three puparia produced two parasites each. Three females, which emerged September 9 and reproduced, and which were not fed, lived respectively 9, 9, and 13 days.

Several insect associates of *P. casei* prey upon it. Chief among these is the clerid beetle *Necrobia rufipes* DeG. (the ham beetle), which is predacious both as adult and larva. Young larvæ of *N. rufipes* are unable to kill migrant skippers, but vigorous migrant skipper maggots are readily killed by larger larvæ of this beetle, and in rearing experiments with the latter skippers have been found to be the best food for larvæ and adults. Table 19 shows the predacity of this beetle, which is also cannibalistic. In the laboratory, colonies of skippers to which these beetles had access were observed to be rapidly depleted. Adult ham beetles also have eaten skipper eggs, dead adults, and puparia.

TABLE 19.—Results of exposure of migrant larvæ of *Piophilæ casei* to larvæ and adults of *Necrobia rufipes*

Number of <i>P. casei</i> larvæ exposed	Number of <i>N. rufipes</i> used	Stage of <i>N. rufipes</i> used	Predacity record after 24 hours
			<i>Per cent</i>
20	4	Full-grown larvæ.....	0
20	2do.....	0
20	4do.....	6
20	2do.....	40
20	3	Half-grown larvæ.....	55
20	3do.....	70
20	2	Adults.....	45
20	4do.....	85
20	2do.....	50
20	4do.....	75
20	9	Adults.....	60
20	3	Full-grown larvæ.....	100
20	9	Adults.....	100
20	3	Full-grown larvæ.....	90
20	12	Adults.....	90
	6	Half-grown larvæ.....	

Adults of *Necrobia ruficollis* Fab., sometimes found in material infested with *P. casei*, are also actively predatory upon these maggot. *Pediculoides ventricosus* Newp., a widespread predacious mite, rarely kills the larvæ and flies.

SMOKEHOUSE CONDITIONS

A variety of types of smokehouses are in use, ranging from chambers the size of a barrel, through the usual wooden or masonry farm smokehouse, to the improved apparatus used by the larger packers (3, pp. 98-102). Some of the improvements in the last class include automatic temperature control, auxiliary heat supply from steam pipes, and gas fuel for burning the smoking sawdust. Some smoke chambers are arranged for continuous operation, the meat being carried up and down during the smoking on a chain conveyor and removed while hot to the hanging room as soon as sufficiently smoked.

The duration of smoking varies from a minimum of about 24 hours for sweet-pickle hams prepared for a market which desires meat with a high water content, to light, intermittent smoking for five or six weeks as in the preparation of Smithfield hams. The best smoking temperature is about 120° F., but as a usual thing there is considerable variation from an even, optimum heat.

The time during which cured meats remain in the smokehouse may be divided for purposes of discussion into two parts. The first period, in which the danger of infestation is comparatively small, begins when the meat, wet from soaking and washing following cure, is hung in the smokehouse to dry, and ends when the heat of the fire drops for the last time below 100° F. The second period, during which, in warm weather, infestation is certain in localities where skippers are found, begins when the first period ends and lasts until the meat is removed from the smokehouse.

After having been washed and hung in the smokehouse, meats need to dry about three hours before the fire is lighted. In view of the fact that dry-salt pork (unsmoked) is sometimes infested, it is

very probable that eggs are occasionally laid on cured meat while it is drying in the smokehouse. There follows the question as to whether any eggs so laid, or laid in times of favorable temperatures during intermittent smoking, can survive the subsequent high temperatures, heavy concentration of smoke, and smothering effect of melted fat. Nothing very definite can be said with respect to this point, principally on account of the lack of uniformity in the degree and duration of the heat produced. In some cases (fig. 10), the heat would be expected to kill any adults, eggs, or young larvæ which might be present.

Throughout the warm months it is clearly apparent that one of the most important flaws in our defense against skipper infestation consists in the commonly unprotected condition of smoked meat dur-

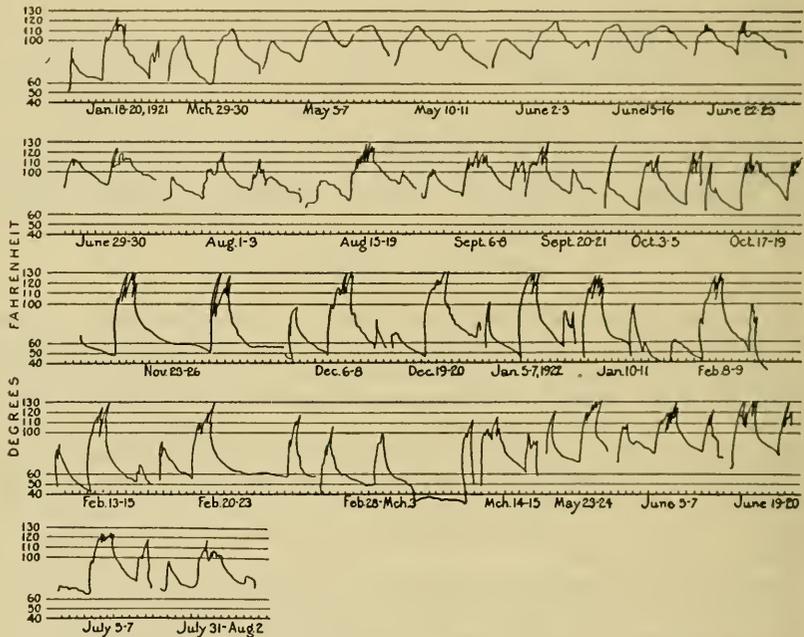


FIG. 10.—Reproductions of thermograph records of smokehouse temperatures. The scale marked on the 40-degree line measures 4-hour intervals

ing the second part of its stay in the smokehouse. From the time the heat drops below 100° F. for the last time until the meat is removed from the smokehouse there is a period of temperatures favorable to egg laying. The above diagram (fig. 10) gives a number of smokehouse records⁵, with the approximate range of reproductive temperatures shown by the wide interval between 60 and 100° F.

As shown in this diagram, there was usually abundant opportunity, so far as temperatures were concerned, for the flies to oviposit

⁵ Pantograph copies of thermograph records obtained through the interest and courtesy of E. Z. Russell, in charge of swine investigations, Animal Husbandry Division, Bureau of Animal Industry. The writer is also indebted to K. F. Warner, of the swine investigations, and to G. A. Anthony, inspector, Washington Center Market, Bureau of Agricultural Economics, for valuable cooperation in many ways.

on the meat after the last record of a temperature of 100° F.; that is, during the second period. But the ends of these records did not always coincide with the removal of the meat from the smokehouse; the thermograph was frequently taken from the smokehouse hours before the meat was removed.

Wilder and Davis (79, p. 366) directed that the fire should be put out when the smoking is completed, the house opened up, and the meats allowed to cool. These writers realized, however, the danger of exposing meats in unprotected smokehouses, and recommended (p. 371) that the windows and doors be finely screened, and that smokehouses should be regularly fumigated with sulphur.

While smoked meats are cooling off in the smokehouse, they are not only at maximum attractiveness for skipper flies but also readily accessible to the flies when unscreened doors, windows, or ventilators are left open. The writer has observed skipper flies upon meats in the smokehouse at this stage, and recommends that the houses be of tight construction and thoroughly screened with wire cloth of at least 30 meshes per inch.

SUMMARY AND CONCLUSIONS

Piophilæ casei (L.), a piophilid fly commonly known in its larval or maggot stage as the cheese skipper and ham skipper, and by other popular names, is widely distributed throughout the world. In the United States it is the chief insect pest in smoked, cured pork, and cheese. It is able to nourish itself in dried beef, salt pork, cured fish, and a variety of inedible animal products.

Medical literature contains records of myiasis caused by the presence of skipper larvæ in the intestines, a condition which probably not infrequently results from the custom of eating infested cheese. There are several published accounts of the presence of this species in exposed human corpses and its remains have been found in graves.

The characteristic injury done to cured hams and shoulders consists of eaten-out areas among the large muscles, and these extend to the center of the meat, close to the bones. Very fat meat, such as bacon, is not extensively injured; the insect prefers connective and muscular tissue.

The adult is a very active, small, tame, shining black fly somewhat resembling a winged ant. It feeds principally on the juices of the larval food, and liquid or semiliquid food is a prerequisite to normal oviposition.

Fertile eggs are laid as soon as 10½ hours after the act of mating, the latter often taking place a few minutes after the female leaves the puparium. Unmated females deposit infertile eggs. The eggs are rapidly scattered about over the surface of the meat or masses of them are concealed in crevices. The maximum number of eggs laid by one female is nearly 500, but the usual number is about 140, laid over a period of three or four days.

Flies kept at low temperatures (48 to 50° F.) may live for more than a month. During hot weather (80 to 90° F.) the usual length of life is three or four days if food and water are not provided. When flies are unfed the females live longer than the males; the

reverse is true when they are fed and mated. In midsummer males in breeding vials lived an average of 8.5 days and females 5.1 days.

Male flies are slightly more numerous than females and they usually require less time for metamorphosis. Both sexes are attracted to light, but this stimulus is not a dominant one in the presence of food odors.

The eggs hatch in about 24 hours at 80 to 90° F. and the larva cluster together for feeding. There appear to be three larval instars. All stages of the larvæ are repelled by light.

After the completion of feeding the full-grown larva leaves its food and seeks a dark, dry spot for pupation. The larval and pupal stages are each five days long in hot weather (80 to 90° F.) when fed on juicy ham. The life cycle occupies a minimum of 12 days, and at Washington the average rapidity of summer increase is two generations per month. The range of temperatures at which reproduction takes place is approximately 56 to 102° F.

Control suggestions come principally under four heads:

1. Preventing adults from entering storage rooms. This may be accomplished by careful screening with 30-mesh wire cloth and by using care that flies do not enter when the doors are opened.

2. Preventing infestation of meats in rooms to which the flies have access. The usual method consists of wrapping each piece of meat in paper and inclosing the whole in a tight cloth sack, often with a coating of yellow wash as additional protection. On farms and in retail stores a closet or cage with sides of 30-mesh wire cloth should be provided for the storage of cured meat. On farms, such a cage would render wrappings, sacks, and washes unnecessary. The prevention of infestation is the essence of skipper control.

3. Killing *Piophilæ casei* in infested meats. The maggots are very difficult to kill, especially when they are feeding in the moist interior of pieces of meat. They are able to withstand extremes of temperatures, starvation, and immersion in water and other liquids for periods which would be fatal to most insect larvæ. Hydrocyanic-acid gas fumigation causes heavy mortality among skippers in meat, but even strong dosages are not certain to kill them all. Inspection of suspected hams and shoulders can not be relied upon to disclose either the minute, concealed eggs or all of the deep-seated feeding larvæ.

4. Killing *Piophilæ casei* in infested rooms. To kill all stages nothing is better than strong dosages of hydrocyanic-acid gas (2 ounces of sodium cyanide per 100 cubic feet) applied for 24 hours.

On account of the large number of skippers which may be produced by a single piece of meat, it is advisable to destroy promptly all infested meat which can not be reconditioned by trimming. Supplies of bones should not be allowed to accumulate near stores of smoked meats.

Where curing and smoking operations are confined to the winter months, in parts of the country where the temperatures are below the minimum reproductive temperature of the skipper (about 56° F.) the danger of early infestation is avoided.

Smokehouses should be well screened. Meats stored in a well-screened farm smokehouse should require no further protection of any kind.

The biology of *Piophilha casei* reveals no excuse for neglecting, during the skipper-fly season, to protect cured meats with fine screens, glass cases, or low temperatures from the time they leave the curing vats until they are either wrapped or rapidly carried through trade channels to the consumer. There may be economic reasons for avoiding the expense of protection, and in each case the risk of loss through skippers should be balanced against the cost of preventing such damage.

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About 170 references to *Piophilha casei* are to be found in the literature of entomology. A few more than half are omitted from the following pages because they largely duplicate previously published data.

Illustrations of the insect which are especially worthy of note are to be found in papers by Alessandrini (5), Banks (10), Dufour (19), Mote (51), Sakharov (67), and Swammerdam (73, pp. 63-75).

The principal contributions to the biology and control include: Alessandrini (4, 5), Bachmann (9), De Ong and Roadhouse (18), Howard (32), Kellogg (37, pp. 114-115), Kessler (38), Krausse (40), Mote (51), Murtfeldt (53), Ormerod (54), Redi (58), Sakharov (67), Swammerdam (73), Willard (80), and Wille (81).

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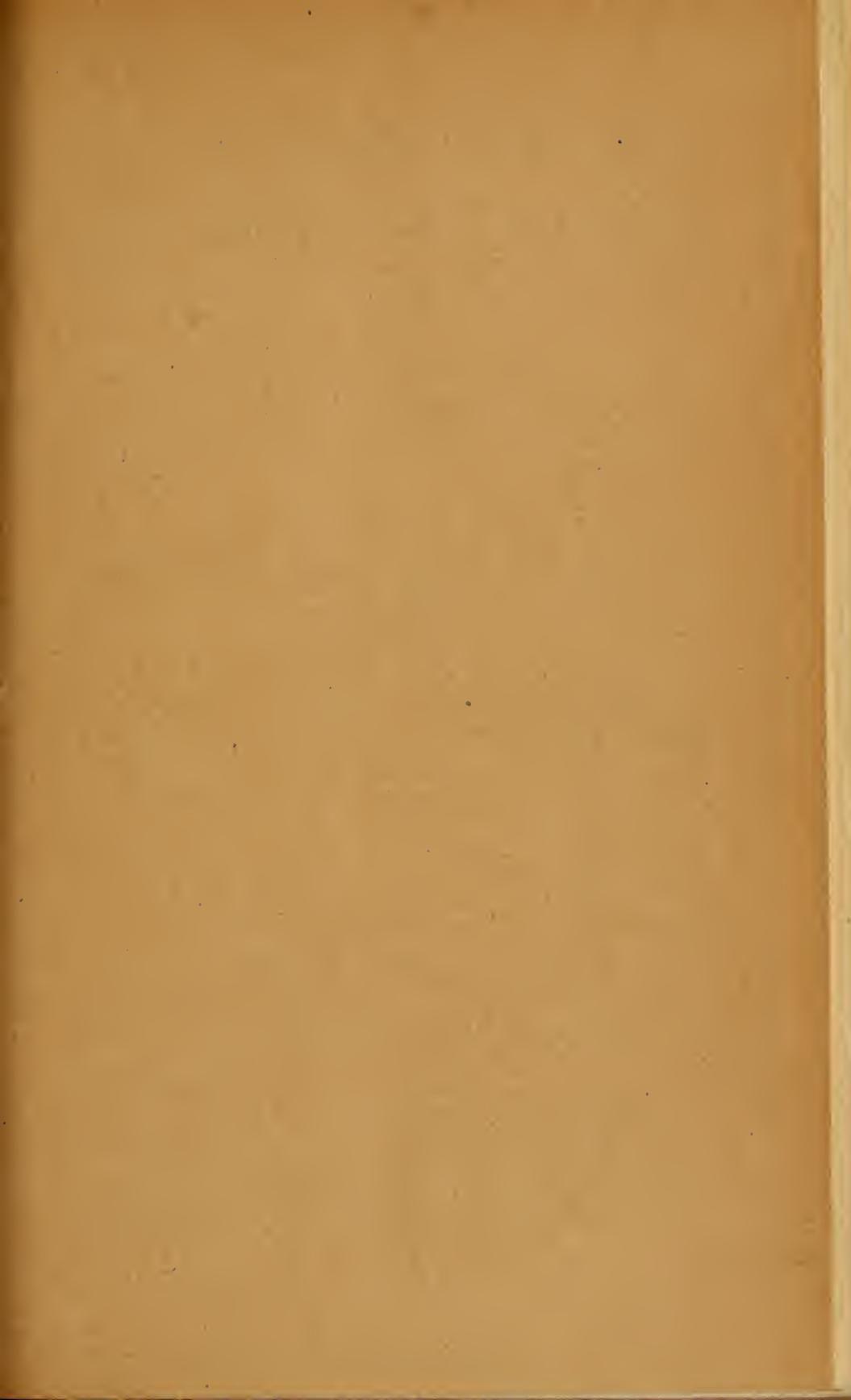
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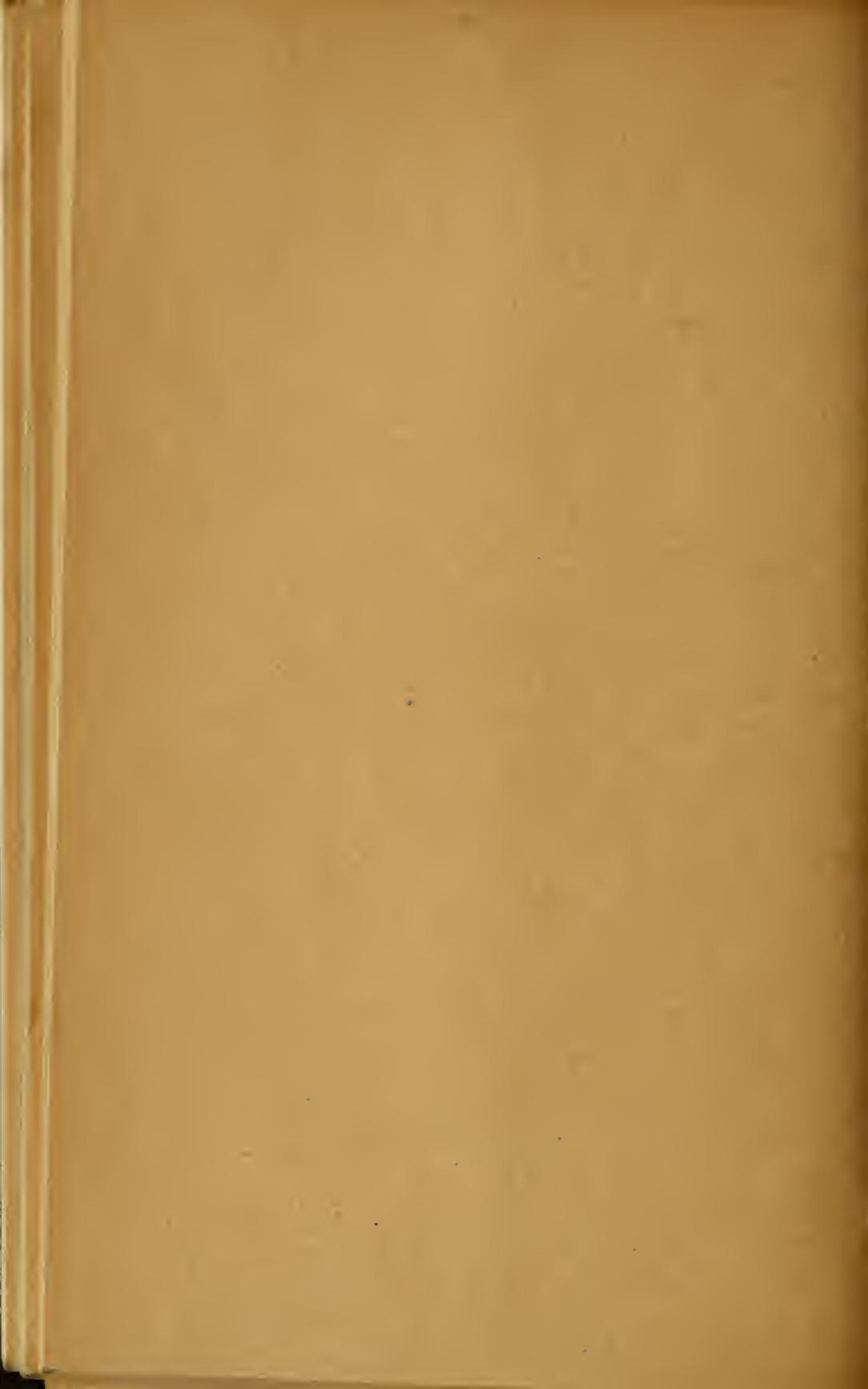
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UNITED STATES DEPARTMENT OF AGRICULTURE



DEPARTMENT BULLETIN No. 1469



Washington, D. C.

February, 1927

THE SATIN MOTH, A RECENTLY INTRODUCED PEST

By A. F. BURGESS, *Senior Entomologist, in Charge*, and S. S. CROSSMAN, *Entomologist, Gipsy Moth and Brown-Tail Moth Investigations, Bureau of Entomology*¹

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INTRODUCTION

On June 22, 1920, H. N. Habberley, at that time superintendent of the Middlesex Fells Reservation of the Metropolitan Park system, brought to the Gipsy Moth Laboratory of the Bureau of Entomology, United States Department of Agriculture, a few larvæ of the satin moth, *Stilpnotia salicis* L. They were found by a crew of park employees, and were defoliating Carolina poplars along the parkway near the Malden-Medford city line, a few miles north of Boston. This parkway is several miles in length and is lined with from two to four rows of Carolina poplars which are about 30 years old.

An investigation made where the caterpillars were collected showed a heavy infestation extending over a small area, and some Lombardy poplars on private property were severely defoliated. The caterpillars were nearly full-grown when the infestation was discovered, and many of them were deserting the trees, swarming over buildings, and in some cases entering houses. (Fig. 3, B. C.) After consultation with the State forester's office and the park superintendent, it was decided to do as much work as was possible to meet the emergency.

The park department began spraying the infested trees in the parkway and stationed a crew of men to patrol the area infested in

¹ After the satin moth was discovered the late F. H. Mosher was detailed to study its life history and habits in connection with his regular duties at the Gipsy Moth Laboratory of the Bureau of Entomology, U. S. Department of Agriculture. He was assisted by J. E. R. Holbrook, who completed certain phases of this work after the untimely death of Mr. Mosher. To these gentlemen credit is given for the life history and information concerning food plants of the insect.

the park and to crush the larva, pupae, and moths and destroy the newly deposited egg clusters. The State forester's office detailed a force of men to search the area outside of the parkway, to determine the immediate limits of the infestation, and to destroy all of the satin moths found. The Bureau of Entomology cooperated by scouting the towns outside of the area where the park department and State forces were working.

The spraying was not so effective as normally, because many larvae had left the trees for pupation or had pupated in the leaves on the trees. However, the infestation was to some extent reduced by spraying and by the other suppressive methods used.

Scouting operations determined that the infestation was of several years' standing and that the insect had spread over a much larger area than had been supposed. In some of the surrounding towns and cities, where a few isolated defoliated Lombardy poplar trees were found, statements were obtained to the effect that this insect had been present the previous year, but had not been recognized as a new insect in the locality.

It is not known when the satin moth arrived in this country, but it must have been present several years prior to 1920. In many locations large larvae and pupae were found in the scouting operations of 1920, indicating that the insect was present in the previous year.

In addition to the suppression and scouting work which was immediately begun, Franklin H. Mosher, of the Bureau of Entomology, stationed at the gipsy-moth laboratory at Melrose Highlands, Mass., investigated the life history of the satin moth and collected data on its habits.

DISTRIBUTION IN EUROPE AND ASIA

This insect is widely distributed throughout Europe and Asia. In some localities it is common and destructive, and a number of distinct varieties or races are recognized in the different regions which it inhabits.

Foreign literature indicates that it is common in central Spain and throughout Italy, also in Russia, the Balkan peninsula, Corsica, Armenia, northeastern Asia Minor, Altai, southeastern Siberia, Urgan, Amur, Chosen (Korea), China, and Japan. It has also been reported from the Arctic region and from the British Isles.

Experts of the Bureau of Entomology, detailed on gipsy-moth work in Europe, report it sparsely distributed over most of France, Germany, Poland, Bulgaria, Spain, Italy, Yugoslavia, Hungary, and Czechoslovakia, and medium to heavy infestations have been reported at Dresden, Germany; Luck and Smogulec, Poland; Sofia, Bulgaria; Prague, Czechoslovakia; and Budapest, Hungary. The infestations observed were on poplar and willow trees planted on roadsides and estates. In foreign literature oak foliage has been included as one of the foods of this insect.

In Europe it is not usually considered a very serious pest, being noticed at times of great abundance, when poplar and willow trees are severely defoliated. There is some confusion in foreign literature as to the manner in which this insect hibernates, but the facts that the moths are strong flyers and that they are attracted to lights are mentioned in many articles referring to the satin moth.

NORTH AMERICAN DISTRIBUTION

IN CANADA

In July, 1920, J. D. Tothill found caterpillars of the satin moth defoliating poplar trees in New Westminster, British Columbia. Anxiety was felt by the Canadian authorities when this insect was discovered within their territory, its close relation to the gipsy moth (*Porthetria dispar* L.) and the brown-tail moth² (*Nygmia phaeorrhoca* Donovan) placing it in a group of notoriously injurious insects.

R. Glendenning, of the entomological branch, Department of Agriculture, Dominion of Canada, has conducted investigations on this insect, the results of which have been published by the Dominion Department of Agriculture.³ Lombardy poplar trees on the grounds of Columbia College, at New Westminster, were found to be heavily infested by the satin moth in July, 1920, and during the summer the insect spread to most of the white and Lombardy poplar trees in the city. A few moths were found in a village about 2 miles east of the city. The following year several infestations were located, the worst one being at Vancouver, British Columbia, which was so severe as to indicate that it was the original infestation and that the infestations at New Westminster and other places had originated from Vancouver. At the time of the preparation of the report the infested area included about 50 square miles on the mainland of British Columbia, with several infestations on Vancouver Island.

In the summer of 1923 the senior author visited some of the infested area in New Westminster and noted partial to complete defoliation of poplar and willow trees.

IN THE STATE OF WASHINGTON

The first record of the satin moth in the State of Washington⁴ was made at Bellingham in 1922 by W. E. Longley. The insect was first seen on a nearly defoliated row of Lombardy poplars. Later in the season it was discovered in several other places. The specimens were identified at the Dominion Museum at Victoria, British Columbia.

Since that time considerable scouting has been done throughout the western part of the State of Washington, under the direction of A. G. Webb, plant quarantine inspector of the Federal Horticultural Board, who has charge of the port of Seattle. The results of this work indicated that the insect had become established in many localities where poplar and willow trees are present, distributed throughout most of the counties from the international line south to Seattle. As a result of this work the Federal quarantine was extended in the

² In American publications the brown-tail moth has been known since its establishment in the United States as *Euproctis chrysorrhoea* L. It is regrettable that the use of a name which has been employed so long and is so well understood should have to be discontinued. However, evidence has been presented to prove clearly that *E. chrysorrhoea* is the name of another common European insect. BARNES, W., and BENJAMIN, F. H. ON THE CORRECT NAME FOR THE BROWN-TAIL MOTIL. Ent. Soc. Wash. Proc. 26:213.

³ GLENDENNING, R. THE SATIN MOTH IN BRITISH COLUMBIA. Canada Dept. Agr. Pamphlet 50, New Series, 14 pp., 1924.

⁴ Acknowledgment is gladly made here of the kindness of E. R. Sasseer, of the Federal Horticultural Board, in allowing the writers to refer to a report by A. G. Webb, associate plant quarantine inspector, in regard to the satin-moth situation in the State of Washington.

State, as shown in Figure 1. The details are given later in this report.

IN THE NEW ENGLAND STATES

Data regarding the distribution of the satin moth in New England have been obtained from several sources. Much of the information for Massachusetts has been obtained from the State forester's office of the commissioner of conservation and from the division of plant pest control of the State department of agriculture. The moth superintendents and tree wardens of many of the towns and cities in the State have reported on the conditions in the towns they represent. Information from the other New England States has been



FIG. 1.—Map of the State of Washington. The shaded portion shows the area in this State quarantined against the satin moth. The plus (+), at Bellingham, in the northwestern part, indicates the location of the first infestation of the satin moth found (in 1922) in the State. The small circles (⊙) denote the known infestations in British Columbia in 1924.

obtained from State entomologists and other interested parties, and these data have been supplemented by scouting work in Maine by State and Federal employees, and in New Hampshire, Connecticut, and Rhode Island by assistants connected with the gipsy moth and brown-tail moth project. Much information has been collected by employees of this division in connection with their regular duties.

The information obtained during the summer of 1920, when extended scouting was done, showed that this insect had spread over an area of 642 square miles, including 60 towns in Massachusetts and 4 in New Hampshire. Some of this spread occurred in the summer of 1920, but the occurrence of large larvae and pupae in the majority of the towns proved that in many cases the insect had been present the previous year.

In 1921, 1922, and 1923 little scouting was done, but an attempt was made to determine the situation in Massachusetts with respect to the satin moth by requesting information from all of the towns known to be infested with it and in a double row of towns bordering the infested territory. The information obtained was furnished by superintendents of local work against the gipsy moth. A similar request for information concerning the situation in the towns in New Hampshire known to be infested, and in those immediately surrounding the infested area, was made to the State entomologist of New Hampshire. As a result of these requests, with information acquired by the Federal force in 1921, four towns in Massachusetts and one in New Hampshire were included in the infested area. In 1922 no newly infested towns were reported. In 1923 two more towns were added to the infested area in Massachusetts; and, of 57 New Hampshire towns that were inspected, 41 were found to be infested.

Very little scouting was done in New Hampshire in 1924, but it resulted in the inclusion of four additional towns in the infested area. In Massachusetts scouting was carried on by inspectors of the State department of agriculture, chiefly in the southern part of the State, by which 34 towns were added to the infested area.

In 1925 many towns were added to the infested territory, and the satin moth was found for the first time in Maine and in Rhode Island. The new records of occurrence of the satin moth were made in 42 towns in Maine, 21 in New Hampshire, 80 in Massachusetts, and 11 in Rhode Island.

Scouting in 1926 resulted in the addition to the area quarantined against this moth of 16 towns in Rhode Island, 2 in Connecticut, 24 in Massachusetts, 24 in New Hampshire, and 32 in Maine.

The present distribution of the satin moth in New England (fig. 2) covers an area of approximately 12,114 square miles. The infested territory lies along the Atlantic coast, covering an area about 60 miles wide and extending from the city of Belfast, Me., to Stonington, Conn.

The spread of this insect in New England has been rapid, and principally toward the north and northeast, as was the case in the dispersion of the brown-tailed moth, the gipsy moth, and several other insects. The record of the yearly distribution, as determined by the reports and scouting records, is merely suggestive of the direction and rapidity of the spread of this insect, for, with the exception of the work done in 1920, 1925, and 1926, no systematic attempt has been made to determine the exact spread of the insect.

DESCRIPTION AND HABITS

THE MOTH

The insect derives its name from the white, satinlike appearance of the moths, which are larger than most of the white moths native to New England and have no colored markings on the wings. (Pl. 1, 3, 4.)

Males 15 to 20 mm., females 20 to 25 mm. in length. Wing expanse 35 to 60 mm. Males slightly smaller than females. Head, thorax, and abdomen black, densely covered with long white hairs and scales, giving the moth a

satinlike luster. Hairs often dense at tip of abdomen, giving it a tufted appearance. Eyes black. Shaft of antennae black, covered dorsally with flat, white scales. Antennae of males bipectinate; of females, bidentate. Pectinations and dentations brown to black. Legs black, femora densely covered

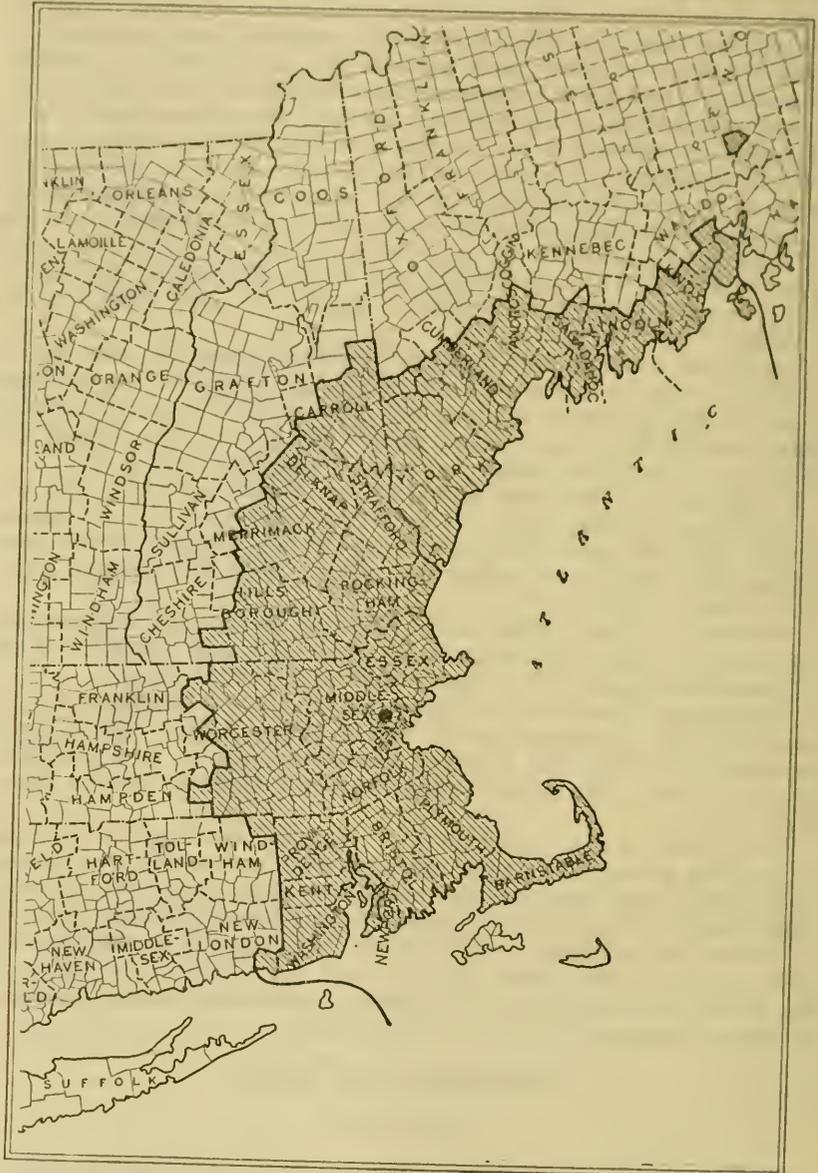


FIG. 2.—Map of the portion of New England in which infestations of the satin moth have been found. The shading indicates the area known to be infested, which is also the area quarantined against this moth. The heavy dot near Massachusetts Bay denotes the location of the original colony, discovered in 1920

with long white hairs. Tibiae and tarsi sparsely covered with white hairs, ringed with white overlapping scales, giving the appearance of alternate bands of black and white.



DIFFERENT STAGES OF THE SATIN MOTH (*STILPNOTIA SALICIS*)

- 1, Full-grown larva. 2, Pupa. 3-4, Moths. 5, An egg cluster on bark. 6, Small larva on leaf. 7, Pupa in its cocoon in partially folded leaf. At right, defoliated poplar, with partially defoliated willows in background.

The moths emerge during a period of three to four weeks, beginning in the latter part of June, and are most abundant in the month of July. Those of both sexes are strong flyers and are attracted to lights, especially in the darkness of the early evening. European records indicate that great numbers of moths fly long distances, but such migrations have not been observed in this country. The moths move about during the day and fly short distances when disturbed, but are more active at night and are often abundant around street lights. In laboratory experiments the females have lived from 6 to 20 days, and the average length of life was 10 days.

MATING AND OVIPOSITION

Mating usually takes place within a few hours after emergence. While the moths are in coitu their heads are in opposite directions, and they may remain in that position for several hours. In a heavy infestation mated pairs may be found in this position on trees, grass, or bushes, and in some cases on electric-light poles, or on buildings near by. Both sexes frequently mate more than once, especially if the female has been disturbed during oviposition. The eggs are sometimes deposited near the place where the female emerged, but in many cases a long flight may be made before the eggs are laid.

Egg laying takes place during July, being at its height about the middle of the month. The clusters of eggs are deposited principally on the trunks, the under sides of the branches, and the leaves of trees; but they are also frequently found on fences, stones, buildings, or electric-light poles that are located near trees or brilliant lights. Glendenning⁵ reports that—

Twenty-five egg masses were counted on July 28, 1921, on the faces of the clock on the tower of the Burns Building, Vancouver, British Columbia. This building is nearly 250 feet high, and the clock is illuminated at night, which probably accounts for the eggs being there. This apparent carelessness is, however, no doubt occasionally the means of dispersal to fresh locations, when the eggs are laid on movable objects.

THE EGG

The eggs are laid in patches which are somewhat oval in form, averaging in size 15 mm. long and 12 mm. wide. Each patch is easily seen, being covered with a satin-white secretion which glistens in the sun. (Pl. 1, 5.)

Eggs spherical, but slightly flattened; light green when freshly laid, gradually becoming brown as embryo develops.

The number of eggs in egg masses deposited in the field averaged 316, as determined by an examination of large numbers of clusters. The largest mass collected in the field contained 412 eggs. There is a great variation in the size of these clusters, owing to the habit of the female of moving about if disturbed and so depositing more than one mass.

In an experiment involving 46 fertilized females, two deposited over 1,000 eggs each. The greatest number deposited by one female was 1,023, and the average number for the experiment was 571. This number is greater than the average for field records.

⁵ Page 10 of publication cited in footnote 3.

Under laboratory conditions hatching occurred in from 12 to 19 days after egg deposition, the average time being 15 days.

THE LARVA

[Pl. 1, *L. 6*; text fig. 3, B, C, D]

There is a slight variation in the markings of the larvæ, as well as in the length and in the width of the head of the different larval stages. The following descriptions and measurements are for the average larvæ in each stage.

FIRST-STAGE LARVA

Newly hatched larva 2.5 mm. long. Head brownish and 0.43 mm. in width; flat on front, with a few short spines. Mouth parts lighter in color. Thoracic legs brown. Body brownish yellow, with rows of darker brown tubercles, thickly studded with short brown spines and with a small number of long hairs. First thoracic segment provided with brownish dorsal shield.

The first-stage larvæ leave the egg mass soon after hatching and begin feeding on either side of the leaf, but more often on the underside. They eat the epidermis only, avoiding even the smaller veins. After five or six days each larva incloses itself within a small web, where it molts. Very soon after molting the second-stage larva crawls from the molting web and begins feeding.

SECOND-STAGE LARVA

Newly molted larva 4 mm. long. Head 0.55 mm. wide, black, with lighter colored mouth parts. Body dark brown, with rows of dark-brown tubercles thickly studded with short brown spines and a few long hairs. Thoracic legs dark brown to black. First thoracic segment with dark-brown dorsal shield, similar to the one in the first-stage larva. Dorsum of the second and third thoracic segments, and the third, fourth, fifth, eighth, and ninth abdominal segments, yellowish white. Dorsum of the sixth and seventh abdominal segments provided with retractile tubercle.

The second-stage larvæ feed for five to six days, in the same manner as do the first-stage larvæ. Since the larvæ of both stages confine their feeding to the epidermis of the leaves, they do not defoliate the trees as do the larger caterpillars. In heavy infestations the feeding by the small larvæ is often severe enough to cause many of the leaves to turn brown and drop, making the trees unsightly. When through feeding, the larvæ construct hibernating webs, in which, soon after their completion, another molting occurs.

HIbernACULUM

The web made by the second-stage larva is much stronger than the molting web of the first-stage larva, and within it the third-stage larva passes the winter. Usually there is a single larva within each web, but occasionally, in heavy infestations, several larvæ hibernate under the same web. The hibernating webs (fig. 3, E) are placed in crevices and depressions, ranging from deep to very slight, in the bark on the tree trunks and branches. They are sometimes found on small twigs, and even on leaf scars, and are present from the top to the bottom of the trees. They are very inconspicuous, closely resembling the color of the bark. In shape they are irregular, with a circular or oval outline, usually about 4 mm. in length and 1 or 2 mm. wide. Occasion-

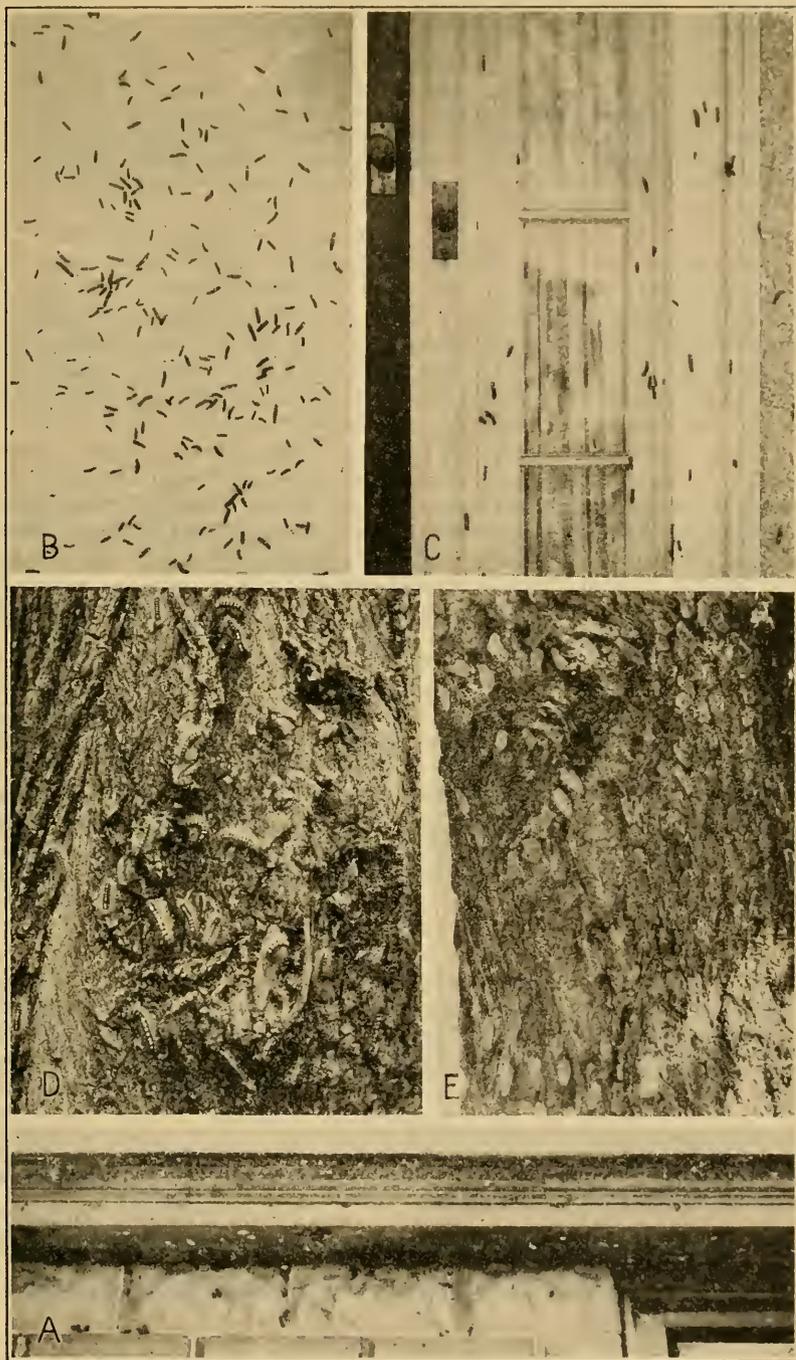


FIG. 3.—A Satin moth pupal cases and egg clusters on garage; B, larvæ on ceiling of porch; C, larvæ on door opening on front porch; D, larvæ on trunk of tree; E, hibernation webs on trunk of tree

ally a small amount of the bark over which the web is constructed appears to have been excavated. The cavity is lined with fine silk.

THIRD-STAGE LARVA

When first molted, the third-stage larva is about 6 mm. long. In its hibernating web it contracts to about 4 mm. in length. Head black, 0.63 mm. wide. Body slightly darker in color than in second stage; being contracted, it appears much more hairy. Contraction of the body makes the light colors on dorsum more pronounced.

Normally the third-stage larvæ do not feed and do not leave their hibernaculum until the following spring. Occasionally they have been observed crawling on the trees on warm days in the late fall and early winter. Such larvæ have not been known to reenter their hibernating quarters, and those observed died without attempting to construct new ones. In the laboratory experiments which have been performed, third-stage larvæ have not fed or left their hibernating webs at any time during the fall or winter.

In the latter part of April the third-stage larvæ begin emerging from hibernation, the emergence continuing through the first three weeks of May, with a maximum early in the month. After five or six days of feeding, under laboratory conditions, the larvæ inclose themselves in rather coarse webs, in which they molt. In the field, just before molting, the larvæ construct for this purpose webs similar in appearance to the hibernating webs. Only the epidermis of the leaf is eaten by third-stage larvæ.

FOURTH-STAGE LARVA

Newly molted larva 8 mm. long. Head black, 0.95 mm. in width. Body similar to that of third-stage larva, with hairs much longer.

Fourth-stage larvæ feed from five to six days, consuming much more food than larvæ in the previous stages. They do not confine their feeding to the epidermis of the leaves, but eat small, irregular holes, avoiding the larger veins. These larvæ prepare slight webs across the fissures of the bark, beneath which they molt.

FIFTH-STAGE LARVA

Newly molted larva 12 mm. long. Head black, with a slight bluish tinge, 2 mm. in width. Body black, mottled with white markings of irregular shape, which form distinct subdorsal lines on each segment. On the dorsum of the first, and that of the last, body segment is a white irregular blotch. On each of the intermediate segments are two white blotches of irregular shape. These are placed anteriorly and posteriorly on the segments, so that the posterior blotch on each segment combines with the anterior blotch of the one following. These white blotches make the caterpillar conspicuous, and are characteristic of this species. Tubercles in this stage reddish brown, and hairs longer than in preceding stage.

In feeding, the fifth-stage larvæ consume the entire leaf with the exception of the larger veins. This stage occupies five to six days, after which the larvæ prepare their molting webs in the fissures on the tree trunks.

SIXTH-STAGE LARVA

Newly molted larva 25 mm. long. Head black with bluish tinge; 3 mm. wide. Markings similar to those of previous stage. White blotches larger and more conspicuous, and brown tubercles brighter in color than on fifth-stage larva. White mottling of black body, giving it a light bluish-gray appearance.

The sixth-stage larvæ feed for five to six days, eating the entire leaf tissue, and leaving only the coarser veins. As in the case with the previous stages, the sixth-stage larvæ construct webs across the fissures of the bark, under which they molt.

SEVENTH-STAGE LARVA

Newly molted larva 35 mm. long. Head black with a bluish tinge. 4.5 mm. wide. The caterpillar has the same appearance as in the sixth stage, but is considerably larger and more conspicuous. (Pl. 1, 1.)

The seventh-stage larva feeds for about seven days, then spins a loose cocoon in which to pupate.

THE PUPA

Pupa (Pl. 1, 2, 7) 20 to 25 mm. long and 5 to 7 mm. wide at base of abdomen. Shining black, covered with tufts of long, silky, white and golden hairs, except on venter, where hairs are scarce. Usually on each abdominal segment occurs a row of two to five light-brownish spots, variable in size and number and occasionally missing.

Pupation takes place after the seven larval stages which have been described, both male and female moths developing from seventh-stage caterpillars. The cocoon, the spinning of which may occupy from several hours to two days, is very loosely made, and the pupa within is plainly visible. It is frequently constructed so as partially to bring together the two edges of a leaf, as shown in Plate 1, 7. The cocoons occur not only on leaves, but are also found in the crevices of bark, in rubbish near trees, and on buildings, fences, and in other convenient places. (Fig. 3, A.) The adult emerges about 10 days, on an average, after construction of the cocoon is begun.

FOOD PLANTS

Field observations and feeding experiments have been made at the Gipsy Moth Laboratory to determine the favored food plants of the satin moth in New England. As a result the trees here named have been listed in the order of their preference as food plants of the satin moth.

FAVORABLE

Lombardy poplar.....	<i>Populus nigra italica</i> DuRoi.
Carolina poplar.....	<i>Populus deltoides</i> Marsh.
Balm of Gilead.....	<i>Populus canadensis</i> Ait.
White poplar.....	<i>Populus alba</i> L.
Large-tooth aspen.....	<i>Populus grandidentata</i> Michx.
Quaking aspen.....	<i>Populus tremuloides</i> Michx.
Golden willow.....	<i>Salix vitellina</i> L.

PARTIALLY FAVORABLE

Scrub oak.....	<i>Quercus ilicifolia</i> Wang.
Black oak.....	<i>Quercus velutina</i> Lam.

NONFAVORABLE

Alder.....	<i>Alnus incana</i> (L.) Moench.
Apple.....	<i>Pyrus malus</i> L.
Gray birch.....	<i>Betula populifolia</i> Marsh.
Elm.....	<i>Ulmus americana</i> L.
Red oak.....	<i>Quercus borealis mexicana</i> (Marsh.) Ashle (<i>Q. rubra</i> nuct.).
White oak.....	<i>Quercus alba</i> L.
Scarlet oak.....	<i>Quercus coccinea</i> Moench.
Pear.....	<i>Pyrus communis</i> L.
Red maple.....	<i>Acer rubrum</i> L.
Paper birch.....	<i>Betula papyrifera</i> Marsh.
White ash.....	<i>Fraxinus americana</i> L.
Hickory.....	<i>Hicoria ovata</i> (Mill.) Britton.

From the time of hatching to the adult stage the larvæ of the satin moth feed on the food plants listed as favorable, but have seldom been observed under field conditions to attack the species listed as partially favorable. Glendenning^a reports that the insect was noted sparingly on the native cottonwood, *Populus trichocarpa* Torr. & Gray, at New Westminster, British Columbia, and A. G. Webb has found the larvæ feeding on this and on willow trees in the State of Washington.

Larvæ of the satin moth have not been reared from hatching to maturity on the trees listed as partially favorable, but fed through the first two fall stages and hibernated successfully with no other food than scrub oak. Emerging in the following spring as third-stage larvæ, they began feeding on scrub-oak leaves in the laboratory, but died without molting. Larvæ which fed on poplar during the first two stages in the fall were successfully reared to maturity on scrub oak the following spring. The feeding experiments have indicated that black oak is less favorable than scrub oak. Larvæ which have had only black-oak foliage for food have been reared through the first two stages and lived through the winter; but in the spring, when black oak was the only food supplied, they died without further development. Larvæ which were fed on poplar only during the first two stages, and hibernated successfully, were fed on black oak during the following spring; they developed slowly, and in no case reached maturity.

The foliage of the trees listed as nonfavorable has been tested for several years as food for larvæ of the satin moth. In no case have caterpillars developed to the hibernating stage when restricted for food to any of the trees listed in this group.

ARTIFICIAL CONTROL

In cases where the satin moth is abundant and many egg clusters are deposited the latter can be destroyed by treating them with creosote. *This treatment should be applied as soon as possible after the eggs are laid, as hatching takes place in from 10 to 20 days after the time of deposit, and after the eggs have hatched the treatment is futile.* Crude coal-tar creosote, to which a small quantity of lampblack is added, so as to leave a black residue on the treated clusters, will be satisfactory. It should be applied with a brush; if this is attached to a pole many of the clusters on the trunks

^a See p. 4 of publication cited in footnote 3.

and lower branches of the trees can be reached. In eastern New England the poplars and willows are usually attacked by borers, so that many of the large limbs are in a weakened condition, and as the wood is naturally very brittle it is usually inadvisable to climb the trees in order to apply treatment.

If the infestation is extremely heavy or the larvæ swarm on buildings or enter houses, they can be swept to the ground and killed by crushing. Cases are on record where the larvæ were washed from buildings by using water pressure, and afterwards were crushed on the ground.

Experience has shown that the most effective treatment for the satin moth is to spray the trees infested by it with arsenate of lead (fig. 4) during the period when the caterpillars are feeding.



FIG. 4.—Carolina poplars. The foliage on the trees in the rear was sprayed with arsenate of lead. The trees in the foreground were not sprayed, and were heavily fed upon by larvæ of the satin moth.

As the eggs are deposited anywhere on the trees, the feeding by the young larvæ is well distributed on the foliage. It is not necessary to spray in August unless the infestation is very heavy. Should this be the case, an even distribution of the poison will give excellent results. If the spray is applied as soon as the larvæ begin to feed it will be most effective. Both sides of the foliage should be sprayed.

Summer spraying will not as a rule be necessary. In the spring, as soon as the trees are in full leaf, treatment should be applied. A high-pressure sprayer is required in order to treat the tops of the trees. A machine of this type, using a solid-stream spray, has given excellent results in Massachusetts, when arsenate of lead was applied at the rate of 6 pounds of powder to 100 gallons of water.

Because of the smooth surface of the foliage of poplar and willow trees, the poison does not adhere to it as well as to other types of foliage. Recent experiments at the Gipsy Moth Laboratory indicate that excellent adhesion can be obtained by adding 3 quarts of

fish oil, or, if this is not available, the same quantity of raw linseed oil, to each 400 gallons of spray. The oil should be poured into the spray tank while it is being filled with water and after the poison has been added. The contents of the tank should be thoroughly agitated while the oil is poured in and until the mixture is applied.

This spray will adhere very closely to the foliage and is affected very little by rain. Care should therefore be exercised to prevent cattle from feeding on the grass beneath sprayed trees. Buildings will be discolored with this spray unless care is taken to wash them with water from a garden hose before any poison adhering to them is thoroughly dried.

NATURAL ENEMIES

One of the interesting features of the introduction of an insect into a new region is the question whether it will be attacked by natural enemies present in its new home.

NATIVE PARASITES

Several native parasites have been found attacking the satin moth in New England, although the rate of parasitism is small. The following species were reared from this insect at the Gipsy Moth Laboratory:

Reared from eggs.—*Telenomus californicus* Ashm.

Reared from larvæ.—*Zenillia blanda* O. S., *Frontina frenchii* Will., and *Phorocera claripennis* Macq.

Reared from larvæ and pupæ.—*Tachina mella* Walk. and *Winthemia quadrifustulata* Fab.

Reared from pupæ.—*Theronia fulviseens* (Cress.), *Ephialtes pedalis* (Cress.), *Hoplectis conquisitor* (Say), and *Dibrachys hemerocampæ* (Girault).⁷

Of native parasites *Telenomus californicus* is the most common. During the summer of 1925, satin-moth egg clusters were received at the laboratory from 66 towns in New England, from 19 of which this egg parasite was recovered. These data are especially interesting, as the collections, each consisting of a single egg cluster, were mostly taken from new infestations in towns on or near the border of infested territory.

Two species of Tachinidae, three species of Hymenoptera, and three sarcophagids have been mentioned as natural enemies of the satin moth in British Columbia. The tachinids *T. mella* Walk. and *T. robusta* Tn. appear to be of considerably more value there than any native parasite has been in New England. Glendenning⁸ writes as follows of observations made in 1922 of infestations in New Westminster, British Columbia, where from 25 to 80 per cent of the caterpillars had tachinid eggs on them:

The majority of these eggs, being laid shortly after the last larval molt, hatched before being shed at pupation, and the great majority thus proved fatal to their hosts and were an appreciable control factor in this location.

Another quotation from Glendenning⁸ follows, indicating the abundance of native tachinids at an infestation on Vancouver Island.

⁷ Determined by A. B. Gahan, of the Bureau of Entomology. The other Hymenoptera and Diptera were determined by C. F. W. Muesebeck, R. T. Webber, and T. H. Jones, of the Gipsy Moth Laboratory.

⁸ See p. 13 of publication cited in footnote 3.

In Nanaimo, in 1922, the white eggs were very abundant, but owing to the immense number of larvæ present the percentage was only about 35 * * * Numbers of larvæ collected here contained so many maggots of apparently equal vigor that very few completed their feeding and but few puparia were obtained.

In addition to *T. mella* and *T. robusta*, three sarcophagids, *S. houghii* Aldr., *S. aldrichii* Pk., and *Agria affinis* Fall., and three Hymenoptera, *Ephialtes pedalis* (Cress.), *Theronia fulvescens* (Cress.), and *Amblymerus liparidis* Vier., are recorded as being parasitic on the satin moth in British Columbia. They were considered to be of little importance as control factors.

PREDATORY ENEMIES

Birds undoubtedly consume many larvæ of the satin moth. Mosher made some special studies to determine the relationship of birds to the satin moth and recorded the following species as feeding on them: Black-billed cuckoo, *Coccyzus erythrophthalmus*; oriole, *Icterus galbula*; blue jay, *Cyanocitta cristata cristata*; starling, *Sturnus vulgaris*, and catbird, *Dumetella carolinensis*. On numerous occasions the junior author has noted blue jays and starlings apparently picking the small satin moth larvæ from their hibernating webs on heavily infested poplar trees. Western robins and bats have been reported as feeding on the satin moth at New Westminster, British Columbia. Toads have been observed to take the larvæ, and several spiders have also been noted as their enemies.

DISEASE

There is no positive evidence that larvæ of the satin moth are attacked in this country by the disease commonly known as "wilt." Larvæ are occasionally observed in the field attached to the tree trunks by their anal prolegs, with the head hanging downward in a position similar in appearance to the characteristic position in which caterpillars are found which have died from the wilt. On two of these occasions, when the situation was further investigated, it was found that in one place the foliage had been sprayed, indicating that the larvæ had been poisoned. At the other location several dead larvæ were examined, and each one was found to contain a tachinid maggot.

In the food-plant experiments which have been carried on at the laboratory for the last few years there has been no evidence that the larvæ die from wilt. However, in some of the large trays used for feeding large numbers of satin moth larvæ which had been collected to obtain *Compsilura* for colonization, caterpillars have been found which had the characteristic appearance of having died from wilt. In the summer of 1925 a number of these dead larvæ were sent for examination to R. W. Glaser, of the Rockefeller Institute, who reported that in this material there was no evidence of the wilt disease.

EFFECT OF INTRODUCED ENEMIES OF THE GIPSY MOTH AND BROWN-TAIL MOTH ON THE SATIN MOTH

The gipsy moth and the brown-tail moth became established in the New England States in the utter absence of the insect enemies which attack them in the Old World, but this is not the case with the satin

moth. Several of the insect enemies of the gipsy moth and the brown-tail moth which have been introduced and established are also enemies of the satin moth.

Numerous observations have been made, and collections of various stages of the satin moth obtained, to determine the status of the natural control of this insect in New England. Absolute records have been obtained showing that *Compsilura concinnata* Meigen, *Calosoma sycophanta* L., and *Blepharipa scutellata* R. D. have attacked the satin-moth larvæ in the field. These three introduced insects are among the most important enemies of the gipsy moth that have been successfully established.

B. scutellata has not as yet been an important enemy of the satin moth, but the fact that it is able to develop as a satin-moth parasite gives it a potential value, and under certain conditions it may become important.

Adults of *Calosoma sycophanta* are often seen climbing over the trees and feeding on satin-moth larvæ. They attack these larvæ readily, and the evidence of their work is often observed. Many satin-moth larvæ which have been killed or injured by the beetles have been found on the tree trunks and on the ground at the base of the trees. The observations which have been made indicate that the *Calosoma* larvæ appear too late in the season to be of primary importance as enemies of the satin-moth caterpillars. Moreover, the habit of many of the satin-moth larvæ of pupating in partially folded leaves protects them still further from the attacks of *Calosoma* larvæ.

TABLE 1.—Parasitism of satin-moth larvæ and pupæ by *Compsilura concinnata* in New England from 1922 to 1924, as shown by rearings

Town	Year	Medium-sized larvæ collected	Compsilura recovered	Large-sized larvæ collected	Compsilura recovered	Pupæ collected	Compsilura recovered
Revere.....	1922	100	1	100	11	100	0
Do.....	1923	100	0	100	7	100	3
Do.....	1924	100	1	100	56	100	5
Meirose.....	1922	100	12	100	44	112	16
Do.....	1923	100	22	100	71	100	29
Do.....	1924	100	2	100	66	100	35
Medford.....	1922	100	10	100	50	100	16
Do.....	1923	100	6	100	63	100	11
Do.....	1924	100	4	100	71	100	0

Up to the present time *Compsilura concinnata* has been the principal insect enemy of the satin moth in New England. Table 1 shows the value of this introduced tachinid as an enemy of the satin moth.

The data obtained during the summer of 1925 from collections of medium-sized and large caterpillars are presented in Table 2.

The larval and pupal collections shown in Tables 1 and 2 were kept in trays at the laboratory, and were cared for until the emergence of the parasites. The recoveries from these collections indicate the abundance of *C. concinnata*, and distinctly show how readily it is attacking the satin moth, but these figures are not presented to show the actual percentage of parasitism of the satin moth

in the localities represented. Sufficient study has not been made to determine that.

TABLE 2.—*Parasitism of satin-moth larvæ by Compsilura concinnata in New England in 1925, as shown by rearings*

Town	Larvæ collected	Compsilura recovered		
Melrose.....	} 10,680	3,062		
Belmont.....				
Haverhill.....				
Revere.....			200	16
Beverly.....			29	1
Eastham.....	54	1		
Total.....	10,963	3,080		

¹In the laboratory experiments several collections from these three towns were combined.

In addition to the larval collections shown in the foregoing tables, dissections were made of medium and large-sized satin-moth larvæ collected at the towns listed in Table 3.

TABLE 3.—*Percentage of satin-moth larvæ parasitized by Compsilura concinnata in New England in 1925, as shown by dissections*

Town	Larvæ collected	Larvæ parasitized	Percentage of larvæ parasitized
Dennis, Mass.....	150	0	0
Westwood, Mass.....	1	0	0
Worcester, Mass.....	200	87	43.50
Lowell, Mass.....	3	2	66.67
Seabrook, N. H.....	200	2	1.00
Concord, N. H.....	50	5	16.00
Laconia, N. H.....	16	6	37.50
Total.....	620	105	16.94

The larval dissections listed in Table 3 show in a number of cases more than one parasitic maggot in each caterpillar. Such superparasitism by *Compsilura* occurs in a number of different hosts, and, although it is a waste, it is not as disastrous as might appear. In the case of the satin moth and of several other species superparasitism is seldom excessive, and the host is large enough to support two and sometimes more *Compsilura* maggots without apparent weakening of the resulting adult parasites.

One hundred satin-moth larvæ were collected at Quincy, Mass., in 1924, and upon dissection were found to have an unusual degree of superparasitism. Forty-two contained no parasites, but the remaining 58 were parasitized by 77 *Compsilura* maggots. It seems evident that *Compsilura* larviposits in its host at random, and in this case an unnecessarily large number of parasites were present in some of the hosts. Each of 35 larvæ contained 1, each of 13 contained 2, and 1 contained 3, first-stage maggots; 7 were found to

contain 1, and 1 to contain 2, second-stage maggots; and 1 larva was parasitized by 1 second-stage and 3 first-stage maggots.

In connection with the gipsy-moth work large collections of gipsy-moth caterpillars have been made each year, from which *Compsilura* have been obtained for colonization. There have been few heavy gipsy-moth infestations in and around Melrose in recent years, and as the satin moth is an attractive host for *Compsilura* large numbers of satin-moth caterpillars have been collected from which *Compsilura* for colonization were obtained. The favorable food plants of the satin moth are often planted in groups, and as only poplar and willow trees have been affected it has been possible to make collections of larvæ very rapidly from a heavily infested locality.

Besides the records obtained pertaining to *Compsilura concinnata*, *Calosoma sycophanta*, and *Blepharipa scutellata*, field observations have strongly indicated that another one of the introduced and established gipsy-moth larval parasites, *Apanteles melanoscelus* Ratz., attacks satin-moth larvæ in the field.⁹

Another species, *Apanteles vitripennis* Hal., a very common braconid parasite of gipsy-moth larvæ in Europe, has been colonized in New England in the last two years. It is not as yet positively established, although since colonization it has passed through a generation in the field. In laboratory experiments it attacks small satin-moth larvæ. It apparently needs a host in which to hibernate, and several unsuccessful attempts have been made to induce it to hibernate in small satin-moth larvæ. It has not been conclusively shown, however, that *A. vitripennis* can not under field conditions pass the winter within hibernating satin-moth larvæ. In the spring of 1925 a few hibernating satin-moth larvæ were collected at North Hampton, N. H., where a colony of *A. vitripennis* was liberated in 1924. Several of these larvæ were dissected by C. F. W. Muesebeck, of the Gipsy Moth Laboratory, and in one of the caterpillars a hibernating *Apanteles* larva was found. It was not possible to determine the species of this braconid and no parasites were reared from the remaining larvæ of the collection.

A parasite of the gipsy-moth egg, *Schedius kuranae* How., introduced from Japan, attacks readily and successfully the satin-moth eggs when they are exposed to it in laboratory experiments, and may under favorable conditions attack them in the field.

Rather limited observations have been made to determine the degree of mortality of hibernating satin-moth larvæ in New England; up to the summer of 1925 it seemed to be slight. Examination of the hibernating larvæ in several localities in the spring of 1926 showed 45 per cent larval mortality. A mortality of 2.6 per cent may be attributed to a fungus associated with a few of the dead larvæ, and a mortality of 20.7 per cent appeared to have been brought about by a small pteromalid. Maggots of this parasite were found feeding externally on the satin-moth larvæ in hibernation webs. On examination of pieces of bark heavily infested with hibernating satin-moth larvæ, many of the caterpillars in small areas on the bark were found to be dead, and apparently flattened, as

⁹CROSSMAN, S. S. APANTELES MELANOSCELUS, AN IMPORTED PARASITE OF THE GIPSY MOTH. U. S. Dept. Agr. Bul. 1028. 25 pp., illus. 1922.

though the body fluids had been extracted. In every such case one of these parasite maggots was found in the immediate area, strongly indicating that the pteromalid parasite travels from one hibernating web to another close by, and in the course of its development consumes several caterpillars.

Adults of these parasites have been determined as *Eupteromalus nidulans* (Foerster),¹⁰ a parasite of the hibernating larvæ of the brown-tail moth which is well established in New England as a result of parasite introduction in connection with work on the gipsy moth and brown-tail moth.

The causes of the remaining 21.7 per cent mortality of the hibernating larvæ are unaccounted for. Part of it may be due to mites which are found in considerable numbers in the webs containing the dead larvæ. It should be noted that in the area where the observations were made no unusual winter temperatures have occurred since these observations were begun.

Mortality in New Westminster, British Columbia, due to *Spicaria* sp., a fungous disease, has been reported by Glendenning¹¹ as amounting to 90 per cent in the season extending from November to March, 1920-21, and again in 1921-22, at Vancouver and New Westminster. At Nanaimo the mortality was not nearly so great. Climatic conditions in this section vary so greatly from those obtaining in the Eastern States that mortality records are not comparable. During the humid season on the Pacific coast conditions are very favorable for the growth of fungous diseases, and this fact accounts for the high mortality recorded.

Individual egg clusters vary greatly in the proportion of eggs that hatch. Of the satin-moth eggs in clusters collected in the field, from 30 to 95 per cent hatched, the average being 80 per cent. Many of the larvæ which hatch from eggs deposited on rocks, fences, buildings, and other objects must die without finding any favorable food plant. Such mortality may be high in heavy infestations.

ECONOMIC IMPORTANCE

It is hazardous to predict the extent of injury likely to be caused by the establishment of a foreign insect in a new environment. The observations made since the satin moth was first discovered in this country indicate that this insect is largely restricted for food to a rather limited group of trees—the poplars and willows. Up to the present time in the infested area most of the feeding has been done on trees planted for shade in parks and along roadways, or on trees planted for ornamental purposes on estates. Most of these trees are of rapid-growing varieties, and many of the small branches on Lombardy poplars have died after suffering severe defoliation. Complete defoliation of large white poplars has caused the death in whole or in part of the trees attacked. In severe infestations the trees are defoliated, and enormous numbers of the large caterpillars migrate in search of food. They then become a nuisance, dropping on pedestrians, crawling up and down trunks of

¹⁰ Determined by P. B. Dowden and A. B. Gahan, of the Bureau of Entomology.

¹¹ See p. 12 of publication cited in footnote 3.

trees, upon sidewalks, fences, and buildings, and even entering dwellings. The feeding of small larvæ in the early fall is sometimes so severe as to cause a browning and premature dropping of the leaves.

No heavy feeding of this insect in New England was observed, except on poplars (fig. 5, B), until the summer of 1925, when willows (fig. 5, A, C) were also severely defoliated. Experiments on food plants have shown that this insect can mature when scrub oak forms a large part of its food. Similar experiments suggest that larvæ of the satin moth might mature when black oak is a part of their diet. Such data, together with a European report including oak as one of the food plants of these larvæ, leave open the possibility that under certain conditions this insect may attack some trees not at present included in the list of its favored food plants.

There are certain areas in this country where poplar is an important pulp tree and is being planted for that reason. In some areas on Cape Cod, Mass., white poplars are the predominating shade trees, and severe injury to them will result from heavy defoliations caused by this insect.

In many sections in the West trees of the genus *Populus* constitute the predominating shade and ornamental trees. Should this insect become established in such areas, it might become a pest of the first magnitude.

QUARANTINE

The habit of this insect of hibernating under very small and inconspicuous webs on the trunks of trees (fig. 3, E) and small branches of its favored food plants makes it impossible to inspect nursery stock properly and be sure that it is free from infestation. In order to protect the territory in this country not infested by this introduced insect, a quarantine, No. 53, was promulgated by the Secretary of Agriculture and made effective on and after January 1, 1922. It has been revised annually, the last revision being effective November 15, 1926. This quarantine prohibits the movements of all species and varieties of poplar (*Populus*) and willow (*Salix*) trees, and parts thereof capable of propagation, from the area designated as infested to noninfested territory.

The area designated as infested by the satin moth comprises the city of Bangor, Me., and the following towns and all the territory between them and the Atlantic Ocean:

Vinal Haven, North Haven, Islesboro, city of Belfast, Northport, Lincolnville, Hope, Union, Waldoboro, Nobleboro, Newcastle, Alna, Dresden, Gardiner, Richmond, Bowdoin, Webster, Greene, Auburn, Poland, Casco, Naples, Sebago, Hiram, and Porter. *Maine*; Eaton, Conway, Madison, Tamworth, Moultonboro, Meredith, Sanbornton, Franklin, Salisbury, Warner, Henniker, Deering, Bennington, Greenfield, Peterboro, Jaffrey, Sharon, and New Ipswich, *New Hampshire*; Ashburnham, Winchendon, Templeton, Phillipston, Athol, Barre, Oakham, Spencer, Brookfield, Brimfield, Sturbridge, Southbridge, and Dudley, *Massachusetts*; Thompson, *Connecticut*; Burrillville, Gloucester, Foster, Coventry, West Greenwich, Exeter, Hopkinton, and Westerly, *Rhode Island*; Stonington, *Connecticut*.

The following counties and all the territory between them and the Pacific Ocean are designated as infested by the satin moth:

Whatcom, Skagit, Snohomish, King, Pierce, Lewis, and Skamania, *Washington*.



FIG. 5.—A, C. Willows; B, Lombardy poplar. These trees, all in New England, were defoliated by the satin moth, the willows in 1925

SUMMARY

The satin moth, a common European insect, was first discovered in the United States near Boston, Mass., in June, 1920. In July of the same year it was found near Vancouver, British Columbia, and was reported in the State of Washington in 1922.

Its principal food plants in Europe and on this continent have been the poplars and willows, although records have been made proving that it can develop when fed for a part of the time on scrub oak.

Spraying with arsenate of lead has proved that when properly applied it will control this insect. Spraying in the spring is recommended, and the addition of fish oil or linseed oil to the spray mixture is strongly advised.

Several of the beneficial insects which have been successfully established as enemies of the gipsy moth and the brown-tail moth, and some native parasites, have been recorded as attacking this recently introduced pest. The parasitism of the satin moth in New England by the imported parasite *Compsilura concinnata* and by two native tachinids in British Columbia has been especially noticeable and has prevented many larvae from maturing.

Long-distance spread of the satin moth is being prevented as a result of the enforcement of the quarantine regulations.

Natural enemies are retarding to some extent the increase of this insect.

Control work in the New England States is performed by individuals or by the local authorities, and although many trees are sprayed annually with excellent results, there are heavily infested sections which receive no treatment at all. This has resulted in the rapid increase of the insect during the last five years and its continued spread to uninfested towns and States.

The States concerned and the local authorities in districts infested or threatened with infestation should take vigorous measures to control this insect, and the Bureau of Entomology will cooperate as far as possible by furnishing the latest information concerning this pest and the proper methods of control.

All citizens, and particularly visitors or tourists, can assist by refraining from transporting willows or poplars from the infested area.

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UNITED STATES DEPARTMENT OF AGRICULTURE**

January 18, 1927

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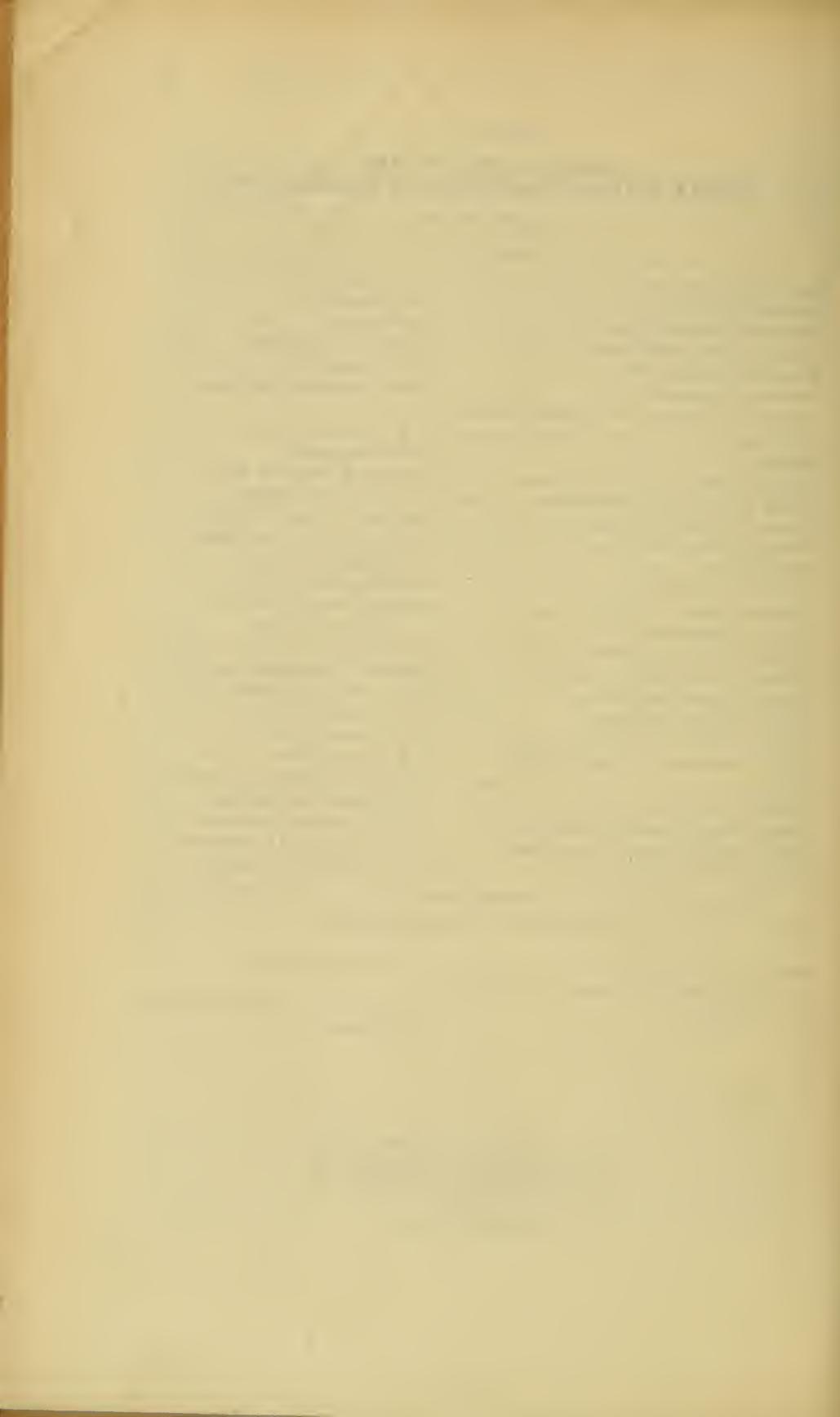
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UNITED STATES DEPARTMENT OF AGRICULTURE



DEPARTMENT BULLETIN No. 1472



Washington, D. C.

March, 1927

CHEMOTROPIC TESTS WITH THE SCREW-WORM FLY

By D. C. PARMAN, *Assistant Entomologist*, F. C. BISHOPP, *Entomologist in Charge*, and E. W. LAAKE, *Associate Entomologist, Investigations of Insects Affecting the Health of Animals, Bureau of Entomology*, and F. C. COOK,¹ *Physiological Chemist*, and R. C. ROARK, *Associate Chemist, Insecticide and Fungicide Laboratory, Miscellaneous Division, Bureau of Chemistry*

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INTRODUCTION

Throughout the southwestern part of the United States heavy losses are suffered each year by the various livestock interests owing to the destructive activities of blowflies. Although the farmers and dairymen have considerable trouble with these insects, the losses are most severely felt by the cattle, sheep, and goat raisers on the ranges.

The species commonly known as the screw-worm fly, *Cochliomyia macellaria* Fab., is by far the most destructive of the blowflies. The average annual loss due to this insect has been estimated at \$4,000,000. It breeds normally in dead or living animal tissue. When the flies are abundant they are strongly attracted to the slightest scratch or blood spot on the skin of an animal. Under favorable conditions oviposition takes place, and the larvæ hatch and start feeding on the living tissues of their host. The larger the wound the more attractive it becomes, and the infestation continues to increase, resulting in extensive destruction of tissue and very often the death of the animal if treatment is not administered within two or three days.

¹ Died June 19, 1923. Since May, 1924, R. C. Roark has been the representative of the Bureau of Chemistry in this investigation.

Certain other species of flies, such as the black blowfly, *Phormia regina* Meig., the green bottle flies *Lucilia sericata* Meig. and *L. cuprina* Meig., and some species of sarcophagids, particularly *S. robusta* Ald., not infrequently infest wounds, but they are much less important than the screw-worm fly. The black blowfly is more inclined to attack old suppurating sores and is most abundant during cool weather, hence it commonly infests animals after dehorning. It also attacks sheep in the early spring, laying its eggs on soiled wool. In this situation it is commonly spoken of as the "wool maggot."

For the control of these blowflies several methods are commonly used. These are (1) the destruction of carcasses in which the flies breed; (2) the prevention of wounds, such as wire cuts, scratches, and bruises, by careful handling at the times when the animals are rounded up, dipped, etc.; (3) the carrying out of the castrating branding, dehorning, and shearing of animals at times when flies are scarce or absent; (4) the trapping of adult flies in traps baited with meat, or, preferably, dried-egg bait; (5) the use of larvicides and repellents on infested wounds on animals.

WORK OF OTHER INVESTIGATORS WITH FLY REPELLENTS

Although the chemotropic responses of many insects have been studied, only a few investigators have experimented with blowflies, and no reference to previous work with repellents for the screw-worm fly has been found.

Cooper and Walling² tested the effect of various chemicals upon blowflies (*Calliphora*) by dusting pieces of meat with a number of different materials incorporated in precipitated chalk. The authors concluded that the following were most suitable as repellents: Methyl salicylate, para-nitraniline, picric acid, creosote, green oil, boracic acid, fusel oil, pine oil, alizarine oil, origanum oil, mustard oil, sod oil, iodoform, dimethylaniline, quinoline, allyl alcohol, aloin, saponin, copper carbonate, nitrobenzene, sinapis oil, and anise-seed oil.

Olive C. Lodge³ reported on some studies of attractive substances which might be used as baits for blowflies and house flies. She found liver to be more attractive than a number of other animal tissues and brought out the fact that the infestations of baits with larvæ caused the baits to become more attractive to the flies. She mentions among the substances showing decided repellent qualities for one species of blowfly (*Protophormia terrae-novae* R. D.), pipendine [piperidine?], oenanthol, xylol, amyl acetate, methyl salicylate, anisole, citral (strong), ethyl sulphocyanide, oil of thyme, of cassia, of Java citronella, of palma rosa, of bay, of heliotrope, of lavender, of cinnamon leaf, of cinnamon bark, of sassafras, of cloves, of camphor. Many other substances tested by her are classed as less repellent or neutral. She also conducted some tests with *Calliphora* and *Lucilia*.

Wardle⁴ tested the repellent effect upon blowflies (*Calliphora*) of various materials by rubbing them upon cotton twine netting of

² COOPER, W. F., and WALLING, W. A. B. THE EFFECT OF VARIOUS CHEMICALS ON BLOW-FLY. *Ann. Appl. Biol.* 2: 166-182. 1915.

³ LODGE, O. C. FLY INVESTIGATIONS REPORTS. IV. SOME ENQUIRY INTO THE QUESTION OF BAITS AND POISONS FOR FLIES, BEING A REPORT ON THE EXPERIMENTAL WORK CARRIED OUT DURING 1915 FOR THE ZOOLOGICAL SOCIETY OF LONDON. *Zool. Soc. London, Proc.* 1916: 481-511. 1916.

⁴ WARDLE, R. A. THE PROTECTION OF MEAT COMMODITIES AGAINST BLOWFLIES. *Ann. Appl. Biol.* 8: 1-9. 1921.

quarter-inch diamond mesh. This netting was tied over the opening of cylindrical glass dishes containing food samples. Oil of star anise was effective in preventing the food from being blown for 24 hours; samples protected with eucalyptus oil, formic acid, and sometimes clove oil remained untouched for 12 hours, while samples protected by oil of almonds, oil of citronella, oil of cinnamon, boracic acid, picric acid, or nitrobenzene were blown within 6 hours.

MATERIALS NOW USED AS SCREW-WORM FLY REPELLENTS

Pine tar, tannic acid, turpentine, kerosene, gasoline, various sheep and cattle dips, hydrated lime, calomel, and other materials have been used in the past with more or less success.⁵ Many home remedies, such as axle grease and lampblack are used by ranchmen, but probably proprietary "screw-worm killers" of one sort or another are now most prevalently used. These consist largely of crude carbolic acid, which, though efficacious in killing all fly larvæ with which it comes into contact, is also very poisonous to animals. As a result, many animals are killed by the treatment. In addition, many ranchmen hesitate to use these carbolic preparations upon their fine stock and confine themselves to the use of chloroform or other larvicides. Although chloroform is in extensive use for killing fly larvæ in wounds, it has no repellent value and does not prevent reinfestation.

The cost of treating an animal for screw-worm infestation has been estimated by several ranchmen to be from 25 to 50 cents for each treatment. A conservative estimate would be 25 cents for each treatment, or \$25 per 100 infested animals per day when treatments are required from once to twice daily. Repeated treatments by improper methods and successive worm infestations occasionally necessitate the treatment of the cases for months.

PURPOSE OF CHEMOTROPIC TESTS

The purpose of this study has been to find a material that will prevent reinfestation for 48 hours or longer. This would relieve the situation to a great extent, as it is not uncommon to find as many as 400 to 500 cases of worms on a single ranch in seasons favorable for the screw worm, and a considerable number of cases on most ranches every season.

The problem involves two objects to be accomplished through the treatment of wounds: (1) The destruction of the larvæ if present, and (2) the protection of the wound from infestation for a reasonable length of time. It is obvious that any treatment which will injure the tissues so as to delay healing or which will act as a local or systemic poison, will defeat the ends in view.

The experience of the writers indicates that there is considerable difficulty in successfully combining a larvicide and a repellent to be used as a single treatment, as the killing properties of the larvicides are too much reduced by the admixture of the repellent material. Hence it is logical to attempt to develop a strong and lasting repellent without larvicidal action.

In this bulletin, therefore, the data given deal essentially with the question of the chemotropic responses of the screw-worm fly to various

⁵ BISHOPP, F. C., MITCHELL, J. D., and PARMAN, D. C. SCREW-WORMS AND OTHER MAGGOTS AFFECTING ANIMALS. U. S. Dept. Agr. Farmers' Bul. 857, 19 p., illus. 1919. (Revised, 1922.)

materials, and contain only incidental information on the toxicity of these materials to the eggs, larvæ, or adults.

From a practical point of view there are a number of factors which must be considered. Among these are availability of the materials, their cost, adhesive qualities, suitability for handling, stability or keeping qualities, whether they stain wool or mohair, and the effect on the animal tissues, which has already been mentioned. Some may feel that the value of a repellent for use on living animals can not be determined by tests conducted with dead tissue. It seemed to the writers, however, that a determination of the reaction of flies toward a large number of materials, exposed under observable conditions, would give, with a minimum expenditure of time and money, the basic information upon which to proceed with other studies. This assumption is being justified by work now in progress. The various practical points mentioned above will be considered in connection with a subsequent report on the treatment of livestock and other uses to which repellents are commonly put. Some of the results of field tests with repellents have been presented.⁶

There are many other uses to which repellents may be put. For instance, there is considerable loss from the infestation of foods by flies, aside from the danger of disease being conveyed to man through eating foods contaminated by them. Throughout the South, and even in the cooler parts of the country, it is often difficult to dress meat on the farm or range or even in well-equipped slaughter houses without having it "blown" by flies. Slaughtering at night, the use of smudges, and other means of avoiding this are practiced, but with only partial success, whereas a good repellent would largely solve the difficulty. Again, tourists and picnic parties are often greatly annoyed and their foods contaminated so as to render life outside of screened houses well-nigh unbearable. The use of an effective repellent under such conditions has been found of great value. Such repellents would serve a useful purpose about the household, dairy, and all establishments where foods are handled or displayed.

Another, though somewhat different, phase of this subject is the use of repellents to protect livestock of all classes from annoyance by flies, especially the blood-sucking forms, such as the horn fly, stable fly, and buffalo gnat. Although this particular series of experiments does not consider, directly, this use of repellents, it is thought that the information gained will aid materially in this field; in fact, the data have already furnished valuable clues which are being followed in the work now under way with sprays for flies on livestock.

This bulletin presents the results of jar tests with the screw-worm fly, *Cochliomyia macellaria* Fab. The results of the tests with the house fly, *Musca domestica* L., the green bottle flies, *Lucilia* spp., and other species will be presented in subsequent papers.

MATERIALS TRIED

As very few observations on the chemotropic responses of blow-flies to various chemicals have been recorded heretofore, the materials used in these tests were selected from a wide range of organic and inorganic compounds in order to reconnoiter the whole field of possible

⁶ LAAKE, E. W., PARMAN, D. C., BISHOPP, F. C., and ROARK, R. C. FIELD TESTS WITH REPELLENTS FOR THE SCREW-WORM FLY, *COCHLIOMYIA MACELLARIA* FAB., UPON DOMESTIC ANIMALS. *Jour. Econ. Ent.* 19: 536-539. 1926.

practical repellents. Representatives of the different classes of the more common and easily procurable organic compounds were selected. The formulæ and boiling points of these are shown in Table 1 with the purpose of ascertaining whether or not there is a relation between the repellent action of organic compounds and their chemical constitution and their volatility (which is measured roughly by their boiling points). On account of the widespread use of certain essential oils, especially citronella and pennyroyal, as mosquito repellents, many tests were made with these. Fish oil, pine tar, and turpentine have been recommended for use in keeping flies off dairy cattle, and it was thought worth while to subject these to careful tests also.

The lubricating oil referred to in the table was automobile motor oil, specific gravity 0.930, Saybolt viscosity at 104° F. 495, manufactured from crude oils of different bases; petrolatum was U. S. P.; the petroleum was north Texas crude which consists principally of paraffin oils. The mineral oil referred to in a few tests was a spindle oil with a specific gravity at 60° F. of about 0.88 and boiling range from 569 to 750° F. Most of the chemical compounds were chemically pure and the essential oils and crude drugs were of the best commercial grade.

PROCEDURE

In some preliminary tests fresh meat was exposed on paper plates in places where flies were abundant, and the materials, the repellent values of which were to be tested, were sprayed with a hand atomizer over the meat until the latter was well covered. About one-half pound of fresh beef was used to each plate. This method proved unsatisfactory, as the number and species of flies present could not be determined accurately.

The baits were next placed in small cone flytraps, but when determination of the flies was made frequently this method was found to be very cumbersome.

The next procedure was to put into a pint Mason jar enough sand to make a layer 1 inch in depth, place 4 ounces of fresh meat on the sand, and then spread a measured quantity of the repellent over the surface of the meat. Rabbit meat was used in some of the tests, but as a rule fresh beef liver was employed. It was found that 5 cubic centimeters of the liquid repellents sufficed to thoroughly cover the meat, and all the tests were accordingly made with this quantity. In the case of the solid materials, 5 grams were used. Since the densities of the liquids differed considerably, the same quantity by weight was not used in the different tests, and in only a few cases did 5 cubic centimeters equal 5 grams. However, for a rapid survey of the field of possible repellents these differences are negligible.

As a rule, each repellent was tested in duplicate at the same time. A series of 30 to 40 jars would be prepared, 2 of which (sometimes 3 to 5) were left untreated and served as checks. The meat in the other jars was covered with the materials to be tested, and the series of jars exposed in a favorable environment where flies were plentiful. Identical tests were made in Dallas and in Uvalde, Tex. In Dallas the jars were exposed in a large roofed shed in the yard of a large packing plant, and were usually first set out about noon. The distance between jars varied from 4 to 6 feet. Observations were

made at two-hour intervals as to the number of each species of fly within the jars. Two observations were made on the day of setting out the jars, four each on the second, third, and fourth days of exposure, and two observations on the fifth and last day of exposure, making 16 observations in all. At the end of each observation period the jars were interchanged in position so as to equalize the conditions of shade and sunlight as much as possible. In Uvalde the jars were set out on the ground in the partial shade of mesquite trees, and examined as described above. The results at the two stations, Dallas and Uvalde, are similar, and in summarizing the data no distinction has been made as to locality.

In this series of experiments no attempt has been made to determine how the meat was rendered unattractive to the flies. It is certain, however, that what has been spoken of as repellent action is a very complicated matter. It is evident that the meat in these tests was protected in several ways by different materials. In some cases the protection was largely mechanical, either by covering the attractive surface or searing the surface so as to denature the meat and stop decomposition; in other cases it was brought about by masking the attractive odor of the baits; and in still others it was due either to a negative chemotropic response on the part of the fly through the sense of smell or an irritation response through the respiratory tract or elsewhere.

METHOD OF COMPUTING RESULTS

The repellent value of a material is determined by the ratio of the number of flies visiting treated meat to the number visiting untreated meat. Owing to the great variation in the prevalence of flies from week to week, several tests made at different times are necessary to accurately gauge the repellent value of any material. In summarizing these data on repellent action the number of flies of the same species visiting all jars treated with the same repellent has been used, and the ratio between this number and the number of flies visiting a comparable number of untreated or check jars has been determined. For example, if the ratios in several tests made at different times are $8/119$, $23/97$, $19/207$, these are combined into the single ratio $50/423$. In this way the observations are weighted according to the abundance of flies, as indicated by the number of flies visiting the untreated meat.

The percentage ratio as given is therefore not the percentage of repellent efficiency directly, but is the percentage of flies entering the treated jars as compared with the number entering the corresponding checks; that is, a percentage ratio of 0 indicates perfect repellent action, 100 shows no effect of the material, and over 100 indicates that the material is attractive.

The percentage ratios for the daily periods have not been computed, but the actual number of flies visiting the jars on each day is given. The figures for the first day really represent only one afternoon, as the tests were usually begun about midday; and the figures for the fifth day usually cover only the forenoon of the last day of exposure, as the tests were usually terminated at noon. It is believed that some idea of the duration of repellent effect may be gained from the comparison of the number of *Cochliomyia* adults

entering the treated and check jars each day, as expressed in the daily ratios.

It was observed in the course of the experiments that when the baits in the check jars became very heavily infested by larvæ, as was often the case, their attractiveness diminished toward the end of the period of exposure and was sometimes completely lost. This tended to place the jars which were treated with a more or less effective repellent, and hence not infested, at a disadvantage when compared with the unattractive check during the last day or two of the test.

In addition to observations of the number of each species of fly present in the jar at two-hour intervals, observations were made as to the presence of eggs or larvæ. The degree of infestation was observed to vary greatly, as indicated by the number of egg masses deposited and the number of larvæ which were present in the different jars at the close of each test. As no effort was made to determine the actual number of eggs deposited, the results are reported as number of infested treated jars over number of infested check jars. Furthermore, since it is impossible by a cursory examination to determine the species of egg or larva, these infestation figures apply to all species, except perhaps the house fly, which infests fresh meat so little that it can be neglected. The species responsible for the infestation was determined by transferring the eggs or larvæ in the jars at the end of the five-day test period to fresh meat and allowing the adults to emerge in screened cages. The emergence data are shown by giving the number of treated jars from which they emerged, no account being taken of the number of flies bred out. The emergence data are incomplete, owing to the difficulties inherent in handling so much material and to the escape of larvæ from the cages.

The fact is recognized that the tests of many of the materials are insufficient both as regards the number of flies present when the tests were conducted and the variety of conditions, such as climatic conditions or dilution of materials, under which a given material was exposed. These matters have been given some consideration in the "Discussion of results," p. 22.

TABULAR STATEMENT OF RESULTS OF TESTS

The results of the chemotropic tests with screw-worm flies are presented in Table 1.

TABLE 1.—Results of chemotropic tests with *Cochliomyia macellaria*

[Number of *Cochliomyia* flies visiting jars containing treated meat as compared with untreated meat during five days' exposure, together with number of treated jars infested over number of check jars infested for each day, and the number of treated jars from which *Cochliomyia* flies emerged over the number of check jars from which they emerged]

Compound	Formula	Boiling point °C.	Total number of treated jars	Total number flies treated jars over checks	Percent- age ratio for entire period	Ratio for flies visiting jars					Ratio for infestation					Ratio for emerge- ence		
						First day	Second day	Third day	Fourth day	Fifth day	First day	Second day	Third day	Fourth day	Fifth day			
Hydrocarbons:																		
Lubricating oil.....			4	18-40	39	0:10	5:10	5:0	0:17	2:0	0:2	1:2	2:4	2:4	2:4	0:2		
Petrolatum.....			6	659:1,085	153	3:185	1,408:774	162:123	22:3	4:0	1:4	4:0	4:0	4:0	4:6	1:3		
Petroleum.....			2	876:505	174	0:0	8:22	390:7	407:443	74:33	0:1	2:2	2:2	2:2	2:2	2:2		
Benzene.....		79.6	2	305:590	70	18:90	199:288	52:84	89:54	7:2	1:1	1:2	2:2	2:2	2:2	2:2		
Toluene.....		110.5	0	120:176	68	50:21	66:148	5:7	0:0	0:0	1:5	2:6	2:6	2:6	2:6	0:0		
Toluene (1) plus pet- rolatum (5), ¹			2	0:5	0	0:0	0:3	0:2	0:0	0:0	0:2	0:2	0:2	0:2	0:2	0:0		
Ortho-xylene.....		144	3	100:213	47	47:02	40:104	4:45	3:2	6:0	2:2	3:3	3:3	3:3	3:3	0:1		
Naphtha, crude sol- vant (60% xylene).			4	26:117	22	5:13	21:97	0:7	0:0	--	2:4	2:4	2:4	2:4	2:4	0:0		
Para-cymene.....		176	7	348:751	46	94:479	180:293	74:32	0:7	--	5:7	6:7	6:7	6:7	6:7	1:1		
Naphthalene.....		217.9	4	13:20	65	3:3	7:13	3:4	0:0	0:0	0:4	2:4	2:4	2:4	2:4	0:0		
Anthracene.....		342	3	0:18	0	0:0	0:0	0:0	0:18	0:0	0:0	0:0	1:1	1:3	1:3	0:2		
Anthracene oil.....			2	48:101	47	17:10	31:86	0:5	0:0	--	1:2	2:2	2:2	2:2	2:2	2:2		
Alpha-pincene.....		154	5	309:692	58	230:471	120:182	43:32	0:7	--	2:4	2:5	2:5	2:5	2:5	0:1		
Bromides:																		
Bromoform.....		150.4	7	499:975	51	18:49	331:380	111:310	34:205	5:22	1:4	3:7	7:7	7:7	7:7	0:3		
Bromoform (1) plus kaolin (4).			1	1:88	1,1	0:17	0:25	0:41	1:4	0:0	0:0	1:1	1:1	1:1	1:1	0:0		
Ethylene bromide.....		131.7	2	8:20	28	4:19	3:10	1:0	0:0	0:0	1:2	2:2	2:2	2:2	2:2	0:0		
Benzyl bromide.....		199	1	1:1	100	0:0	0:0	0:0	0:1	0:0	0:0	0:0	0:1	0:1	0:1	0:0		
Para-xylol bromide.....		220.7	4	1:017	0,2	2:0	0:15	0:215	0:315	1:71	0:0	0:0	0:0	0:4	0:4	0:4		
Para-xylol bromide (1) plus lubricating oil (6).			2	62:17	365	2:0	57:0	2:0	1:17	0:0	0:0	1:0	1:0	1:2	1:2	0:2		
Para-xylol bromide (1) plus inbricating oil (69).			2	52:17	306	3:0	43:0	0:0	0:17	6:0	0:0	0:0	0:0	1:2	1:2	0:2		
Alpha-bromonaphtha- lene.		281.1	5	67:91	7,1	8:130	10:388	16:274	25:127	8:22	0:3	3:5	3:5	3:5	3:5	0:3		
Chlorides:																		
Chloroform.....		61.2	1	285:154	192	150:54	89:53	13:45	16:2	27:0	1:1	1:1	1:1	1:1	1:1	0:1		
Carbon tetrachloride.....		76.8	2	94:154	61	44:54	9:33	27:45	9:2	5:0	1:1	1:1	1:1	1:1	1:1	1:1		
Hexachlorthane.....		185	1	16:154	10	0:5	0:72	8:11	2:2	8:11	0:1	2:2	2:2	2:2	2:2	2:2		
Benzyl chloride.....		179.4	4	5:617	8	0:1	0:15	2:215	2:315	1:71	0:0	0:0	0:0	0:2	0:4	0:4		

TABLE 1.—Results of chemotropic tests with *Cochliomyia macellaria*—Continued

Compound	Formula	Boiling point	Total number of treated jars	Total number of flies treated jars over checks	Percentage ratio for entire period	Ratio for flies visiting jars					Ratio for infestation				Ratio for emergence		
						First day	Second day	Third day	Fourth day	Fifth day	First day	Second day	Third day	Fourth day		Fifth day	
Phenols—Continued.																	
Safral (1) plus petrolatum (5).		° C.	1	1:96	1.0	0:1	0:38	1:53	0:2	0:2	0:1	1:1	1:1	1:1	1:1	1:1	1:1
Safral (1) plus kaolin (4).			2	8:168	4.8	0:2	0:63	6:93	1:7	1:3	0:0	0:2	1:2	2:2	2:2	0:1	0:1
Thymol.	$(\text{CH}_3)_2\text{CHC}_6\text{H}_5(\text{CH}_3)\text{OH}$.	231.8	3	61:304	16	13:288	43:106	5:0	1:1	1:1	2:3	2:3	2:3	2:3	2:3	0:2	0:2
Thymol (1) plus pine oil (5).			2	16:59	27	0:8	16:51	0:0	0:0	1:1	1:1	1:1	1:1	1:1	1:1	0:1	0:1
Thymol in benzene (saturated solution).			3	205:277	74	18:221	120:55	67:1	1:1	1:1	1:3	2:3	3:3	3:3	3:3	0:1	0:1
Thymol in alcohol (saturated solution).			2	24:101	24	7:10	10:86	1:5	6:0	1:1	1:2	2:2	2:2	2:2	2:2	0:1	0:1
Carvaerol.	$(\text{CH}_3)_2\text{CHC}_6\text{H}_5(\text{CH}_3)\text{OH}$.	237.9	6	117:442	26	20:81	33:264	24:42	16:54	24:1	2:5	5:0	6:6	6:6	6:6	2:1	2:1
Aldehydes:																	
Formaldehyde (40 per cent solution in water).	HCHO .		7	50:349	16	24:77	31:104	1:62	0:15	0:1	5:7	6:7	6:7	6:7	6:7	0:1	0:1
Formaldehyde (1 plus petrolatum (5)).			2	0:5	0	0:0	0:3	0:2	0:0	0:0	1:2	1:2	1:2	1:2	1:2	0:0	0:0
Butyraldehyde.	$\text{CH}_3(\text{CH}_2)_3\text{CHO}$.	75.7	4	225:357	63	0:1	9:28	162:236	47:02	7:0	1:3	2:4	4:4	4:4	4:4	1:4	1:4
Crotonaldehyde.	$\text{CH}_3\text{HC}=\text{CHCHO}$.	104	4	23:357	6.4	0:1	0:28	3:236	17:02	3:0	0:3	3:4	4:4	4:4	4:4	0:4	0:4
Heptaldehyde.	$\text{CH}_7(\text{CH}_2)_6\text{CHO}$.	155	5	126:358	35	0:1	9:28	75:237	25:02	17:0	0:2	1:5	4:5	5:5	5:5	0:4	0:4
Citral.	$\text{C}_{10}\text{H}_{16}\text{O}$.	229	2	18:101	18	4:10	12:86	2:5	0:0	1:1	0:1	1:2	2:2	2:2	2:2	0:1	0:1
Citronellal.	$\text{C}_{10}\text{H}_{18}\text{O}$.	208	1	37:52	45	0:4	2:40	32:53	3:7	1:1	1:1	1:1	1:1	1:1	1:1	0:1	0:1
Furfural (1) plus mineral oil (5).	$\text{C}_4\text{H}_3\text{O}_2\text{CHO}$.	161.7	17	81:1,527	5.3	4:126	25:559	13:398	33:437	6:25	3:12	10:11	14:27	15:17	16:17	0:7	0:7
Furfural (1) plus petrolatum (5).			3	1:75	.2	0:67	1:366	0:41	0:1	0:0	0:2	0:3	1:3	1:3	1:3	0:1	0:1
Furfural (3) plus petrolatum (1) plus kaolin (1).			1	0:96	0	0:1	0:38	0:53	0:2	0:2	0:0	0:1	0:1	1:1	1:1	0:1	0:1
Furfural (1) plus kaolin (4).			4	23:640	3.6	0:69	2:427	7:133	2:8	12:3	0:2	0:4	2:4	3:4	3:4	1:1	1:1
Benzaldehyde.	$\text{C}_6\text{H}_5\text{CHO}$.	179.5	2	11:505	2.2	0:0	0:22	1:7	9:443	1:33	1:1	2:2	2:2	2:2	2:2	1:3	1:3
Salicylic aldehyde.	$\text{OHC}_6\text{H}_4\text{CHO}$.	196.5	9	88:668	13	0:55	5:231	35:392	45:16	3:1	0:7	2:9	4:9	6:9	7:9	1:3	1:3
Salicylic aldehyde (1 plus mineral oil (5)).			1	30:96	31	0:1	0:38	7:53	21:2	2:2	0:0	0:1	1:1	1:1	1:1	1:1	1:1

TABLE 1.—Results of chemotropic tests with *Cochliomyia macellaria*—Continued

Compound	Formula	Boil- ing point	Total num- ber of treated jars	Total num- ber flies, treated jars over checks	Percent- age ratio for entire period	Ratio for flies visiting jars					Ratio for infestation					Ratio for emer- gence			
						First day	Second day	Third day	Fourth day	Fifth day	First day	Second day	Third day	Fourth day	Fifth day				
Chlorine substituted ketones—Continued.																			
Chloroacetophenone (1) plus petrolatum (2).		° C.	1	0:455	0	0:64	0:354	0:37	0:0	0:0	0:0	0:1	0:1	1:1	1:1	0:1	0:1		
Chloroacetophenone (1) plus kaolin (1).			3	2:084	.3	0:05	1:376	1:242	0:1	0:0	0:2	0:3	1:3	2:3	2:3	0:3	0:3		
Acids:																			
Normal-valeric.....	$\text{CH}_3(\text{CH}_2)_2\text{CO}_2\text{H}$	187	2	97:61	159	49:42	48:19	--	--	--	2:2	2:2	2:2	2:2	2:2	2:2	2:2	2:2	2:2
Normal-caproic.....	$\text{CH}_3(\text{CH}_2)_5\text{CO}_2\text{H}$	202	2	21:59	35	0:8	21:51	0:0	0:0	0:0	1:2	1:2	1:2	1:2	1:2	1:2	1:2	1:2	1:2
Normal-caprylic.....	$\text{C}_{11}\text{H}_{23}\text{O}_2$	237.5	3	30:61	49	13:42	17:19	--	--	--	3:3	3:3	3:3	3:3	3:3	3:3	3:3	3:3	3:3
Esters:																			
Normal-butyl acetate.	$\text{CH}_3\text{COOC}_4\text{H}_9$	126.5	1	0:1	0	0:0	0:0	0:0	0:0	0:0	0:1	0:1	0:1	1:1	1:1	0:1	0:1	1:1	1:1
Amyl acetate.....	$\text{CH}_3\text{COOC}_5\text{H}_{11}$	142.5	6	132:176	75	39:21	91:148	2:7	0:0	--	2:4	6:5	6:5	6:5	6:5	1:2	1:2	1:2	1:2
Amyl acetate (1) plus petrolatum (5).			2	0:5	0	0:0	0:3	0:2	0:0	0:0	1:2	1:2	1:2	1:2	1:2	0:0	0:0	0:0	0:0
Amyl butyrate (1)	$\text{C}_4\text{H}_9\text{COOC}_4\text{H}_9$	178.6	2	99:101	98	18:10	73:86	3:5	5:0	--	1:2	2:2	2:2	2:2	2:2	1:2	1:2	1:2	1:2
Amyl butyrate (1) plus petrolatum (5).			2	0:5	0	0:0	0:3	0:2	0:0	0:0	1:2	1:2	1:2	1:2	1:2	0:0	0:0	0:0	0:0
Methyl salicylate.	$\text{OHC}_6\text{H}_4\text{COOCH}_3$	223.3	7	70:244	29	15:51	28:102	11:79	15:11	1:1	2:5	5:7	6:7	7:7	7:7	1:3	1:3	1:3	1:3
Amyl salicylate.		273	2	40:61	69	22:42	18:19	--	--	--	2:2	2:2	2:2	2:2	2:2	2:2	2:2	2:2	2:2
Halogens substituted es- ters:																			
Beta-chloroethyl ace- tate.	$\text{ClCH}_2\text{COOC}_2\text{H}_5$	145	4	22:617	3.6	0:1	0:15	3:215	17:315	2:71	0:0	0:0	1:2	1:4	1:4	0:4	0:4	0:4	0:4
Beta-chloroethyl ace- tate (1) plus lubri- cating oil (9).			2	3:17	18	0:0	1:0	0:0	2:17	0:0	0:0	0:0	0:0	0:2	0:2	0:2	0:2	0:2	0:2
Beta-bromoethyl ace- tate.	$\text{C}_{11}\text{H}_{21}\text{BrO}_2$	70 ²	4	2:617	.3	0:1	0:15	1:215	1:315	0:71	0:0	1:0	1:2	1:4	1:4	0:4	0:4	0:4	0:4
Beta-bromoethyl ace- tate (1) plus lubri- cating oil (9).			2	2:17	12	0:0	1:0	0:0	1:17	0:0	0:0	0:0	0:0	0:2	0:2	0:2	0:2	0:2	0:2
Ethers:																			
Beta-naphthyl ethyl ether	$\text{C}_{10}\text{H}_7\text{O}_2\text{C}_2\text{H}_5$	282	9	60:1,506	4	4:128	16:738	21:465	9:175	7:0	1:5	1:9	3:9	5:9	7:9	0:6	0:6	0:6	0:6
Beta-naphthyl ethyl ether (1) plus petro- latum (5).			1	0:1	0	0:0	0:0	0:0	0:1	0:0	0:0	0:1	0:1	1:1	1:1	0:0	0:0	0:0	0:0

	10	1005:1,107	9.5	0.79	28:474	35:322	30:210	12:22	0.7	2:10	6:10	7:10	9:10	1:3
Clove, <i>Eugenia aromatica</i> L. (Fam. Myrtaceae).														
Clove (1) plus mineral oil (4)	1	10:96	20	0:1	0:38	1:53	18:2	0:2	0:0	0:1	1:1	1:1	1:1	--
Clove (3) plus petrolatum (1)	2	1:113	9	0:5	0:47	0:36	0:3	0:2	0:1	0:2	1:2	2:2	2:2	--
Clove (1) plus kaolin (3)	2	3:113	2.7	0:15	0:47	2:36	7:3	0:2	0:1	0:2	2:2	2:2	2:2	--
Clove (1) plus benzene (2)	1	77:65	118	0:10	20:41	50:5	7:0	1:1	-1	-1	-1	-1	-1	--
Clove (1) plus petrolatum (2) plus citronellal (1)	1	3:65	4.0	0:10	0:41	0:5	2:0	1:1	-1	-1	-1	-1	-1	--
Clove bud (3) plus petrolatum (1)	5	54:803	6.0	12:230	30:277	11:162	0:104	1:21	0:4	3:5	3:5	4:5	5:5	0:2
Clove bud (1) plus kaolin (3)	1	0:455	0	0:64	0:54	0:37	0:0	0:0	0:0	0:1	0:1	0:1	0:1	0:1
Clove bud (1) plus kaolin (3)	1	1:455	2	0:64	1:354	0:37	0:0	0:0	0:0	0:1	0:1	0:1	0:1	0:1
Copaiba, <i>Copaiba langsdorffii</i> (Fam. Lecythaceae)	3	126:209	60	0:26	5:92	33:87	65:4	23:1	0:1	2:3	3:3	3:3	3:3	--
Coriander, <i>Coriandrum sativum</i> (Fam. Umbelliferae)	7	67:1,331	5.0	0:133	17:595	22:327	21:254	7:22	0:3	2:7	5:7	6:7	6:7	1:4
Coriander (1) plus mineral oil (4)	1	80:96	83	0:1	0:38	48:53	23:2	0:2	0:0	1:1	1:1	1:1	1:1	--
Coriander (1) plus kaolin (3)	1	106:96	110	0:1	0:38	10:53	89:2	7:2	0:0	0:1	1:1	1:1	1:1	--
Cumin, <i>Cuminum cyminum</i> (Fam. Umbelliferae)	10	179:889	20	19:506	39:281	111:95	10:17	--	2:9	5:10	8:10	8:10	8:10	--
Eucalyptus, <i>Eucalyptus</i> spp. (Fam. Myrtaceae)	4	148,349	42	1:30	63:150	76:153	7:15	1:1	1:2	3:4	4:4	4:4	4:4	1:1
Eucalyptus (1) plus kaolin (3)	1	7:72	9.7	0:1	0:25	0:41	0:4	7:1	0:0	0:1	0:1	1:1	1:1	1:0
Fennel, <i>Foeniculum capillatum</i> (Fam. Umbelliferae)	16	152:1,345	11	15:532	57:426	57:370	23:16	0:1	1:13	10:16	12:16	13:16	14:16	2:3
Fennel (1) plus mineral oil (4)	1	58:96	60	0:1	4:38	36:53	5:2	13:2	0:0	0:1	1:1	1:1	1:1	--
Fennel (3) plus petrolatum (1)	4	14:118	12	0:5	0:50	11:58	2:3	1:2	0:3	0:4	2:4	2:4	4:4	0:0
Fennel (1) plus kaolin (3)	2	31:113	30	0:5	6:47	20:56	6:3	2:2	0:1	1:2	2:2	2:2	2:2	--
Geranium, rose, <i>Palargonium</i> spp. (Fam. Geraniaceae)	5	91:1,136	7.6	0:108	16:510	56:245	15:251	4:22	0:2	1:5	2:5	4:5	4:5	1:4
Hemlock, <i>Abies canadensis</i> Mtxch. and <i>Picea alba</i> and <i>P. nigra</i> L. (Fam. Pinaceae)	2	118:105	61	0:25	7:84	73:82	31:4	7:0	1:1	2:2	2:2	2:2	2:2	--
Juniper wood (artificial)	4	122:610	20	49:467	64:142	9:1	--	--	3:4	4:4	4:4	4:4	4:4	--
Lavender, garden (artificial)	1	79:366	22	0:36	59:234	8:40	10:55	2:1	0:0	0:1	1:1	1:1	1:1	0:1
Lavender, spike, <i>Lavandula spica</i> D. C. (Fam. Labiatae)	2	144:380	38	1:37	116:212	12:45	9:55	6:1	1:0	2:2	2:2	2:2	2:2	1:1
Lemon, <i>Citrus medica</i> var. <i>limonum</i> Hooker (Fam. Rutaceae)	3	67:277	24	30:221	19:55	18:1	--	--	2:3	2:3	2:3	2:3	2:3	--
Lemongrass, <i>Andropogon citratus</i> Stapf. (Fam. Gramineae)	3	154:277	56	5:221	134:55	15:1	--	--	2:3	3:3	3:3	3:3	3:3	--
Nutmeg, <i>Myristica fragrans</i> Houttuyn (Fam. Myristicaceae)	2	15:154	9.7	0:5	2:65	2:72	6:11	5:1	0:1	1:2	1:2	2:2	2:2	0:1
Origanum, <i>Origanum hirtum</i> (Fam. Labiatae)	6	111:177	63	41:55	64:115	3:7	3:0	--	4:5	6:6	6:6	6:6	6:6	1:2
Origanum (3) plus petrolatum (1)	2	0:5	0	0:0	0:3	0:2	0:0	0:0	0:2	0:2	1:2	1:2	1:2	0:0
Pennyroyal, American, <i>Hedeoma pulegioides</i> L. (Fam. Labiatae)	11	206:2,269	9.3	122:1,871	61:230	22:8	1:0	--	5:10	5:11	5:11	5:11	5:11	0:2
Peppermint, <i>Mentha piperita</i> L. (Fam. Labiatae)	7	363:689	53	135:479	153:188	72:9	3:13	--	4:7	5:7	6:7	6:7	6:7	--

¹ The botanical origin and principal constituents of these essential oils are taken mainly from Van Nostrand's Chemical Annual, fifth issue, 1922.

TABLE 1.—Results of chemotropic tests with *Cochliomyia macellaria*—Continued

Essential oil and botanical origin ¹	Principal constituents ¹	Total number of treated jars	Total number of flies treated for jars over checks	Percentage ratio for entire period	Ratio for flies visiting jars							Ratio for emergence			
					Ratio for infestation										
					First day	Second day	Third day	Fourth day	Fifth day	First day	Second day		Third day	Fourth day	Fifth day
Rosemary, <i>Rosmarinus officinalis</i> L. (Fam. Labiateæ).	Pinenes, camphene, cineol, camphor, borneol, bornyl acetate.	2	104:195	53	0:25	15:84	56:82	33:4	-:-	0:1	2:2	2:2	2:2	2:2	-:-
Sandalwood, <i>Santalum album</i> L. (Fam. Santalaceæ).	Santal alcohols, santalol, esters of santal alcohols.	6	233:1,331	18	13:133	74:595	90:327	49:254	5:22	0:3	2:6	5:6	6:6	6:6	1:4
Sassafras, <i>Sassafras varifolium</i> O. (Fam. Lauraceæ).	Safrol, eugenol, camphor, pinene, phellandrene.	8	144:1,312	11	8:487	26:397	42:208	13:198	55:22	1:6	5:8	5:8	5:8	5:8	0:2
Kuntze (Fam. Lauraceæ).		1	44:96	46	0:1	4:38	33:53	4:2	3:2	0:0	0:1	1:1	1:1	1:1	-:-
Sassafras (1) plus mineral oil (4)		3	9:563	1.0	0:68	2:402	2:93	5:3	0:2	0:1	1:3	2:3	3:3	3:3	0:1
Sassafras (3) plus petrolatum (1)		2	93:113	82	0:5	1:47	5:56	7:13	16:2	0:1	2:2	2:2	2:2	2:2	0:2
Sassafras (1) plus kaolin (3)		5	115:828	14	0:47	3:317	40:245	62:199	10:30	0:2	0:4	1:4	2:4	3:4	0:2
Sassafras, artificial.		1	1:455	.2	0:64	1:354	0:37	0:0	0:0	0:0	0:1	1:1	1:1	1:1	0:1
Sassafras, artificial (1) plus kaolin (3).		9	119:1,561	7.6	0:134	8:617	52:533	53:255	0:22	0:5	5:9	8:9	9:9	9:9	1:6
Spearmint, <i>Mentha viridis</i> L. (Fam. Labiateæ).	Carvone, limonene, pinene	5	33:161	20	8:18	25:138	0:5	0:0	-:-	2:4	5:5	5:5	5:5	5:5	0:0
Tansy, <i>Tanacetum vulgare</i> L. (Fam. Compositæ.)	Thujone, camphor, borneol	10	394:1,492	26	5:151	175:733	89:331	100:254	25:23	1:6	6:10	8:10	9:10	9:10	0:4
Thyme, <i>Thymus vulgaris</i> L. (Fam. Labiateæ.)	Thymol, carvacrol, eucymene, linalol, borneol.	11	212:832	25	51:527	101:299	59:0	1:0	-:-	2:10	8:11	9:11	9:11	9:11	1:2
Wormseed, American, <i>Chenopodium neupodium</i> (anthelminticum) L. (Fam. Chenopodiaceæ.)	Ascaridol.....														
Material		Total number of treated jars	Total number of flies treated for jars over checks	Percentage ratio for entire period	Ratio for flies visiting jars							Ratio for emergence			
					Ratio for infestation										
First day	Second day	Third day	Fourth day	Fifth day	First day	Second day	Third day	Fourth day	Fifth day						
Fatty oils:															
Almond.....		3	88:900	42	21:26	58:92	4:87	5:4	-:-	1:2	2:3	3:3	3:3	3:3	-:-
Fish.....		8	269:771	34	176:485	89:240	0:0	0:0	-:-	4:8	6:8	7:8	7:8	7:8	-:-
Fench Kernel.....		2	30:195	15	0:25	5:84	23:82	2:4	-:-	0:1	1:2	2:2	2:2	2:2	-:-

TABLE 1.—Results of chemotropic tests with *Cochliomyia macellaria*—Continued

Material	Total number of treated jars	Total number of jars over checks	Per-cent- ratio for entire period	Ratio for flies visiting jars						Ratio for infestation					Ratio for emer- gence
				First day	Second day	Third day	Fourth day	Fifth day	First day	Sec- ond day	Third day	Fourth day	Fifth day		
Pine products—Continued.															
Pine tar, heavy (1) plus pinap (1).....	2	0.32	0	0:0	0:29	0:2	0:0	0:1	0:1	2:2	2:2	2:2	2:2	0:0	
Pine tar (1) plus borax (1).....	3	11.688	1.6	0:19	9:247	2:202	0:198	0:27	0:1	0:3	2:3	2:3	2:3	0:2	
Pine tar (1) plus borax (1) plus kaolin (2).....	1	3.455	.66	0:64	2:554	1:37	0:0	0:0	0:0	1:1	1:1	1:1	1:1	0:1	
Pine tar (1) plus borax (1) plus petrolatum (2).....	1	7.455	1.5	0:64	5:554	2:37	0:0	0:0	0:0	1:1	1:1	1:1	1:1	0:1	
Pine tar, medium.....	4	0.160	0	0:0	0:35	0:33	0:91	0:1	0:1	1:4	3:4	4:4	4:4	1:2	
Pine tar, thin.....	4	0.160	0	0:0	0:35	0:33	0:91	0:1	0:1	1:4	3:4	4:4	4:4	0:2	
Turpentine, crude.....	7	21.747	2.8	0:4	6:97	8:71	7:541	0:34	1:3	6:7	7:7	7:7	7:7	1:5	
Turpentine, gum.....	2	3.505	.6	3:0	0:3	0:2	0:0	0:0	1:2	1:2	1:2	1:2	1:2	0:0	
Rosin residue (1) plus pine oil (1).....	2	3.505	.6	0:0	0:22	1:7	2:443	0:33	0:1	0:1	1:2	1:2	1:2	0:2	
Rosin spirits, crude.....	1	61.72	8.5	0:1	0:25	0:41	0:4	61:1	0:0	0:1	1:1	1:1	1:1	0:0	
Rosin spirits, crude (1) plus kaolin (3).....	1	9.82	1.1	0:4	4:40	5:31	0:7	--	0:0	1:1	1:1	1:1	1:1	0:1	
Pine-oil foots (1) plus furfural (1).....	2	9.505	1.8	0:0	0:22	2:7	6:443	1:33	2:1	2:2	2:2	2:2	2:2	0:2	
Wood naphtha.....	4	46.116	40	2:13	44:97	0:6	0:0	--	1:4	4:4	4:4	4:4	4:4	0:1	
Wood naphtha (1) plus kaolin (3).....	1	19.82	23	0:4	1:40	9:31	9:7	--	0:1	0:1	1:1	1:1	1:1	0:1	
Wood naphtha (1) plus petrolatum (5).....	1	0.5	0	0:0	0:3	0:2	0:0	0:0	0:2	0:2	0:2	0:2	0:2	0:0	
Wood tar oil.....	6	9.625	1.4	4:470	3:152	2:3	--	--	0:5	4:5	4:5	4:5	4:5	0:0	
Wood creosote.....	7	35.465	7.5	6:92	18:234	7:133	4:5	0:1	0:1	5:7	5:7	6:7	6:7	0:0	
Wood creosote (1) plus kaolin (3).....	1	13.82	16	0:4	0:40	10:31	3:7	--	0:1	1:1	1:1	1:1	1:1	0:1	
Wood creosote oil.....	2	0.505	0	0:0	0:22	0:7	0:443	0:33	0:0	0:2	2:2	2:2	2:2	0:2	
Wood creosote (1) plus petrolatum (5).....	2	0.5	0	0:0	0:0	0:2	0:0	0:0	0:2	0:2	0:2	0:2	0:2	0:0	
Wood creosote (1) plus glycerin (1).....	2	58.229	38	0:1	0:22	58:205	29:1	1:0	0:2	1:2	2:2	2:2	2:2	1:9	
Pine-tar oil, refined.....	9	1.999	.1	0:18	0:244	0:347	1:369	0:21	0:4	2:9	7:9	8:9	9:9	0:5	
Pine-tar oil, refined (1) plus petrolatum (5).....	2	0.456	0	0:64	0:354	0:37	0:1	0:0	0:0	0:2	0:2	0:2	0:2	0:1	
Pine-tar oil, refined (1) plus kaolin (3).....	1	0.455	0	0:64	0:354	0:37	0:0	0:0	0:0	0:1	0:1	0:1	0:1	0:1	
Pine-tar oil, commercial.....	12	35.798	4.4	0:53	4:208	8:346	10:190	4:1	1:6	7:12	10:12	12:12	12:12	0:3	
Pine-tar oil, crude.....	10	0.491	0	0:19	0:45	0:102	0:319	0:6	0:5	2:10	7:10	8:10	8:10	1:6	
Pine-tar oil, crude (1) plus petrolatum (5).....	2	0.10	0	0:0	0:0	0:0	0:10	0:0	0:0	0:2	0:2	0:2	0:2	0:0	
Commercial pine-tar oil, refined.....	3	0.6	0	0:0	0:3	0:2	0:1	0:0	0:2	0:3	0:3	0:3	0:3	0:0	
Pine-tar oil (3) plus chloroform (1).....	2	0.0	0	0:0	0:0	0:0	0:0	0:0	0:0	0:2	1:2	2:2	2:2	0:2	
Pine-tar oil (3) plus furfural (1) plus stearic acid (1).....	2	0.302	0	0:0	0:0	0:0	0:28	0:5	0:2	0:2	0:2	0:2	0:2	0:2	
Pine-tar oil (3) plus furfural (1) plus camphor saasy (1).....	2	0.302	0	0:0	0:0	0:0	0:28	0:5	0:2	0:2	0:2	0:2	0:2	0:2	
Pine-tar oil (1) plus furfural (1) plus creosote dip (1).....	2	0.258	0	0:0	0:0	0:0	0:69	0:28	0:5	0:2	0:2	0:2	0:2	0:2	
Pine-tar oil (1) plus furfural (1).....	4	3.302	1.0	0:0	0:1	0:154	0:83	0:0	0:2	0:2	2:2	2:2	2:2	0.0	
Pine-tar oil (3) plus furfural (1).....	2	0.1	0	0:0	0:0	0:09	2:288	1:5	0:2	0:4	2:4	3:4	3:4	1:4	
Pine-tar oil (4) plus furfural (1).....	2	0.1	0	0:0	0:0	0:0	0:0	0:0	0:0	0:1	0:1	0:1	0:1	0:0	
Pine-tar oil (10) plus furfural (1).....	2	0.302	0	0:0	0:0	0:0	0:28	0:5	0:2	0:2	1:2	1:2	1:2	0:2	

DISCUSSION OF RESULTS

COMPOUNDS

HYDROCARBONS

Petrolatum is the only hydrocarbon exhibiting a decided repellent action, and this persists during the first day of exposure only. However, since 1,636 flies out of the total number of 1,659 visited one of the six jars, and 1,454 of these appeared on the second day, it is possible that the meat in this jar was incompletely covered with the petrolatum, and that additional tests will show petrolatum to have a repellent action persisting during the entire time of exposure. The tests with lubricating oil, toluene mixed with petrolatum, naphthalene, and anthracene were made at times when the number of screw-worm flies present was insufficient to yield an accurate result.

The hydrocarbons are not effective in preventing infestation. The best from this standpoint is toluene, since only two out of six jars treated with this compound were infested.

BROMIDES

Para-xylyl bromide is one of the strongest repellents against screw-worm flies discovered in the course of this investigation, its coefficient of attractiveness being only 0.16. Its repellent action persists during five days of exposure. Although it seemingly loses its repellent action when mixed with lubricating oil, these tests were made when too few flies were available for drawing a conclusion. Alpha-bromonaphthalene also is a good repellent against *Cochliomyia* flies, and its action persists for at least three days. The tests with bromoform mixed with kaolin, ethylene bromide, and benzyl bromide were made at times when the number of screw-worm flies present was insufficient to yield an accurate result.

Para-xylyl bromide is very effective in preventing infestation. None of the meat treated with the pure compound was infested with any species of fly, and none of the meat treated with para-xylyl bromide in lubricating oil, either in 1 per cent or 10 per cent solution, hatched out *Cochliomyia* flies. Alpha-bromonaphthalene prevented infestation of meat till the third day of exposure, and no *Cochliomyia* emerged from any of the jars treated with it.

CHLORIDES

A single test with chloroform indicates that it is attractive to screw-worm flies. Pinene hydrochloride and benzyl chloride are the most strongly repellent of the chlorides tested and are effective over the entire period of five days' exposure. Hexachloroethane is effective over a period of three days. Para-xylyl chloride is very much less effective than the corresponding bromide. The tests with benzyl chloride mixed with lubricating oil, para-xylyl chloride mixed with lubricating oil, and chlorinated naphthalene are inconclusive, owing to the absence of an adequate number of flies at the times the tests were carried out.

Benzyl chloride and benzyl chloride in lubricating oil were effective in preventing infestation by any species of fly, and para-xylyl chloride

effectively prevented infestation by *Cochliomyia* even when mixed with lubricating oil in 10 per cent solution.

IODIDES

Iodoform is a very good repellent, either alone or mixed with kaolin or with petrolatum. It is not effective in preventing infestation, but no *Cochliomyia* flies emerged from iodoform-treated meat.

ALCOHOLS

Denatured alcohol appears to be slightly attractive to screw-worm flies, and dextro-borneol, when dissolved in alcohol, becomes more attractive to them. Alpha-terpineol and dextro-borneol are the only compounds in this group exhibiting more than a slight repellent action. The tests with fusel oil, glycerin, and linalool are inconclusive, owing to an insufficient number of flies.

Nearly all of the jars treated with alcohols were infested, but in the case of linalool and menthol this was by species other than *Cochliomyia*.

PHENOLS

Guaiacol is the most effective compound in this group as a repellent for screw-worm flies. Its action persists over five days of exposure. Safrol is effective for the first and second days of exposure, but after that it loses its strength. Tests with ortho-cresol and with thymol plus pine oil are inconclusive because of an insufficient number of flies.

The phenols are surprisingly poor in preventing infestation. While the two jars of meat treated with guaiacol were infested, there was no emergence of *Cochliomyia* from them; neither did any *Cochliomyia* emerge from thymol-treated meat.

ALDEHYDES

Benzaldehyde and furfural are the most effective repellents in this group. Cinnamic aldehyde is a good repellent for two days, and crotonaldehyde and salicylic aldehyde are effective over a period of three days' exposure. The test with formaldehyde mixed with petrolatum is inconclusive, as there were almost no flies at that time.

None of the aldehydes are effective in preventing infestation. No *Cochliomyia* emerged from meat treated with formaldehyde, crotonaldehyde, citronellal, or furfural, but the emergence data on these compounds are meager.

CHLORINE SUBSTITUTED ALDEHYDES

Chloral hydrate is of no value in repelling *Cochliomyia* flies, neither does it prevent infestation.

KETONES

All of the materials in this group appear valueless both as repellents against screw-worm flies, and in preventing infestation.

CHLORINE SUBSTITUTED KETONES

As a group, this is the most effective class of compounds tested, both in repellent action and in preventing infestation. The tests with chloroacetone in lubricating oil (1 per cent and 10 per cent solutions), and with chloroacetophenone in lubricating oil (1 per cent and 10 per cent solutions) are inconclusive on account of lack of flies. Both chloroacetone and chloroacetophenone when used undiluted not only kept over 99 per cent of the flies away, but also prevented any emergence of *Cochliomyia*, and the former compound prevented all infestation.

ACIDS

Although the number of tests with organic acids is inadequate for generalizing, it appears that valeric acid is attractive to screw-worm flies.

ESTERS

The esters tested appear to be neutral rather than repellent to *Cochliomyia* and do not prevent infestation.

HALOGEN SUBSTITUTED ESTERS

Both the beta-chloroethyl and beta-bromoethyl acetates are quite effective in repelling screw-worm flies; and both are quite effective in preventing infestation, not only in undiluted form, but also in combination with lubricating oil (10 per cent solution). There was no emergence of *Cochliomyia* from any of the jars treated with these compounds. The bromo compound is a more effective repellent than the chloro compound. This is in harmony with the results obtained with para-xylyl chloride and para-xylyl bromide.

ETHERS

Beta-naphthylethyl ether is a very good repellent for use against screw-worm flies, being effective over four days' exposure. The tests with this compound mixed with petrolatum and with mineral oil were made when an insufficient number of flies was present for an accurate result. Beta-naphthylethyl ether does not prevent infestation. There was no emergence of *Cochliomyia* from these jars.

CHLOROHYDRINS

Only one compound belonging to this group, namely epichlorohydrin, was tested, and though very few flies were available at the time of the test, the compound exhibits no worth-while repellent action; neither does it prevent infestation.

NITRO COMPOUNDS

Nitrobenzene and alpha-nitronaphthalene were good repellents over the entire period of the test. Nitrocymene is an excellent repellent during the first two days' exposure, but loses its effectiveness on the third day. In preventing infestation, all the nitro compounds show up poorly. The emergence data with this group of compounds are incomplete, but no *Cochliomyia* emerged from meat treated with nitrobenzene.

MIXED NITRO COMPOUNDS

Picric acid, and chloropicrin in lubricating oil in dilutions of 1 in 10 and 1 in 25, are very effective repellents during five days' exposure. Chloropicrin in dilutions of 1 in 50 and 1 in 100 of lubricating oil are effective over the first and second days of exposure. Although the number of screw-worm flies available at the time the tests with para-nitroaniline were made was very small and no generalization can be made, this compound does not look promising for use as a repellent.

Picric acid is not of value in preventing infestation, but chloropicrin in dilutions of 1 in 10 and 1 in 25 of lubricating oil prevented all infestation and emergence.

AMINES

Dimethylaniline, both undiluted and in combination with petrolatum and kaolin, is a good repellent for the first two days of exposure only. One test with alpha-naphthylamine indicates that it has good repellent value over the entire five-day period.

Dimethylaniline is of little value in preventing infestation after the first day of exposure. The jar treated with alpha-naphthylamine was not infested till the fourth day. No *Cochliomyia* emerged from meat treated with any of the amines.

MISCELLANEOUS NITROGENOUS COMPOUNDS

Pyridine is a very good repellent against screw-worm flies, and although all 10 jars were infested by the third day, there was no emergence of *Cochliomyia*.

Nicotine sulphate is of no value either as a repellent or in preventing infestation.

SULPHUR COMPOUNDS

Ethyl mercaptan is one of the most strongly attractive compounds to screw-worm flies tested. The results with allyl isothiocyanate are not consistent; when diluted with either mineral oil, petrolatum, or kaolin it appears a stronger repellent than when undiluted. An interesting contrast between the action of compounds very similar in chemical constitution is shown by ethyl and butyl mercaptans. The ethyl compound is strongly attractive to the flies, the meat treated with it is infested as soon as the untreated meat, and *Cochliomyia* emerged from both of the two jars treated with it. On the other hand, butyl mercaptan is a pretty good repellent for the first two days of exposure, and though all the jars were infested on the second day, there was no emergence of *Cochliomyia*. There was no emergence of *Cochliomyia* from meat treated with allyl isothiocyanate, either.

SELENIUM COMPOUNDS

The data on these compounds are too few for generalization, but are indicative that the selenium compounds are repellent for the first day of exposure only, and have no action on infestation.

INORGANIC COMPOUNDS

Some of the inorganic compounds tested exhibit repellent action for a few days. For example, antimony trichloride is repellent for two days, bleaching powder for three days, copper sulphate for three days, and potassium sulphide for two days. Even the odorless and chemically inactive powder kaolin, for the first day of exposure, repels three-fourths of the screw-worm flies normally present. The strong repellent action of copper carbonate, which persists throughout the five days of exposure, is one of the most puzzling results obtained in the investigation, and required further testing. None of the inorganic compounds are effective in preventing infestation. No *Cochliomyia* flies emerged from jars treated with borax or lead acetate.

ORGANIC PRODUCTS

ESSENTIAL OILS

The following essential oils when undiluted exhibit a coefficient of attractiveness toward screw-worm flies of 10 or less: Star anise, 9.8; bergamot, 6; cade, 4.9; cinnamon, 10; citronella (Ceylon), 2.8; clove, 9.5; clove bud, 6.1; coriander, 5; rose geranium, 8; nutmeg, 9.7; pennyroyal, 9.3; spearmint, 7.6. Tests with Java citronella oil and also with citronella oil of unknown geographical origin show them to have only moderate repellent value (coefficients 75 and 19, respectively) so that the high repellent value found for Ceylon citronella oil requires confirmation. In addition to the above oils, camphor by-product, cassia, copaiba, cumin, fennel, hemlock, and sassafras exhibit good repellent action (coefficient about 10 or less) for the first and second days of exposure only.

None of the essential oils were successful in preventing infestation, but whether the infestation was by *Cochliomyia* or not is difficult to say because the emergence data are very meager. There was no emergence of screw-worm flies, however, from meat treated with the following oils: Star anise, bergamot, cade, camphor, cedar leaf, cinnamon, citronella, clove bud, nutmeg, pennyroyal, sassafras, or thyme.

FATTY OILS

Peach-kernel oil is a good repellent for the first two days of exposure only. None of the fatty oils prevents infestation.

MISCELLANEOUS VEGETABLE PRODUCTS

Clove powder, derris, and pyrethrum are effective repellents for the entire five-day period. Cinnamon powder is effective for the first two days, as are also sassafras bark and wormseed; and lupulin powder is effective over a three-day period. A single test with powdered deer-tongue leaves indicates that they have considerable repellent value.

Although clove powder, derris, and pyrethrum did not prevent infestation, this was by species other than the screw-worm fly, as there was no emergence of *Cochliomyia* from any of the jars treated with these materials. The alcoholic and kerosene extracts of pyrethrum also prevented emergence of *Cochliomyia*.

PINE PRODUCTS

Nearly all of the pine products are very good in repelling screw-worm flies. Although most of the meat treated with pine products showed infestation, this was by species other than *Cochliomyia*.

FURFURAL MIXTURES

All of the furfural mixtures are excellent repellents and are also effective in preventing infestation by *Cochliomyia* (but not by other species).

COAL-TAR CREOSOTES

The coal-tar creosotes are very effective in repelling screw-worm flies and also in preventing infestation by this species.

BONE MEAL

Bone meal repels five-sixths of the screw-worm flies normally visiting meat during the first day of exposure.

BEST REPELLENTS

The most effective repellents against the screw-worm fly are listed in Table 2 in the order of decreasing effectiveness. Only those materials whose coefficient of attractiveness is 10 or less, and in the tests of which not less than 100 flies visited the check jars, are considered. The infestation at end of fifth day and emergence data are also shown for each material in the table. It should be distinctly understood that these statements are not generalizations, but apply only to the tests herein described, and that under other conditions, especially when the substances are used on wounds, very different valuations might be obtained.

TABLE 2.—*Best repellents against Cochliomyia macellaria*

Material	Coefficient ¹	Number of treated jars	Number of flies in treated jars over checks	Infestation: Number of infested treated jars over checks	Emergence, treated over check jars
Salicylic aldehyde (1) plus petrolatum (5).....	0	2	0:113	0:2	0:-
Chloroacetophenone.....	0	3	0:770	2:3	0:3
Chloroacetophenone (1) plus petrolatum (2).....	0	1	0:455	1:1	0:1
Camphor oil by-product (1) plus bone meal (3).....	0	1	0:455	0:1	0:1
Clove-bud oil (3) plus petrolatum (1).....	0	1	0:455	1:1	0:1
Clove powder (1) plus petrolatum (2).....	0	2	0:456	2:2	0:1
Wood naphtha.....	0	4	0:160	4:4	0:2
Pine tar, heavy.....	0	4	0:160	4:4	0:2
Pine tar, medium.....	0	4	0:160	4:4	1:2
Pine tar, thin.....	0	4	0:160	4:4	0:2
Pine-tar oil, refined (1) plus petrolatum (5).....	0	2	0:456	0:2	0:1
Pine-tar oil, refined (1) plus kaolin (3).....	0	1	0:455	0:1	0:1
Pine-tar oil, commercial.....	0	10	0:491	8:10	1:6
Pine-tar oil, commercial (3) plus furfural (1) plus star anise oil (1).....	0	2	0:302	0:2	0:2
Pine-tar oil, commercial (3) plus furfural (1) plus camphor-sassy oil (1).....	0	2	0:302	0:2	0:2
Pine-tar oil, commercial (3) plus furfural (1) plus a creosote dip (1).....	0	2	0:302	1:2	0:2
Pine-tar oil, commercial (1) plus furfural (1).....	0	2	0:238	2:2	0:0
Pine-tar oil, commercial (10) plus furfural (1).....	0	2	0:302	1:2	0:2
Pine-tar oil, commercial (20) plus furfural (1).....	0	2	0:302	0:2	0:2
Pine-tar oil, commercial (3) plus furfural (1) plus fennel oil (1).....	0	2	0:302	0:2	0:2

¹ The figures in this column correspond to those in column 6 of Table 1, i. e., percentage ratio for the entire period.

² The sign (-) means no record.

TABLE 2.—Best repellents against *Cochliomyia macellaria*—Continued

Material	Coefficient ¹	Number of treated jars	Number of flies in treated jars over checks	Infestation Number of Infested treated jars over checks	Emergence, treated over check jars
Pine-tar oil, commercial (3) plus furfural (1) plus safrol (1).....	0	2	0:302	0:2	0:2
Pine-tar oil, commercial (3) plus furfural (1) plus artificial sassafras oil (1).....	0	2	0:302	0:2	0:2
Pine-tar oil, commercial (3) plus safrol (1) plus camphor-sassy oil (1).....	0	2	0:302	1:2	0:2
Pine-tar oil, commercial (3) plus safrol (1) plus fenel oil (1).....	0	2	0:302	0:2	0:2
Pine-tar oil, commercial (3) plus safrol (1) plus salicylic aldehyde (1).....	0	2	0:238	0:2	0:0
Pine-tar oil, commercial (3) plus salicylic aldehyde (1).....	0	4	0:238	3:4	0:2
Pine-tar oil, commercial (3) plus safrol (1).....	0	4	0:302	2:4	0:4
Pine-tar oil, commercial (10) plus safrol (1).....	0	2	0:302	2:2	0:2
Pine-tar oil, commercial (20) plus safrol (1).....	0	2	0:302	0:2	0:2
Furfural (2) plus pine-tar oil (3) plus zinc stearate (2).....	0	2	0:505	2:2	0:2
Furfural (1) plus castor oil (1) plus grafting wax (2).....	0	2	0:505	2:2	0:2
Wood-cresote oil.....	0	2	0:505	2:2	0:2
Coal-tar cresote (1) plus kaolin (3).....	0	1	0:455	0:1	0:1
Pine-tar oil, refined.....	.10	9	1:999	9:1	0:5
Copper carbonate.....	.10	3	1:996	3:3	1:3
Para-xylyl bromide.....	.16	4	1:617	0:4	0:4
Chloroacetone.....	.16	6	1:634	0:6	0:6
Furfural (1) plus petrolatum (2) plus zinc oxide (1).....	.20	2	1:505	2:2	1:2
Furfural (1) plus castor oil (1) plus rosin (1).....	.20	2	1:505	2:2	0:2
Pine oil No. 4.....	.21	10	2:932	8:10	0:4
Furfural (1) plus petrolatum (5).....	.21	3	1:475	1:3	0:1
Sassafras oil, artificial (1) plus kaolin (3).....	.22	1	1:455	1:1	0:1
Clove-bud oil (1) plus kaolin (3).....	.22	1	1:455	0:1	0:1
Coal-tar cresote (1) plus petrolatum (5).....	.22	2	1:456	1:2	0:1
Pine oil, refined.....	.23	8	1:427	6:8	0:2
Camphor, artificial (pinene hydrochloride).....	.27	1	1:366	1:1	0:1
Chloroacetophenone (1) plus kaolin (1).....	.29	3	2:684	2:3	0:3
Beta-bromoethyl acetate.....	.32	4	2:617	1:4	0:4
Pine-tar oil (3) plus safrol (1) plus anise oil (1).....	.33	2	1:302	1:2	0:2
Gualacol.....	.40	2	2:505	2:2	0:2
Pine oil No. 4 (1) plus pine-tar oil (1).....	.42	2	1:238	2:2	0:0
Coal-tar cresote.....	.41	3	4:982	0:3	0:3
Camphor oil by-product (3) plus petrolatum (1).....	.3	4	3:1,023	2:4	0:2
Rosin residue (1) plus pine oil (1).....	.59	2	3:505	2:2	0:2
Pine tar (1) plus borax (1) plus kaolin (2).....	.66	1	3:455	1:1	0:1
Pine-tar oil (3) plus safrol (1) plus artificial sassafras oil (1).....	.66	2	2:302	1:2	0:2
Iodoform (1) plus petrolatum (2).....	.66	1	3:455	1:1	0:1
Benzyl chloride.....	.81	4	5:617	0:4	0:4
Clove oil (3) plus petrolatum (1).....	.88	2	1:113	2:2	-----
Clove powder (1) plus kaolin (4).....	.88	1	4:455	1:1	0:1
Pine oil (steam distilled).....	.99	2	5:505	2:2	0:2
Pine-tar oil (3) plus furfural (1).....	1.0	4	3:302	3:4	1:4
Allyl isothiocyanate (1) plus kaolin (3).....	1.1	4	7:640	4:4	0:1
Sassafras oil (3) plus petrolatum (1).....	1.6	3	9:568	3:3	0:2
Pine-tar (1) plus borax (1).....	1.6	3	11:688	2:3	0:1
Pine oil No. 4 (1) plus refined tar oil (1).....	1.7	2	4:238	2:2	0:0
Pine-tar oil (1) plus safrol (1).....	1.7	2	4:238	2:2	0:0
Pine-tar (1) plus borax (1) plus petrolatum (2).....	1.5	1	7:455	1:1	1:1
Pine-oil foots (1) plus furfural (1).....	1.8	2	9:505	2:2	0:2
Wood-tar oil.....	1.4	6	9:625	4:6	0:0
Furfural (1) plus gum galbanum (1).....	1.2	2	6:505	2:2	0:2
Picric acid.....	2.0	3	19:996	3:3	2:3
Benzaldehyde.....	2.2	2	11:505	2:2	1:2
Nitrobenzene (1) plus kaolin (4).....	2.3	3	14:623	3:3	0:1
Chloroquin (1) plus lubricating oil (24).....	2.3	2	14:600	0:2	0:2
Pine oil, crude.....	2.3	2	14:616	2:2	1:2
Pine-tar acid.....	2.4	2	12:505	2:2	1:2
Nitrobenzene (1) plus petrolatum (5).....	2.4	2	13:551	2:2	0:1
Iodoform (1) plus kaolin (4).....	2.6	1	12:455	1:1	0:1
Alpha-naphthylamine.....	2.6	1	4:151	1:1	0:1
Clove oil (1) plus kaolin (3).....	2.7	2	3:113	2:2	-----
Citronella oil (Ceylon).....	2.8	3	6:212	3:3	-----
Turpentine, crude.....	2.8	7	21:747	7:7	1:5
Furfural (1) plus petrolatum (1) plus grafting wax (2).....	2.0	2	11:505	2:2	0:2
Camphor oil by-product (1) plus kaolin (3).....	1.7	5	19:1,095	2:5	0:2
Furfural (1) plus petroleum (1).....	3.2	2	16:505	2:2	0:2
Furfural (1) plus kaolin (4).....	3.6	4	23:640	3:4	1:1
Beta-chloroethyl acetate.....	3.6	4	22:617	1:4	0:4

¹ The figures in this column correspond to those in column 6 of Table 1, i. e., percentage ratio for the entire period.

TABLE 2.—*Best repellents against Cochliomyia macellaria*—Continued

Material	Coefficient ¹	Number of treated jars	Number of flies in treated jars over checks	Infestation: Number of infested treated jars over checks	Emergence, treated over check jars
Pine tar	3.9	16	93:2, 373	11:16	0:6
Beta-naphthylethyl ether	4.0	9	60:1, 506	7:9	0:6
Pine-tar oil	4.4	12	35:798	12:12	0:3
Powdered deer-tongue leaves	4.4	1	16:366	1:1	1:1
Clove powder	4.7	12	71:1, 502	9:12	0:4
Pyridine	4.7	10	68:1, 447	10:10	0:4
Derris powder	4.7	5	30:634	5:5	0:4
Safrol (1) plus kaolin (4)	4.8	2	8:168	2:2	0:-
Cade oil	4.9	11	59:1, 207	11:11	0:6
Salicylic aldehyde (1) plus kaolin (4)	4.9	3	9:185	2:3	0:-
Coriander oil	5.0	7	67:1, 331	6:7	1:4
Furfural	5.3	17	81:1, 527	16:17	0:7
Pyrethrum powder	5.8	6	50:862	6:6	0:6
Bergamot oil	6.0	1	22:366	1:1	0:1
Clove-bud oil	6.1	5	54:893	5:5	0:2
Citronella oil (Ceylon) (3) plus petrolatum (1)	6.2	2	7:113	2:2	-----
Citronella oil (Ceylon) (1) plus kaolin (3)	6.2	2	7:113	2:2	-----
Crotonaldehyde	6.4	4	23:357	4:4	0:4
Pine oil, pure steam distilled	6.5	8	42:647	4:8	1:4
Alpha-nitronaphthalene	6.6	1	10:151	1:1	1:1
Iodoform	6.8	4	76:1, 116	4:4	0:4
Alpha-bromonaphthalene	7.1	5	67:941	5:5	0:3
Wood creosote	7.5	7	35:465	6:7	0:1
Spearmint oil	7.6	9	119:1, 561	9:9	1:6
Star-anise oil (1) plus kaolin (3)	8.0	2	9:113	2:2	-----
Rose-geranium oil	8.0	5	91:1, 136	4:5	1:4
Pine oil, pure amber steam distilled	8.3	3	51:617	2:3	0:2
Pennyroyal oil	9.3	11	206:2, 209	5:11	0:2
Clove oil	9.5	10	105:1, 107	9:10	1:3
Wood naphtha (1) plus pine-tar oil (1)	9.6	2	19:198	2:2	0:0
Nitrobenzene	9.6	16	132:1, 378	13:16	0:5
Nutmeg oil	9.7	2	15:154	2:2	0:1
Star anise oil	9.8	11	142:1, 456	7:11	0:4
Hexachloroethane	10	2	16:154	2:2	1:1
Cinnamon oil	10	12	196:1, 969	10:12	0:4

¹The figures in this column correspond to those in column 6 of Table 1, i. e., percentage ratio for the entire period.

These best repellents may be classified in the following groups:

Halides. Benzyl chloride, para-xylyl bromide, iodoform, hexachloroethane, alpha-bromonaphthalene.

Phenols. Guaiacol.

Aldehydes. Furfural, benzaldehyde, salicylic aldehyde.

Chlorine substituted ketones. Chloroacetone, chloroacetophenone.

Halogen substituted esters. Beta-bromoethyl acetate, beta-chloroethyl acetate.

Ethers. Beta-naphthylethyl ether.

Nitro compounds. Nitrobenzene, chloropicrin (trichloronitromethane), picric acid (trinitrophenol), alpha-nitronaphthalene.

Amines. Alpha-naphthylamine.

Miscellaneous nitrogenous compounds. Pyridine.

Inorganic compounds. Copper carbonate.

Essential oils. Clove-bud oil, artificial sassafras oil, clove oil, Ceylon citronella oil, cade oil, coriander oil, bergamot oil, spearmint oil, star-anise oil, rose-geranium oil, pennyroyal oil, nutmeg oil, cinnamon oil.

Miscellaneous vegetable products. Pyrethrum, derris, clove powder, powdered deer-tongue leaves.

Pine products. Pine oil, pine tar, pine-tar oil, turpentine, etc.

It will be noted that one of the halides (alpha-bromonaphthalene), the only ether studied (beta-naphthylethyl ether), one of the nitro compounds (alpha-nitronaphthalene), and the better of the two amines studied (alpha-naphthylamine) are all naphthalene derivatives. Naphthalene itself was tested at times when too few screw-worm flies were present to enable a conclusion to be drawn.

The following compounds were used during the World War as "tear gases" and are characterized by causing intense irritation to the eyes: Benzyl chloride, para-xylyl bromide, chloroacetone, chloroacetophenone, beta-chloroethyl acetate, beta-bromoethyl acetate, and chloropicrin.

In regard to attractiveness for the screw-worm fly, ethyl mercaptan was the best in this respect. Chloroform shows some attractiveness, also denatured alcohol and valeric acid.

Practically all of the materials which are effective in repelling screw-worm flies are also very effective in preventing the deposition of eggs. The emergence data show that almost no *Cochliomyia* emerged from any of the jars treated with these repellents. In other words, the fly-repellent value of a material is an index of its value in preventing infestation by *Cochliomyia*.

MATERIALS EXHIBITING A PERFECT REPELLENT ACTION FOR PERIODS OF FROM TWO TO FIVE DAYS

Each of the following materials was tested not less than four times, and when the number of flies visiting all the comparable check jars was 100 or over:

(1) Materials which repelled all flies for a period of two days: Allyl isothiocyanate plus kaolin, and cade oil.

(2) Materials which repelled all flies for a period of three days: Pine-tar oil, refined.

(3) Materials which repelled all flies for a period of four days: Para-xylyl bromide, refined pine oil, and pine oil No. 4.

(4) Materials which repelled all flies for a period of five days: Wood naphtha, heavy pine tar, medium pine tar, thin pine tar, commercial pine-tar oil, commercial pine-tar oil (3) plus safrol (1), commercial pine-tar oil (3) plus salicylic aldehyde (1).

Inasmuch as both allyl isothiocyanate and fennel oil, when applied undiluted to meat, failed to keep all screw-worm flies away for the first two days, it is probable that additional tests with mixtures of these compounds with kaolin and petrolatum will indicate that they have less repellent value than present tests show.

The above grouping of materials is of interest because it is the experience of stockmen that a material which effectively repels flies for at least two days is suitable for use on animals as a fly-repelling wound dressing, provided, of course, there are no practical objections to its use, such as injurious effects on the animal tissues.

RELATION BETWEEN REPELLENT ACTION OF COMPOUNDS AND THEIR CHEMICAL CONSTITUTION AND VOLATILITY

An examination of the data fails to show any consistent relation between the fly-repellent properties of the compounds and their chemical constitution. There is no clear difference in the repellent action of the aliphatic and aromatic compounds, nor in that of the various classes of compounds, such as aldehydes, phenols, etc.

The introduction of a halogen atom into a compound in some cases greatly increases its repellent action toward screw-worm flies. For example:

Compound	Coefficient	Compound	Coefficient
Toluene.....	68	Benzyl chloride.....	0.8
Dextro-pinene.....	58	Pinene hydrochloride.....	27
Naphthalene.....	65	Alpha-bromonaphthalene.....	7.1
Acetone.....	76	Monochloroacetone.....	16

On the other hand, in some cases the halogen derivative has almost the same repellent value as the parent hydrocarbon. For example:

Compound	Coefficient	Compound	Coefficient
Crude solvent naphtha (mixture of xylenes)-----	22	Para-xylyl chloride-----	16
Naphthalene-----	65	Chlorinated naphthalene-----	60
Benzene-----	70	Para-dichlorobenzene-----	82

Bromine has a more marked action in enhancing the repellent action of a compound than chlorine. For example:

Compound	Coefficient	Compound	Coefficient
Para-xylyl chloride-----	16	Para-xylyl bromide-----	0.16
Beta-chloroethyl acetate-----	3.6	Beta-bromoethyl acetate-----	.32

Iodine is even more powerful than bromine in increasing the repellent action of compounds. Compare:

Chloroform, 192; bromoform, 51; iodoform, 6.8.

The introduction of a nitro (NO₂) group into a compound increases its repellent action toward screw-worm flies. For example:

Compound	Coefficient	Compound	Coefficient
Benzene-----	70	Nitrobenzene-----	9.6
Para-cymene-----	46	Nitrocymene-----	39
Naphthalene-----	65	Alpha-nitronaphthalene-----	6.6
Chloroform-----	192	Chloropicrin (nitrochloroform)--	0

There is no correspondence in the repellent action of the compounds tested and their boiling points. While in the homologous series benzene, toluene, and ortho-xylene an increase in boiling point is accompanied by an increase in repellent action upon screw-worm flies, this is so slight as to be within the limit of error in the results.

	Boiling point (° C.)	Coefficient
Benzene-----	79.6	70
Toluene-----	110.5	68
Orthoxylyene-----	144	47

The following examples show how little relation there is between the repellent action and boiling points of compounds:

(1) Compounds boiling between 142.5° and 161.7° C.:	Boiling point	Coefficient
Amyl acetate-----	142.5	75
Allyl isothiocyanate-----	150.7	16
Alpha-pinene-----	154	58
Furfural-----	161.7	5.3
(2) Compounds boiling between 202° and 220.7° C.:		
Normal-caproic acid-----	202	35
Guaiacol-----	205.1	0.4
Citronellal-----	208	45
Camphor-----	209.1	29
Nitrobenzene-----	210.9	9.6
Menthol-----	212	98
Dextro-borneol-----	213.5	13
Naphthalene-----	217.9	65
Alpha terpineol-----	219.8	12
Para-xylyl bromide-----	220.7	0.16

Obviously the boiling point would have a relationship to the persistence of the repellent effect, and materials with a very low boiling point would be too volatile to be of practical value as repellents.

SUMMARY

In an investigation having as its object the discovery of a repellent for blowflies suitable for application upon wounds on domestic

animals, the chemotropic responses of three species of blowflies (the screw-worm fly, *Cochliomyia macellaria* Fab.; the green-bottle fly, *Lucilia sericata* Meig.; and the black blowfly, *Phormia regina* Meig.), and the house fly (*Musca domestica* L.) to a wide range of organic and inorganic compounds, essential oils, plant products, and pine-distillation products have been determined.

The repellent or attractant action of 353 compounds and mixtures upon the screw-worm fly, *Cochliomyia macellaria* Fab., is reported in this bulletin.

The chemotropic effect of these materials was tested by smearing 5 cubic centimeters of the liquids or 5 grams of the solids over 4 ounces of fresh beef liver contained in a pint Mason jar. These jars were then exposed in the proximity of a packing house or other environment where flies were abundant. Tests were made at Dallas and Uvalde, Tex., during the summer months. Untreated meat was exposed at the same time, and the chemotropic effect of the materials is calculated by the ratio of the number of flies visiting the treated jar over the number of flies visiting the untreated or check jar. A total of 1,152 treated jars are reported in this bulletin.

About 20 of the organic compounds diminish the normal attractiveness of beef liver to *Cochliomyia* flies from 100 to 10 or less. These are representative of nine different classes of organic compounds. Four of these compounds are naphthalene derivatives, and seven others are characterized by causing intense irritation to the eyes of man, and were used during the World War as "tear gases." There are not sufficient data on the organic compounds to show clearly any consistent relation between chemical constitution and repellent value. There appears to be no relation whatever between the repellent action of the organic compounds tested and their boiling points.

Only one inorganic compound, copper carbonate, is an effective repellent for screw-worm flies. A number of the essential oils are good repellents, among which are Ceylon citronella oil and American pennyroyal oil, commonly used as mosquito repellents. Powdered pyrethrum and derris, both of which are valuable contact insecticides, are effective in repelling screw-worm flies.

Except for the conclusion presented in the following paragraph, no attempt is made to draw conclusions as to the practicability of utilizing on livestock the substances tested. The results herein presented serve as a basis for tests on living animals, which are now under way. Furthermore, it is felt that these studies are a step in the direction of obtaining a better insight into the fundamental principles underlying the chemotropic responses of insects.

Of all the materials tested as repellents against the screw-worm fly, certain products obtained from the pine are among the best. These include pine oil, both the destructively and steam distilled, crude turpentine, pine tar, and pine-tar oil. In view of the cheapness, availability, nontoxicity, and adhesiveness of pine-tar oil, the writers are of the opinion that this is the best material among all of those tested to use upon wounds of domestic animals to protect them against the screw-worm fly.

UNITED STATES DEPARTMENT OF AGRICULTURE



DEPARTMENT BULLETIN No. 1476



Washington, D. C.



February, 1927

A PROGRESS REPORT ON THE INVESTIGATIONS OF THE EUROPEAN CORN BORER

By

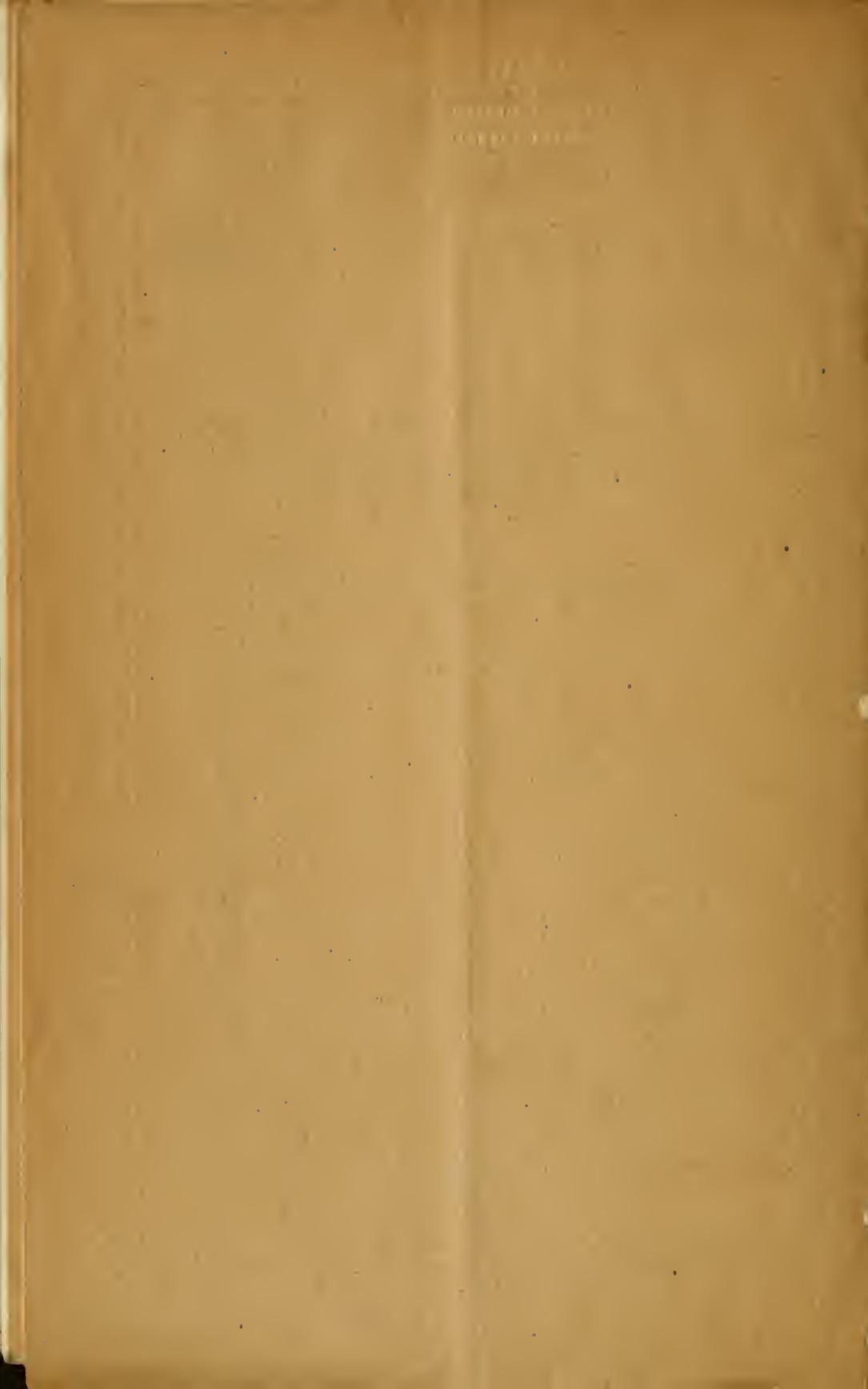
D. J. CAFFREY, Entomologist in Charge, Corn Borer Investigations, and
L. H. WORTHLEY, Administrator in Corn Borer Control, Bureau of Entomology

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WASHINGTON
GOVERNMENT PRINTING OFFICE

1927



UNITED STATES DEPARTMENT OF AGRICULTURE



DEPARTMENT BULLETIN No. 1476



Washington, D. C.

February, 1927

A PROGRESS REPORT ON THE INVESTIGATIONS OF THE EUROPEAN CORN BORER

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INCEPTION AND SCOPE OF THE WORK ¹

The discovery of the European corn borer (*Pyrausta nubilalis* Hüb.) in the vicinity of Boston, Mass., during the summer of 1917, was the first definite intimation that this dangerous foreign pest had gained a foothold on the North American Continent. Stuart C. Vinal,² of the Massachusetts Agricultural Experiment Station, who discovered the presence of the insect (70),³ immediately began a preliminary survey and investigation to determine its distribution, biology, economic importance, and methods of possible control or repression under American conditions. This investigation was continued during 1918 in cooperation with the Bureau of Entomology (71). In 1919 the project was taken over by the bureau and has since been continued on that basis.

¹The investigations reported in this bulletin, covering the period from the spring of 1918 to fall of 1924, have been conducted by D. J. Caffrey and L. H. Worthley, under the direction of W. R. Walton, formerly entomologist in charge, and George A. Dean, senior entomologist in charge, cereal and forage insect investigations, to whom many thanks are expressed for their advice, constructive criticism, and supervision. The section on distribution and scouting in the United States was prepared by Mr. Worthley, assisted by R. A. Vickery. The sections on seasonal history, seasonal development, and winter mortality of larvae in stored material were conducted and prepared by K. W. Babcock, following the methods suggested by Victor E. Shelford, of the University of Illinois. The descriptions were prepared by W. O. Ellis. The data on seasonal occurrence, and most of the data on life history, habits, predators, and dispersion by water drift, were prepared by G. W. Barber, assisted by W. O. Ellis, K. W. Babcock, L. H. Patch, R. H. Van Zwaluwenburg, D. H. Craig, L. B. Scott, F. L. O'Rourke, J. J. McCarthy, and B. W. Banks. The data pertaining to host plants, infestation and injury to vegetables, flowers, field crops, etc., were prepared by B. E. Hodgson, assisted by F. W. Grigg, L. B. Sanderson, F. S. Vidler, and O. J. Teel. The work on parasites was conducted and reported by D. W. Jones, assisted by H. L. Parker, R. C. Ellis, H. E. Smith, C. W. Smith, and A. N. Vauce.

The purpose of this publication is to record the more important results of the investigations upon the bionomics of the insect. The data pertaining to control, as well as to the quarantine and scouting operations, will be issued in a separate publication. Most of the information contained herein has accrued since 1918, through investigations carried on at bureau laboratories located at Arlington, Mass., Silver Creek, Schenectady, and Scotia, N. Y., Sandusky, Ohio, and Hyères, Var, France, together with data obtained during the field control, scouting, and quarantine operations. The information obtained during the cooperative work with the Massachusetts Agricultural Experiment Station (71) has also been freely drawn upon, as well as the original report from that station (70) announcing the discovery of the insect.

SYSTEMATIC HISTORY AND SYNONYMY

Until the latter part of the nineteenth century not a little confusion existed in foreign literature concerning the systematic history and synonymy of the insect that is now known in America as the European corn borer (*Pyrausta nubilalis* Hübn.).

In 1796 Hübner (26, figs. 94, 116) described and figured a male moth from Hungary as *Pyralis nubilalis*. (Hüb., fig. 94.) At the same time he described and figured a female moth from Austria as *P. silucealis*. (Hüb., fig. 116.) The food plant was not mentioned in either instance. It was afterwards shown by Treitschke (67, p. 81) in 1829 that these supposed "species" merely represented opposite sexes of a single species. According to the law of priority, therefore, the name *nubilalis* is retained for Hübner's species. The error by Hübner, however, led several succeeding workers to adopt the name *silucealis*, which fact contributed to the confusion regarding its synonymy in Europe.

The information pertaining to the eastern New York area was reported by C. F. Turner, J. H. Barman, E. M. Searls, T. R. Richardson, H. D. Smith, J. J. Kelly, and H. P. Wood. In the western New York and Pennsylvania area the information was obtained and reported by H. N. Bartley, L. B. Scott, C. E. Hofer, L. H. Patch, J. J. McCarthy, George Wishart, and H. H. Hodgkiss; and from Ohio and Michigan by F. W. Poos, L. H. Patch, P. A. Howell, H. P. Wood, H. S. Peters, O. L. Cartwright, and E. G. Moore.

Carl Heinrich kindly reviewed the section on systematic history and synonymy. He has also determined larvae, pupae, and adults of *Pyrausta nubilalis*, as well as closely allied species which were reared or collected during the progress of the investigations. J. M. Aldrich, of the United States National Museum; A. B. Gahan and R. A. Cushman, of the taxonomic staff of the bureau in Washington; and C. F. W. Muesebeck, of the gipsy-moth laboratory, have determined the parasitic insects mentioned herein.

Much of the information on the corn borer in Europe has been taken from an unpublished manuscript written (in his capacity as collaborator of the Bureau of Entomology) by J. Jablonowsky, director of the Hungarian Agricultural Experiment Station, Budapest, Hungary. (Jablonowski, J., The European Corn Borer and Its Control in Hungary. [Unpublished manuscript. Abstracted by W. K. Walton and J. S. Wade. Mimeographed.]) Professor Jablonowsky has studied *P. nubilalis* in Hungary for more than 25 years, and his manuscript includes valuable and complete information relative to the history and distribution of the corn borer in Europe, as well as details concerning its biology in Hungary and the methods of control practiced in that country.

W. R. Thompson, in charge of the European parasite laboratory conducted by the Bureau of Entomology at Hyères, Var, France, has contributed most of the data relative to the parasites of *P. nubilalis* in Europe, as well as a portion of the information pertaining to its habits, seasonal history, economic status, and distribution in France, Belgium, and Italy.

K. W. Babecek, of the Arlington, Mass., laboratory, who began environmental research studies upon *P. nubilalis* in Europe during the spring of 1924, has also contributed information relative to the seasonal history, habits, economic status, and distribution of the borer in Hungary, Italy, Rumania, Yugoslavia, Germany, and France.

²Mr. S. C. Vinal, who conducted the initial investigations of this pest with great ability and zeal, died Sept. 27, 1918. It is believed that his untimely death was due largely to his intense devotion to the work. Had he lived to complete his task there is no doubt that he would have contributed largely to the success of the project.

³Italic numbers in parentheses refer to "Literature Cited," p. 143.

Haworth (22, p. 380), 1811, described a species from England as *Pyralis glabratis*. This later was accepted as a doubtful synonym by Hampson (21, p. 435) and others, although the description is at variance with Hübner's species.

Treitschke (67, p. 81), 1829, and Duponchel (15, p. 121, CCXVII, 4), 1831, adopted the name *Pyralis silacealis* Hübner, although recognizing that *nubilalis* of Hübner was the male of *silacealis*. Freyer (18, p. 96), 1831, Kollar (34, p. 108), 1840, Herrich-Schaeffer (25, p. 30), 1849, and Snellen (59, p. 49) as late as 1882, designated the species as *silacealis* and referred it to the genus *Botys* erected by Latreille (38), 1805.

Guenée (20, p. 331), 1854, accepted the species as being identical with *Phalaena lupulina* Clerck, illustrated in the *Icones Insectorum* of Clerck (11) in 1759. He therefore designated it as *Botys lupulinis*. A study of Clerck's figure, however, convinced later workers that Clerck's *lupulina* was not identical with Hübner's species. This interpretation by Guenée, nevertheless, led to the acceptance of the name *lupulina* by several succeeding workers. Heinemann (23, pp. 1, 2, 70), 1865, designated a species from Switzerland as *Botys lupulina*. This is now listed as a synonym of Hübner's species. Butler (10, p. 19), 1889, referred to the species as *Hapalia lupulina* (non Clerck).

Guenée (20, p. 332), 1854, described a species from the East Indies as *Botys zealis*, which he regarded as being very close to his *B. lupulinis*, asserting, "it may be simply a variation of our *lupulinis*." This species is now listed as a synonym of Hübner's species, although some authors are not convinced of its validity.

Lederer (39, p. 372), 1863, retained the species of *Botys* and accepted the figure of Hübner's *nubilalis* as truly representing the species. This designation was accepted by Staudinger and Wocke (62, p. 209), 1871, Jourdhueille (32, p. 129), 1883, Robin and Laboulbène (52), 1884, and by Leach (46, p. 32, IV, 4), 1886.

Moore (48, p. 222, pl. VII, fig. 28), 1888, described a species from Kashmir, India, as *Hapalia kasmirica*. This is now listed by Hampson (21, p. 435) and others as a synonym of Hübner's species. (Specimen in collection of Doctor Staudinger.)

Meyrick (45, p. 416), 1895, removed the species to the genus *Pyrausta*, erected by Schrank (55) in 1802, and retained *nubilalis* of Hübner, an action which has since been followed by Hampson (21, p. 435), 1896, and by Staudinger and Rebel (61, p. 65), 1901.

In 1905 Dyar (16, p. 955) described a species from Japan as *Pyrausta polygoni* (type a ♀). The specimens were reared from *Polygonum tinctorum*. Dyar differentiated his species from *nubilalis* on several characters, chief among which was the similar coloring of males and females, which character would indeed exclude it as a synonym of *nubilalis*. According to Carl Heinrich, however, the male paratype is badly faded and rubbed, which may account for the lack of characteristic coloring. Its genitalia are identical with *nubilalis* and on that account Mr. Heinrich is of the opinion that *polygoni*, with some reservation, should be considered a synonym of *nubilalis*.

Schultze (56, p. 35), 1908, described a male and female reared from corn at Manila, Philippine Islands, as *Pyrausta vastatrix* (type a ♀). The very brief description of the male poorly applies

to *nubilalis*, but according to Mr. Heinrich, a female in the United States National Museum received from the Philippines as *vastatrix* agrees in oral and genitalic characters with typical *nubilalis*. Mr. Heinrich is of the opinion that *vastatrix*, with some reservation, should be considered a synonym of *nubilalis*.

Reference to the species *Pyrausta nubilalis* Hübner may, therefore, be arranged as follows:

- Pyrausta nubilalis* Hübner (26, figs. 94, 116).
Pyralis silacealis Hübner (26, figs. 94, 116).
Pyralis glabrata Haworth (22, p. 389).
Botys silacealis Freyer (18, p. 96).
Botys lupulina Guenée (20, p. 331).
Botys zealis Guenée (20, p. 332).
Botys nubilalis Lederer (39, p. 372).
Botys lupulina Heinemann (23).
Hupalia kasmirica Moore (48, p. 222, pl. VII, fig. 28).
Hupalia lupulina Butler (10, p. 19).
Pyrausta nubilalis Meyrick (45, p. 416).
Pyrausta polygوني Dyar (16, p. 955).
Pyrausta vastatrix Schultze (56, p. 35).

DISTRIBUTION

FOREIGN DISTRIBUTION

Hübner (26, figs. 94, 116) in his original record of the species gave its habitat as "Europe, western Asia, the Himalayas, and Assam" (northern India). Foreign literature also refers, in general terms, to the range of *Pyrausta nubilalis* as central and southern Europe (45, p. 416), Asia Minor (61, p. 65), west-central and northern Asia (45, p. 416), northwestern Himalayas (21, p. 436), northern India (61, p. 65), Siberia (61, p. 65), Japan (45, p. 416), the East Indies (20, p. 332), the Philippine Islands (56, p. 35), and Guam (8, p. 39-40).

The published records and correspondence of various foreign writers mentioning more in detail the distribution of *P. nubilalis* in the Old World indicate that it is widely distributed in certain districts of the Netherlands, Belgium, France, Italy, Germany (Bavaria), Austria (Vienna district), Hungary, Czechoslovakia (Bohemia), Yugoslavia (Slavonia and Carniola), Rumania (Transylvania and Wallachia), southern and southwestern Russia, including Trans-Caucasia, with apparently isolated areas of infestation in the irrigated regions near the city of Astrakan, and in Livonia (67, p. 81; 20, p. 331).

Meyrick (45, p. 416) mentioned the occurrence of the species in England (Middlesex, Isle of Wight, Lancashire)—"probably a casual immigrant only."

The species has also been reported from Switzerland (23, p. 1, 2, 70) and Portugal (44), and in 1920 the Bureau of Entomology received specimens of *P. nubilalis* larvae from Spain (Madrid). It has also been recorded from the Erivan district of Armenia (68); from the Province of Ferghana in Turkestan (69); from the Provinces of Kashmir (48, p. 122, pl. VII, fig. 28); from Sikkim, Manipur and the Khasi Hills (21, p. 436) in northern India; from Cairo, Egypt (19, p. 270); and from the Province of Amur in Siberia (61, p. 65).

In Japan the occurrence of the species is mentioned by Meyrick (45, p. 416) and by Takahashi (64). During 1922 adults were submitted to the Bureau of Entomology from Yokohama, Japan. Briggs (8, p. 39-40) recorded severe damage by the European corn borer to corn in the island of Guam during the period from 1917 to 1919. Specimens from Guam were submitted to the Bureau of Entomology during 1918 and identified as *P. nubilalis*. A species reared from corn at Manila, P. I., was described as *Pyrausta vastatrix* by Schultze (56, p. 35) in 1908. This name is now believed to be a synonym of *P. nubilalis*.

Additional distribution records of the species in Germany and Austria were secured by K. W. Babcock during the summer of 1924. He collected specimens of the eggs, larvae, and pupae in the vicinity of Berlin and examined specimens in the museum at Berlin that were collected near Danzig and at other points throughout northern Germany. Records were also obtained of the presence of the species near Hamburg and in Wurtemberg. In southeastern Austria Mr. Babcock observed *P. nubilalis* in the regions of Gratz, Bruck, Kapfenberg, Boden, and Affenz, and he received reports showing that the species was present at Klagenfurt, and at Marburg in Yugoslavia. In correspondence W. R. Thompson states that according to a report received by him from Doctor Isaakides, of the Greek phytopathological service, the species frequently causes important damage in the Provinces of Trikkala, Karditza, and Karpenissi in Greece.

By reviewing the foregoing, it will be noted that *P. nubilalis* has a wide geographic range in the Northern Hemisphere extending from approximately latitude 58° north (Livonia) to 13° north (Guam and the Philippines). Its climatic range embraces a very wide contrast of meteorological conditions varying from the dry steppes of southeastern Russia (Tsaritsyn), where the annual mean temperature averages 44.6° F. and the precipitation 13.11 inches annually, to the warm equable temperatures of Guam, with an average annual mean of 81.7° F. and a mean precipitation of 97.27 inches annually. The species is also present in certain irrigated areas, notably in Egypt, Trans-Caucasia, and southern France, where the temperature is relatively high, but where the rainfall in some cases is not sufficient to mature ordinary crops without irrigation. Riazan in Russia, with an annual mean of 40.3° F., and Guam with an annual mean of 81.7° F., represent approximately the lowest and highest temperature limits within which the insect is known to exist. Judging from this facile adaptability to a wide range of climatic conditions exhibited by the species, it appears reasonable to assume that there would be no climatic barrier to prevent *P. nubilalis* from becoming established over the greater part of the arable regions of the United States wherever its host plants can be grown. In this contingency the economic status of the species undoubtedly would vary in certain areas representing widely different climatic and cultural conditions comparable to the apparent variation in its status within the different areas of its occurrence abroad.

ECONOMIC HISTORY IN THE OLD WORLD

The status of *P. nubilalis* as a serious enemy of corn, hops, millet, and hemp has long been recognized in the Old World, although there are no existing records of it as an important economic pest prior to 1835. At that time it was recorded by Schmidt (54) as causing severe injury to millet (*Panicum miliaceum*) in Carniola (Yugoslavia). This author states that, under conditions favorable to the larva, the yields of millet fields attacked by it were reduced by one-twelfth or perhaps even one-eighth. Subsequent foreign literature contains a large number of references to the occurrence of and serious injury by *P. nubilalis* in fields of corn, hops, millet, and hemp; especially in Hungary, Rumania, Yugoslavia, Russia, and France. Some of these reports give definite estimates concerning the degree of actual economic loss sustained, but in many instances the details regarding percentage of infestation and injury are lacking. Mention is frequently made in some of the foreign references, dealing particularly with certain areas where hops, millet, hemp, and broomcorn are attacked by *P. nubilalis*, that the insect is widely distributed in these areas, but that it is normally not abundant enough to be of practical importance.

Judging from all available information it is apparent that in certain areas of the Old World, particularly where corn is grown, *P. nubilalis* becomes periodically abundant and causes severe losses, whereas in other areas it is a widely distributed pest which normally does not cause severe economic losses and seldom becomes destructively abundant.

Most of the foreign authors agree that corn is injured by *P. nubilalis* to a greater extent than any of its other cultivated hosts, although some instances are cited of serious injury to hops, millet, and hemp.

One of the first records pertaining to the European corn borer as a pest in Hungary was by Linderman, early in the nineteenth century, who mentioned it as a pest of Indian corn. Emich (17) recorded damage in Hungary to corn, millet, and hemp during the period from 1871 to 1884. Szaniszlo (63) reported slight injury to corn and millet at Kolozsvár during 1884. In 1886 Jablonowski (27) asserted that some damage was wrought to corn in the Banhegyes district of Hungary. During the period from 1891 to 1893 the same author recorded severe damage to corn from several localities in Hungary, where, in badly infested fields the loss amounted to one-third of the yield, and in at least one field under observation, consisting of about 70 acres, a total loss of the grain was sustained. According to Jablonowski (28) the insect was again very injurious to corn in Hungary during 1897. He observed severe injury to corn in at least 11 localities and estimated that the average damage throughout the country was at least one-fourth of the grain. At this time complaints were received from 1,600 to 1,800 official agricultural correspondents concerning the damage caused by this pest. The same author (30) recorded another severe outbreak in Hungary during 1915 and 1916. The damage during that period was reported as being particularly severe in the Bačka, one of the principal corn-growing regions of Hungary. Jablonowski asserts that in 1916 the large landowners of this region estimated their total losses

due to corn-borer damage as equivalent to from \$8,000,000 to \$10,000,000, estimating the value of the corn at war prices. That author estimated the loss in different fields of the Baeska region as ranging from 5 to 60 per cent of the grain during 1916. Bakó (4) estimated that 50 per cent of the corn in the Baeska region was destroyed in 1917. In correspondence dated November 16, 1921, Joblonowski stated that the damage in Hungary from *P. nubilalis* had reached its culmination in 1919 and was now diminishing. He considers the loss to be unimportant during 1921.

During 1924 Mr. Babcock conducted observations in the principal corn-growing areas of Hungary, and his reports show that the corn borer caused serious damage to corn in restricted areas of the Great Plain of Hungary during that season, although it was not considered to be a favorable year for the insect. According to Mr. Babcock, appreciable damage occurred throughout the southern and central parts of the country, but that part of southern Hungary lying between Bekes and Novi Sad (including the contiguous areas of Rumania and Yugoslavia) was practically the only region observed, or reported, during 1924, where the corn borer caused serious interference with the growth of corn. Detailed studies of the actual losses caused by the corn borer in the corn-fields of this region showed an average estimated loss of 23.9 per cent in 38 fields in the vicinity of Mezöhegyes, 18.9 per cent loss in 12 fields near Novi Sad, 18.4 per cent loss in 19 fields at Bankut, and losses ranging from 14.2 to 5.5 per cent in other districts of this region. A combination of fungus and borer injury was rather widespread in this region during 1924, and in the majority of instances where the grain had been injured by the borer the fungus developed and rendered the injury more serious. In seven fields of broomcorn examined near Mezöhegyes and Bankut, Mr. Babcock found that the stalk infestation ranged from 7.4 to 54.8 per cent, with a general average of 24.5 per cent and an average of 34.3 borers per 100 plants. An examination of five fields of hemp near Mezöhegyes showed an average stalk infestation of 14.5 per cent and an average of 17.4 borers per 100 plants. An examination of a 35-acre millet field at Mezöhegyes showed that 8.1 per cent of the plants were infested. In a 2-acre field of feterita at Bankut 3 per cent of the plants were infested.

Köppen (35) in 1880 first summarized the statements of various authors regarding *P. nubilalis* as a pest in Russia. He reported that the insect, though rather scarce, was well dispersed in that country. This same author refers to Widhalm, who reported that in 1879 the cornfields in the district of Odessa looked as though trampled by cattle and that millet was also injured in that district. Köppen also referred to Linderman, who mentioned severe damage to hemp in the government of Tula, and to Cancrin, who recorded severe injury to millet in the government of Jekaterinoslav. Kurjumov (37) in 1913 enumerated the damaged plants from Poltava as maize, millet, hemp, and hops. During the period from 1913 to 1920 there were many reports by Russian entomologists relative to the injury caused by *P. nubilalis* in Russia. Particular reference was made of serious damage to corn in Bessarabia during 1914 and 1915. Other reports from various localities in southern Russia mentioned injury (presumably to corn) varying from 20 to 90

per cent. Vassiliev (69) stated that in Kiev during 1914 Indian corn was injured more than millet and that the damage was confined chiefly to the stalk. According to this authority the insect was very injurious to corn in Jekaterinoslav during 1914, the grain being totally destroyed in some localities. Averin (3) recorded serious injury to maize in Charkov during 1915 and mentioned that in some cases 90 per cent of the stalks were infested. Uvarov (68) reports great damage to maize during 1916 and 1917 in Tiflis and Erivan. In correspondence dated December 20, 1921, D. N. Borodin asserted that according to his personal observation *P. nubilalis* is widely distributed in Russia, but is not a serious pest of corn, although it is injurious to millet, hemp, and hops. Dobrodeiv (14) records that it is found "as an injurious insect" in the following Provinces of European Russia: Minsk, Volhynia, Podolia, Kiev, Cherson, Poltava, Chernigov, Ekaterinoslov, Charkov, Kursk, Orel, Kaluga, Tula, Riazan, Tambov, Simbirsk, Voronej, Saratov, Don, and Kuban, and in Turkestan. Millet, maize, cotton, hemp, hops, and sunflowers are mentioned by this author as the principal economic crops attacked in Russia, but he does not give specific instances of damage except in the fields of the Voronej Agricultural Institute, where the infestation in different varieties of millet ranged from 14 to 63 per cent of the stems. Incidentally he mentions that the varieties of millet possessing a close growing habit were more susceptible, under Russian conditions, than varieties possessing "a branching widespread" habit.

In France the insect was first recorded as a pest by Duponchel (15, p. 121, CCXVII, 4), 1831, who mentioned it as being injurious to hops. Several French writers subsequently recorded *P. nubilalis* as a pest of maize, hops, and hemp, but no details concerning the extent of the injury are given. Robin and Laboulbène (52) reported damage to maize in the Department of the Aisne during a period of several years prior to and including 1879. No definite estimates of damage are given. The same authors mention that hemp was seriously injured in the Department of Lot-et-Garonne in 1878. P. Chretien (in correspondence dated May 20, 1919) mentions severe damage to corn in the Department of Aveyron during 1889. He records one cornfield of this district where nearly all of the stalks were infested and 75 per cent of the stalks bore atrophied ears. Schonfeld mentioned *P. nubilalis* as being very injurious to hops in Alsace during 1893. Vuillet (72, p. 105) reported in 1913 that the insect was injurious in the southwestern part of France and was the principal enemy of corn, yet the damage caused by it was small and often passed unnoticed. During this same year Marchal (43) reported that maize was seriously injured in the Department of Gers. In 1917 it was stated by Noël that maize and hemp were attacked, but the locality and degree of injury were not indicated. Chretien (in correspondence) reported severe damage to corn in the Department of Basses-Pyrenees during 1918, and that 20 per cent of the stalks were broken over in some of the cornfields. Rives (51) observed severe damage to maize near Toulouse during 1919 and mentioned one field of maize in which 60 per cent of the "roots" were infested.

The first statement regarding damage by *P. nubilalis* in Italy appears to be that of Targioni-Tozzetti (65, p. 28) in 1884, who mentioned that hemp was attacked by the insect. In 1911 Silvestri (19,

p. 270) reported it as damaging maize (Turkish wheat). During the summer of 1920 L. O. Howard, Chief of the Bureau of Entomology, made a general survey of the status of *P. nubilalis* in Italy and determined that the insect occurred throughout the entire Italian peninsula, but was not abundant. He found it principally in cornfields. K. W. Babcock made examinations of cornfields in the vicinity of Milan during the middle of July, 1924, and found thus early in the season an average stalk infestation of 38.6 per cent in 23 fields, with an average of 104.2 borers per 100 stalks. At Bergamo Mr. Babcock found an average stalk infestation of 40.6 per cent, with an average of 138 borers per 100 stalks. One field of early planted corn at Bergamo showed a stalk infestation of 83 per cent and an ear infestation of 14 per cent. In the fields around Florence the infestation was found to be very light. From notes contributed by W. R. Thompson and H. L. Parker, regarding the infestation in the cornfields of northern Italy during late June and early July, 1924, it is stated that in 5 fields near Turin the stalk infestation ranged from 20 to 49 per cent, in 4 fields at Novara the stalk infestation ranged from less than 1 to 82 per cent, and in 23 fields of the Bergamo region from 25 to 62 per cent of the stalks were infested. In the cornfields of the Pavia region an average of about 15 per cent of the stalks were infested, and in the region of Vicenza the infestation was very light. Doctor Thompson also reports that during some years the corn borer is said to be rather injurious to hemp in the region of Bologna.

In Bavaria *P. nubilalis* was recorded during 1880 as occurring in hops and hemp, but the injury was of no practical importance. Schonfeld, however, reports very severe injury to hops in Bavaria during 1886.

According to Schonfeld the hop fields of Bohemia were seriously injured by *P. nubilalis* during 1879 and 1880. Buzek, a schoolmaster of Rakonic, recorded that the entire hop yield was destroyed in some of the fields of the Rakonic district during 1879.

In Belgium *P. nubilalis* is reported by De Crombrugghe de Picquendael (13) as being abundant in the vicinity of Brussels, but no mention is made of injury to economic plants.

Briggs (8, p. 39-40) reported from the island of Guam that in 1919 fully 50 per cent of the corn crop was damaged in certain portions of the island. He also mentioned that grain sorghums and rice were attacked by the insect, and that 100 larvae were found in a single stalk of kafir corn.

DISTRIBUTION IN THE UNITED STATES

At the close of 1924 the European corn borer was known to be present in three large and two small separate areas of the United States (see map, fig. 1), comprising a total of 24,773 square miles. These figures relate to townships where the corn borer has actually been found and do not include certain townships which have been included in the quarantined area. The three large areas mentioned above are located (1) in eastern New England, (2) eastern New York and southwestern Vermont, and (3) in a narrow strip along the American shore of Lake Erie, comprising portions of the States of New York, Pennsylvania, Ohio, and Michigan. The two small areas

of infestation are located (1) at Brooklyn, N. Y.; Staten Island, N. Y.; and Little Neck, N. Y.; and (2) in Nelson Township, Madison County, N. Y., respectively.

DISCOVERY AND DISTRIBUTION IN NEW ENGLAND

In 1917, when the presence of the European corn borer in the United States was first discovered, it was found to be distributed over an area of approximately 100 square miles located immediately north and northwest of Boston, Mass. According to Vinal (70), who first discovered the presence of the insect and secured its identification, the fields of early sweet corn in market gardens 10 or 12 miles inland were reported by the owners as having been seriously injured by this pest for three or four years prior to 1917. During this period, however, the depredator was not recognized as being a

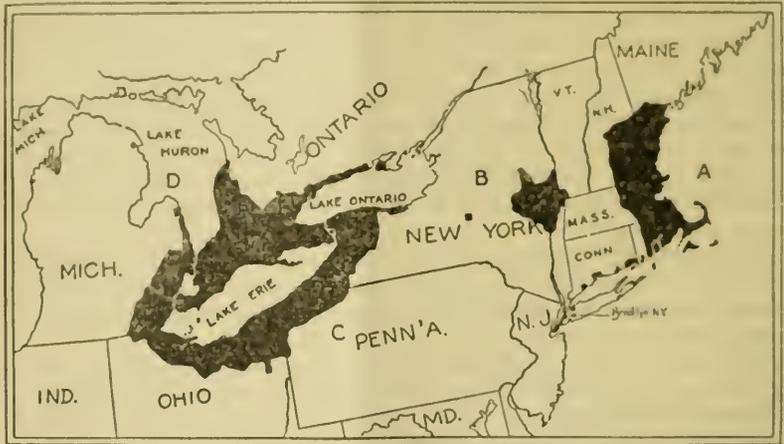


FIG. 1. Map showing areas of European corn-borer infestation in North America as known January 1, 1925. A, New England area; B, eastern New York area in the vicinity of Schenectady and Albany; C, Lake Erie area, including western New York and a strip along the lake in Pennsylvania, Ohio, and Michigan; D, Canadian area of infestation. Small areas of infestation at Brooklyn, N. Y.; Staten Island, N. Y.; Little Neck, Long Island; and Nelson Township, N. Y., are also indicated.

foreign pest. Judging by the intensity of the infestation in 1917 and by the size of the area infested at that time, as well as from the reports concerning the activity of the pest prior to 1917, Vinal was of the opinion that it had been imported about 1910, although realizing that this was only a conjecture. The investigations since 1917 have indicated that Vinal's estimate was probably very nearly correct, although the exact date is still unknown.

In 1916 specimens of dahlia stems infested by lepidopterous larvae were sent to the Massachusetts Agricultural Experiment Station from three localities near Boston, Mass. Adults were reared from this material, but their identity as *P. nubilalis* was not established until after adults had been reared from sweet corn by Vinal in 1917.

At the end of 1924 a total of 5,661 square miles was known to be infested by the European corn borer in this eastern New England area (see map, fig. 1), as shown by Mr. Worthley's field scouts, including eastern Massachusetts, the adjoining portion of New

Hampshire, southern Maine, seven townships in Rhode Island, and six scattered townships along the shore line of Connecticut. An infestation was also found during the summer of 1923 by scouts of the Federal Bureau of Entomology on Fishers Island, N. Y., which is located only about 7 miles offshore from the Connecticut infestation.

DISCOVERY AND DISTRIBUTION IN EASTERN NEW YORK

The insect was discovered during the latter part of January, 1919, at Scotia, N. Y., one of the suburbs of Schenectady, by F. V. Osterhoudt, in his garden at 223 Sanders Avenue. Mr. Osterhoudt had observed unfamiliar worms injuring the sweet corn in his garden during the previous summer, and when a popular article on the corn borer by R. H. Allen, of the Massachusetts State Department of Agriculture, appeared in the *Country Gentleman* the descriptions and illustrations led Mr. Osterhoudt to believe that this foreign pest was present in his corn. He sent specimens of the larva to C. R. Crosby, of Cornell University, who in turn referred them to the Lepidoptera specialist, W. T. M. Forbes. Doctor Forbes recognized in these the larvae of *P. nubilalis*, a determination which later was confirmed by Carl Heinrich,⁴ of the Federal Bureau of Entomology. Professor Crosby immediately notified the Bureau of Entomology of this discovery on January 29, 1919.

Subsequent scouting by State and Federal men showed that a sparse but widespread infestation existed in the region surrounding Schenectady and portions of the Mohawk and Hudson River Valleys, together with adjacent territory. By the end of 1924, 72 townships and cities, containing 2,882 square miles, were known to be infested in this region. This area also included two adjoining townships containing 90 square miles in southwestern Vermont. (See map, fig. 1.)

DISCOVERY AND DISTRIBUTION IN THE LAKE ERIE SECTION

During the latter part of September, 1919, an infestation was discovered on the farm of Alfred Morrison at North Collins, Erie County, N. Y., about 25 miles south of Buffalo and a short distance from Lake Erie. Specimens of the larvae were collected by Mr. Morrison and sent to Cornell University, where they were identified as *P. nubilalis* by W. T. M. Forbes. This discovery was reported to the bureau by E. P. Felt, State entomologist of New York. Larvae and adults were later submitted to Carl Heinrich, who confirmed the determination.

In September, 1919, an infestation was also found on the farm of a Mr. Eagley of North Girard, Erie County, Pa., by D. M. DeLong, J. R. Eyer, and H. E. Bachus, of the Bureau of Plant Industry, Pennsylvania State Department of Agriculture. Specimens of the larvae were forwarded to Washington, through P. T. Barnes.

Subsequent scouting during 1919 and 1920 revealed that the infestation in the Buffalo section was very extensive, whereas the Girard infestation was very sparse and confined to a single field; in fact no specimens of *P. nubilalis* were found in the Pennsylvania

⁴Mr. Heinrich has also been responsible for the determination of all other corn-borer material mentioned in this review of the occurrence of the pest in the United States to date.

area during 1920. The scouting during 1921 and 1922, however, disclosed that a sparse but extensive infestation had occurred in all the Pennsylvania townships bordering Lake Erie and adjacent thereto.

During the summer of 1921 the insect was discovered (May 3, 1921) by scouts of the Federal Bureau of Entomology on the farm of Peter Sontz, East Point Road, Middle Bass Island, Ohio, in Lake Erie. This island is located about 7 miles from the Ohio shore. Subsequent scouting during the summer of 1921 revealed sparse infestations in most of the townships bordering Lake Erie in Ohio and Michigan, and also on the islands in the western end of the lake. The borers were more numerous on the islands at this time than on the mainland.

At the close of 1924 *P. nubilalis* was known to be present in practically all of the territory along the American shore of Lake Erie and extending a short distance inland. (See map, fig. 1.) This area includes 4,812 square miles in western New York; 1,999 square miles in northwestern Pennsylvania; 6,591 square miles in northern Ohio; and 2,828 square miles in southeastern Michigan, a total of 16,230 square miles in the Lake Erie section. The presence of the European corn borer in Pennsylvania, Ohio, and Michigan establishes the pest within a short distance of the large and extremely important corn-growing areas of the Middle West and also provides a possible means of natural dispersion southward because of the presence of the insect in the territory drained by the headwaters of the Ohio River.

DISCOVERY AND DISTRIBUTION IN OTHER AREAS

During the late summer of 1923 a small area of infestation was discovered in the Bay Ridge section of Brooklyn, N. Y., by scouts of the Federal Bureau of Entomology. Limited infestations were also found during 1924 on the northeastern side of Staten Island, N. Y., just across the channel from the Brooklyn area, and at Little Neck, Long Island. Many of the larvae found in this region were inhabiting weeds, and evidences were also present that the insect had undergone two generations in this area during 1923 and 1924. It is believed that this infestation is of great importance since rather extensive sweet corn growing areas are present on Long Island and in the near-by districts of New Jersey and Connecticut. The situation may become especially serious if two generations should continue to develop each year in this area.

A single specimen of *P. nubilalis* pupa was discovered during July, 1923, in Nelson Township, Madison County, N. Y., by W. L. Miles, a former employee of the Bureau of Entomology. This area is located about 50 miles west of the main eastern New York area. A few specimens of the larvae were found later in a near-by field by a scout of the Federal Bureau of Entomology. Only two infested fields were found in this area.

Extensive scouting operations have been maintained during the period from 1921 to 1924 in the territory surrounding and adjacent to the infested areas of New England, New York, Pennsylvania, Ohio, and Michigan, as well as along the main lines of travel, river valleys, water routes, the vicinity of broom factories, and other susceptible localities in those States. Scouting operations have also included field examinations in susceptible localities in the territory

east of and including the Mississippi River basin States, as well as in Texas, New Mexico, and Arizona. Particular attention has been given localities where imported broomcorn was known to have been received, as well as to sections producing field corn, sweet corn, and broomcorn. Special scrutiny has been given the territory adjacent to ocean and river ports and railroad centers and along the main railroad, highway, and water routes.

DISTRIBUTION IN THE DOMINION OF CANADA

During August, 1920, the Canadian authorities reported the discovery of an infestation by the European corn borer in Welland County, Ontario, along the Niagara River immediately opposite the western New York area of infestation, and another larger and more heavily infested area along the Canadian shore of Lake Erie, with its apparent center near St. Thomas, Ontario.

At the close of 1924 the pest was present in an area of approximately 18,000 square miles, comprising the entire southern Ontario peninsula bordering Lake Erie and including Pelee Island in the lake. The area of infestation in Ontario was practically continuous with the area of infestation on the United States side of Lake Erie. (See map, fig. 1.)

The character of the infestation in Middlesex and Elgin Counties, Ontario, was more severe than in any of the areas in the United States, with the exception of that existing in New England, and, according to Crawford and Spencer (12), very severe losses occurred to flint field corn and to sweet corn, whereas dent field corn in general suffered to a lesser extent.

The presence of this large and severely infested area directly across Lake Erie from American territory constitutes a source of possible further dispersion to the lake regions of New York, Pennsylvania, Ohio, and Michigan, through both the natural and artificial spread of the insect. The severe character of the infestation in part of Ontario is also indicative of conditions which may be expected eventually to develop on the American side of the lake, as the climatic and agricultural conditions are similar.

PROBABLE MANNER OF IMPORTATION

The precise manner in which the European corn borer gained entrance to the United States is not definitely known, but as a result of investigations conducted since its original discovery in New England, it is believed that broomcorn which was imported for manufacturing purposes from Hungary or Italy during the period from 1909 to 1914 was the probable carrier (58). At this time the conditions of the trade were such that unusually large quantities of broomcorn were imported, the report of the Bureau of Foreign and Domestic Commerce, Department of Commerce, showing that at least 12,000 tons were received during this period. Broomcorn is known to be commonly infested by *P. nubilalis* in both Hungary and Italy, where much of this material originated. The inspection service was not authorized by law until 1913, and therefore it was not possible to intercept this material upon its arrival at the ports of entry.

Parts of these importations were received at broom factories located at Everett, Mass., near the apparent center of the original New England infestation, and at Amsterdam, N. Y., near the apparent center of the eastern New York infestation. The remainder of these importations were traced to many different parts of the United States, but subsequent extensive scouting in localities where they were known to have been received has failed to reveal any additional infestations.

Raw hemp was formerly believed to be the most likely medium through which the European corn borer gained entrance to this country, but in the light of our present knowledge this theory appears untenable, and broomcorn appears to have been the probable vehicle in which it entered America.



FIG. 2.—Broomcorn butts sectioned to show typical injury by European corn borer and borers in position at base of hurls. Medford, Mass., November, 1921. Broomcorn infested in a similar manner, originating in Hungary and Italy, has been intercepted at the port of New York by inspectors of the Federal Horticultural Board.

broomcorn in passengers' baggage arriving at New York from Italy and Germany.

An investigation of the broom industry indicated that the customary methods of handling raw broomcorn afforded an opportunity for the dispersion of the insect if contained within the material. The fact was determined that the foreign broomcorn, previously mentioned as having been received at Everett, Mass., was kept in storage for several years before being used, thus giving every opportunity for any larvae contained therein to complete their development and emerge as moths. During the process of manufacture a section sev-

The supposition that *P. nubilalis* was originally imported in broomcorn received an apparent confirmation during February and March, 1920, in April, 1922, and again in March, 1923, when commercial shipments of broomcorn from Hungary and Italy were intercepted by inspectors of the Federal Horticultural Board at the port of New York and were found to contain many living larvae of the pest. This broomcorn was in the raw, or unmanufactured state, and consisted of about 30 inches of the upper part of the broomcorn plant, including the "hurles" or that portion usually incorporated in ordinary house brooms and the upper part of the stalk or "butt." Corn-borer larvae were found throughout the length of the "butt" proper, and also within the extreme upper tip of the terminal internode beyond the point where the "hurles" or broom splints are attached. (Fig. 2.) During March, 1923, the inspectors also intercepted living larvae of *P. nubilalis* in stalks of

eral inches long often is removed from the base of the "butt" and discarded as refuse. Infested refuse of this character, unless promptly destroyed, may become a source of danger, especially when dumped along the banks of water courses. The original infestation in eastern New York, along the Mohawk River, is believed to be directly traceable to infested refuse from the broom factory at Amsterdam, previously mentioned as having received foreign importations. It was also determined that occasionally the raw material is made into large brooms, for stable or other rough use, without any preliminary process or manufacture, and in such a manner that opportunity is afforded for the dispersion of any corn-borer larvae that might be contained therein. Moreover, it was determined that the sulphuring and other processes undergone by the broomcorn during manufacture was not always sufficient to insure the destruction of all the larvae contained therein. Consequently there is a possibility that some kinds of brooms manufactured from infested material may serve to disseminate the insect.

Concerning the infestations on the islands and along the shore of Lake Erie in Michigan, Ohio, and Pennsylvania, it is believed that they may have originated from the intensely infested area directly across the lake in the Province of Ontario. The history and intensity of this infestation near Saint Thomas and Port Stanley, Ontario, indicate it as probably the oldest colony of the pest in this region. The infestation in western New York possibly may have originated from this same source, although its origin is more obscure.

The method of dispersion from Ontario may have been by flight of the moths or by drift of infested plant material in the waters of Lake Erie. A study of the wind and water currents in the Lake Erie region, in relation to the known habits of the insect, show the possibility of such dispersion through either of these agencies, as will be discussed in greater detail in another part of this bulletin.

The origin of the Ontario infestation is thought by McLaine (41) to be possibly traceable to large importations of broomcorn into Elgin and Middlesex Counties from central Europe during the period from 1909 to 1910, although no conclusive evidence has been obtained upon this point.

HOST PLANTS

HOST PLANTS IN FOREIGN LANDS

According to foreign authorities the most common economic host plants of *P. nubilalis* in the Old World are corn (or maize), hops, millet (*Panicum miliaceum* L.), hemp (*Cannabis sativa* L.), and broomcorn. Indian corn, or maize, however, appears to be the preferred host of the species in the Old World and is usually mentioned as being more severely injured than any of its other hosts. Hop is considered to be second in importance as a host of the species, while millet, hemp, and broomcorn are commonly attacked when grown within the range of distribution of the insect. In regions where for climatic reasons corn can not successfully be grown, particularly along the northern limit of distribution of the insect, it is able to subsist upon other plants, notably millet and hops, thus demonstrating that in its native habitat the species is not dependent

upon corn. Owing to its status as a pest of millet and hops it is frequently mentioned in foreign literature as the "millet borer" and the "hop-vine borer." The original host of the species is a matter of conjecture, but it is believed by different authorities to have been either the hop plant or some one of the larger Asiatic or European grasses or grasslike plants. The fact that corn is of American origin precludes the possibility that this plant was the original host of *P. nubilalis*. The insect was first found in middle Europe living in millet (*P. miliaceum*) and in maize. Judging from the known history and habits of the insect and the history of its more susceptible hosts, there appear to be good reasons for considering wild hop as the original host. Hop affords excellent opportunities for the survival of the insect, since it is a perennial, whereas millet and hemp, two other possible original hosts, are annuals. Millet is said to derive its origin from Egypt and Arabia and hemp from Dauria and Siberia, but the hop is indigenous to Europe.⁵

De Crombrughe de Picquendaele (15) records that in Belgium, mugwort (*Artemisia vulgaris* L.) is the chief host plant. P. Chretien, curator of the National Museum of Natural History at Paris, also states in correspondence that this plant is the favorite host in northern France. This and allied species are mentioned as hosts by several other writers. Pigweed (*Amaranthus retroflexus* L.) is recorded as a frequent host by Jablonowski (29) and has been found commonly infested near Hyères, France, by W. R. Thompson, of the Bureau of Entomology.

Foreign literature contains reference to a great variety of occasional or minor host plants, including oats (49), barley (49), cotton (69), rice (8, pp. 39-40), kafir (8, pp. 39-40), bean pods (52), sunflower (36), mustard (36), barnyard grass (*Echinochloa crus-galli* (L.) Beauv.) (33), giant reed (*Arundo donax* L.) (47), fuller's teasel (*Dipsacus fullonum* L.) (29), green foxtail (*Chaetochloa viridis* (L.) Scrib.) (52), stinging nettle (*Urtica urens* L.) (50, p. 16), thistles (*Cirsium* or *Carduus* spp.) (29), ploughman's spikenard (*Inula conyza* D. C.) (13), stiff inula (*Inula squarrosa* L.) (72, p. 106), and common reed (*Phragmites communis* Trin.) (13). K. W. Babcock recorded an infestation in feterita at Mezöhegyes, Hungary.

Professor Chretien, in correspondence, mentioned thistle (*Carduus tenuiflorus* Curtis) and garden orach (*Atriplex hortensis* L.) as hosts in northern France. W. R. Thompson, in correspondence, has recorded bean pods, tomato fruits, tumble weed (*Amaranthus gracilis* L.), wood amaranth (*Amaranthus silvestris* Desf.), and *Pieris spinulosa* Guss. as hosts in the vicinity of Hyères, France, and he observed eggs on dock (*Rumex* sp.) in the Paris region. From Ekaterinoslaw, Russia (46), it is mentioned as a "market garden pest." Jablonowski⁵ has cited an instance where grapevines (*Vitis vinifera* L.) were heavily infested by *P. nubilalis* larvae which had migrated from near-by cornstalks. The species has also been found in oak galls (52). The adults have been observed upon heather (32) and upon virgin's bower (*Clematis vitalba* L.) (29), but there is no record of the larvae being found in these plants. Sand (53, p. 121) and Vuillet (72) have recorded the larvae from several of the Gramineae.

⁵ See footnote 1.

It is probable that some of the plants recorded as hosts of *P. nubilalis* in the Old World serve primarily as shelter plants rather than as food, a condition which is known to prevail in the infested areas of America.

HOST PLANTS IN AMERICA

In general, corn appears to be the preferred host of the European corn borer in America and is more seriously injured by the insect



FIG. 3.—Cocklebur (*Xanthium* sp.), a susceptible weed host of the European corn borer

than any other cultivated crop attacked. This includes sweet corn, field corn (both dent and flint), and pop corn. In the heavily infested area of eastern New England the pest also attacks and frequently causes serious injury to a great variety of other economic plants, including several of the field crops, vegetables, flowers, and

grasses. The infestation in crops, other than corn, is especially likely to occur (1) when corn is growing near by, (2) when the infested crop remnants and weeds from previous crops on the same or adjacent areas have not been destroyed, and (3) when susceptible weeds are growing in the field or in its immediate vicinity. Many weeds are included as hosts, thus serving to complicate the control of the



FIG. 1.—Smartweed (*Polygonum* sp.), a favorite weed host of the European corn borer

pest and aiding in its multiplication and dispersion. Occasionally in certain fields some of these weeds, notably cocklebur (*Xanthium* spp., fig. 3), barnyard grass (*Echinochloa crus-galli* (L.) Beauv.), and smartweed (*Polygonum* spp., fig. 4), appear to be preferred as hosts rather than corn.

In some cases it seems that the species of plant selected as food or as shelter depends more upon its location with reference to other heavily infested plants or plant material than upon its character as a plant. The protection afforded to gravid females also appears to be a determining factor in some instances, since eggs are deposited freely upon certain large-leaved plants, rhubarb for example, which afford protection to the females during the day. Moreover, some plants in which the larvae are not known to feed are occasionally utilized for egg deposition, as will be shown in this discussion.

In New York, Pennsylvania, Ohio, and Michigan, and in Ontario, the infestation to date has been confined mostly to corn, with comparatively slight infestation in the more susceptible weeds. Occasional borers also have been found in some of the economic plants in the Lake Erie region and in Ontario. During 1923 and again in 1924 two commercial fields of broomcorn in western New York sustained infestations which were nearly equal to those of field corn in the vicinity. Probably the intensity and variety of infestation in susceptible weeds, vegetables, field crops, and flowering plants eventually will increase in these areas if the insect should become more numerous. It is possible also that the comparatively restricted list of host plants in these areas, as compared to New England, may be influenced by the fact that in New England two generations usually occur annually, whereas in the more western areas and in Ontario only one generation has yet been observed, except in favorable seasons when a few individuals of a second generation have developed. Under two-generation conditions the insect begins its feeding activity much earlier in the season than where but one generation occurs, and continues feeding actively throughout a longer total period for the season. Therefore it is able to use as hosts during the early part of the season, and again during the late season, many plants which are not available in an attractive or susceptible stage of growth during the period when the single-generation adults and larvae are most active.

NEW ENGLAND

In this section, up to January 1, 1924, the European corn borer has been found inhabiting a total of 215 different species and varieties of plants, some of which apparently serve primarily as shelter rather than food for the borers.

The relative degree of susceptibility of these host plants to *P. nubilalis*, and the parts attacked, are shown in the following list (Table 1) compiled for the New England area. In genera where two or more species were found to be hosts of *P. nubilalis*, usually only the generic name is listed.

TABLE 1.—Classified list of *P. nubilalis* host plants

CLASS 1.—PLANTS SEVERELY ATTACKED	
Name of plants	Parts attacked
Barnyard grass (<i>Echinochloa crus-galli</i> (L.) Hitchc.)	Stems
Beggar-ticks (<i>Hedysc. spp.</i>) ¹	Do
Bromus (<i>Hedysc. sorghum</i> L.) ¹	Stalks
Cockspur (<i>Xanthox. spp.</i>) ¹	Stems, burs
Corn (<i>Zea mays</i> L.) (dent, dent, pop, sweet) ¹	All parts except fibrous roots.
Dahlia (<i>Dahlia</i> spp.)	Stalks, flowers
Doek (<i>Rumex</i> spp.)	Stems.
Field ragweed (<i>Helianthus scaberrimus</i> Nutt.)	Do.
Indian sorghum (<i>Hedysc. sorghum</i> L.) (keterita, hegarl, milo, kafir) ¹	Stalks, seed heads.
Henop (<i>Cenchrus ciliaris</i> L.) ¹	Do.
Japanese hop (<i>Humulus japonicus</i> Sieb. & Zucc.)	Stems
Japanese millet (<i>Echinochloa crus-galli edulis</i> Hitchc.) ¹	Do.
Pigweed (<i>Amaranthus retrofractus</i> L.)	Stems, flowers.
Prince's plume (<i>Polygonum orientale</i> L.)	Stalks, flower stems.
Ragweed (<i>Ambrosia</i> spp.) ¹	Stems.
Rhubarb (<i>Rheum raphanistrum</i> L.)	Leaf stalks.
Smartweed, Knotweed (<i>Polygonum</i> spp.) ¹	Stems.
Wormseed (<i>Chenopodium ambrosioides</i> L.)	Do.

CLASS 2.—PLANTS FREQUENTLY ATTACKED

Barley (<i>Hordeum vulgare</i> L.) ¹	Stems
Bean (<i>Phaseolus</i> spp.) (kidney, lima, scarlet runner) ¹	Stalks, pods, seeds.
Beet (<i>Beta vulgaris crassa</i> Alef.)	Leaf stalks, rarely beet roots.
Broomcorn millet (<i>Panicum miliaceum</i> L.) ¹	Stems.
Burlock (<i>Arctium</i> spp.) ¹	Do.
Celery (<i>Celeri gracilens</i> (L.) Tritton)	Leaf stalks.
China aster (<i>Callistemma chinensis</i>)	Stalks, flower stems.
Chrysanthemum (<i>Chrysanthemum</i> spp.)	Stalks, flowers.
Cotton (<i>Gossypium hirsutum</i> L.) ¹	Stalks, bolls.
Cowpea (<i>Vigna sinensis</i> (L.) Endl.) ¹	Stalks, pods.
Fireweed (<i>Erigeron canadensis</i> L.)	Stems.
Japanese fleuce flower (<i>Polygonum sieboldii</i> De Vriese)	Do.
Jimson weed (<i>Datura</i> spp.) ¹	Stems, seed pods.
Pepper (<i>Capicum annuum</i> L.)	Stalks, fruit.
Potato (<i>Solanum tuberosum</i> L.)	Stalks.
Sorgho (<i>Hedysc. sorghum</i> L.)	Do.
Sunflower (<i>Helianthus annuus</i> L.)	Do.
Swiss chard (<i>Beta vulgaris cicla</i> Moq.)	Leaf stalks.
Tansy (<i>Tanacetum vulgare</i> L.)	Stems.
Teosinte (<i>Euchlaena mexicana</i> Schrad.) ¹	Stems, leaf blades.
Wormwood (<i>Artemisia</i> spp.) ¹	Stems.
Zinnia (<i>Zinnia elegans</i> Jacq.)	Stalks, flower stems.

CLASS 3.—PLANTS OCCASIONALLY ATTACKED

Aster (<i>Aster</i> spp.) ¹	Stems.
Boltonia (<i>Boltonia heteroides</i> (L.) L'Her.)	Stalks.
Broad grass (<i>Panicum</i> spp.) ¹	Stems.
Buckwheat (<i>Fagopyrum vulgare</i> Hill) ¹	Do.
Calendula (<i>Calendula officinalis</i> L.)	Stalks, flower stems.
Canna (<i>Canna</i> spp.)	Stalks, leaves, flowers.
Cockscumb, common (<i>Croton cristata</i> L.) ¹	Stems, flowers.
Cockscumb, feather (<i>Croton argentea</i> L.) ¹	Do.
Coleus (<i>Coleus</i> spp.)	Stems.
Cosmos (<i>Cosmos bipinnatus</i> Cav.)	Stalks.
Crab grass (<i>Syntherisma sanguinalis</i> (L.) Dulac)	Stems.
Eggplant (<i>Solanum melongena</i> L.)	Stems.
Feverfew (<i>Chrysanthemum parthenium</i> (L.) Bernh.) ¹	Fruit.
Fireweed (<i>Erechtites hieracifolia</i> (L.) Raf.)	Stalks, flower stems.
Galinsoga (<i>Galinsoga</i> sp.)	Stalks.
Geranium (<i>Pelargonium hortorum</i>)	Stems.
Gladiolus (<i>Gladiolus</i> spp.)	Stalks.
Golden Glow (Hort. var. of <i>Eudbeckia laciniata</i> L.)	Stalks, flowers.
Goldenrod (<i>Solidago</i> spp.) ¹	Stalks, flower stems.
Hollyhock (<i>Athaea rosea</i> Cav.)	Stems.
Hop, common (<i>Humulus lupulus</i> L.) ¹	Stalks, leaf stems.
Jerusalem artichoke (<i>Helianthus tuberosus</i> L.)	Stems.
Lamb's quarters (<i>Chenopodium album</i> L.)	Stalks.
Mallow (<i>Malva</i> spp.) ¹	Stems.
Mangel (<i>Beta vulgaris crassa</i> Alef.) ¹	Do.
Motherwort (<i>Leonurus cardiaca</i> L.)	Leaf stalks.
Mustard (<i>Brassica</i> spp.) ¹	Stems.
	Do.

¹ Two or more species or varieties are grouped under this common name. The names of these species will be furnished to interested persons.

² Plants occurring rarely or grown only in the experimental fields. These plants are classified according to their susceptibility rather than the frequency in which they are found infested.

TABLE 1.—Classified list of *P. nubilalis* host plants—Continued
CLASS 3.—PLANTS OCCASIONALLY ATTACKED—Continued

Names of plants	Parts attacked
Nettle (<i>Urtica lyallii</i> Wats.)	Stems.
Oat (<i>Avena sativa</i> L.)	Do.
Orach (<i>Atriplex</i> sp.)	Do.
Prickly lettuce, Wild L. (<i>Lactuca</i> sp.)	Do.
Purslane (<i>Portulaca oleracea</i> L.)	Do.
Salvia, scarlet sage (<i>Salvia splendens</i> Ker-Gawl.)	Stalks, flower stems.
Sow thistle (<i>Sonchus</i> spp.) ¹	Stems.
Spinach (<i>Spinacia oleracea</i> L.)	Leaf stems.
Strawflower (<i>Helichrysum bracteatum</i> Andr.) ¹	Stalks, flower stems.
Thistle (<i>Cirsium</i> spp.) ¹	Stems.
Tomato (<i>Lycopersicon esculentum</i> Mill.)	Stalks, fruit.
Velvetleaf (<i>Abutilon theophrasti</i> Medic.) ²	Stems.
Yarrow (<i>Achillea millefolium</i> L.)	Do.

CLASS 4.—PLANTS BARELY ATTACKED

Ageratum (<i>Ageratum houstonianum</i> Mill.)	Stalks, flower stems.
Apple-of-Peru (<i>Nicandra physalodes</i> (L.) Pers.) ²	Stems.
Ailanthus (<i>Ailanthus</i> sp.) ²	Leaf stems.
Apple (<i>Pyrus malus</i> L.)	Fruit (wind-falls).
Asparagus (<i>Asparagus officinalis</i> L.) ³	Mature stalks.
Balsam (<i>Impatiens balsamina</i> L.)	Stems.
Blackberry (<i>Rubus</i> sp.) ³	Canes.
Black-eyed Susan (<i>Rudbeckia hirta</i> L.)	Stems.
Blister cress (<i>Cherimia cheiranthoides</i> (L.) Link.)	Do.
Blue vervain (<i>Verbena hastata</i> L.)	Do.
Cabbage (<i>Brassica oleracea capitata</i> L.) ³	Stalks.
California poppy (<i>Eschscholtzia</i> sp.)	Stems.
Candytuft (<i>Iberis</i> sp.)	Do.
Cardoon (<i>Cynara cardunculus</i> L.) ¹	Leaf stalks.
Catnip (<i>Nepeta cataria</i> L.) ²	Stems.
Cat-tail (<i>Typha latifolia</i> L.)	Do.
Cauliflower (<i>Brassica oleracea botrytis</i> DC.)	Leaf stalks.
Celandine (<i>Chelidonium majus</i> L.) ³	Stems.
Chicory (<i>Cichorium intybus</i> L.)	Do.
Clover, Alsike (<i>Trifolium hybridum</i> L.)	Do.
Coltsfoot (<i>Tussilago farfara</i> L.) ²	Leaf stalks.
Cornflower (<i>Centaurea cyanus</i> L.)	Stems.
Cucumber (<i>Cucumis sativus</i> L.)	Fruit.
Cup-plant (<i>Silphium perfoliatum</i> L.) ²	Stems.
Daisy, ox-eye (<i>Chrysanthemum leucanthemum</i> L.)	Flower stems.
Elder (<i>Sambucus canadensis</i> L.) ³	Branches.
Endive (<i>Cichorium endivia</i> L.) ^{2, 3}	Stalks, seed heads.
Evening primrose (<i>Oenothera</i> sp.) ³	Stems.
False dragon head (<i>Physostegia virginiana</i> (L.) Benth.) ²	Stems.
Fleabane (<i>Erigeron annuus</i> (L.) Pers.)	Do.
Foxtail, green (<i>Chaetochloa viridis</i> (L.) Scribn.)	Stems, seed heads.
Foxtail, yellow (<i>Chaetochloa lutescens</i> (Weigel) Stuntz)	Do.
Grape, Concord (Hort. var. of <i>Vitis labrusca</i> L.)	Stems, fruit.
Groundsel, common (<i>Senecio vulgaris</i> L.) ²	Stems.
Hedge mustard (<i>Sisymbrium</i> sp.) ³	Do.
Heliotrope (<i>Heliotropium peruvianum</i> L.)	Flower stems.
Horsetail (<i>Equisetum</i> sp.)	Stems.
Jerusalem cherry, false (<i>Solanum capsicastrum</i> Link.)	Fruit.
Jewelweed (<i>Impatiens biflora</i> Walt.)	Stems.
Joe-pye weed (<i>Eupatorium</i> sp.)	Do.
Johnson grass (<i>Holcus halepensis</i> L.) ²	Do.
Knapweed (<i>Centaurea nigra</i> L.) ³	Do.
Locust, common (<i>Robinia pseudoacacia</i> L.)	Sprouts.
Love-lies-bleeding (<i>Amaranthus caudatus</i> L.) ²	Stems.
Mallow (<i>Hibiscus</i> sp.) ³	Do.
Maple-leaf goosefoot (<i>Chenopodium hybridum</i> L.) ²	Do.
Marigold, Aztec or African (<i>Tagetes erecta</i> L.)	Stalks.
Mayweed (<i>Anthemis cotula</i> L.)	Stems.
Mignonette (<i>Reseda odorata</i> L.)	Stalks
Milkweed (<i>Asclepias</i> spp.) ³	Stems.
Millet, golden wonder (<i>Chaetochloa italica germanica</i> (Mill.) Farwell) ²	Do.
Millet, Hungarian (<i>Chaetochloa italica</i> (L.) Scribn.) ²	Do.
Millet, pearl (<i>Pennisetum glaucum</i> (L.) R. Br.) ²	Do.
Mint (<i>Mentha</i> spp.) ¹	Stalks.
Night-flowering catchfly (<i>Silene noctiflora</i> L.) ¹	Stems.
Nightshade, black (<i>Solanum nigrum</i> L.)	Do.
Okra or gumbo (<i>Hibiscus esculentus</i> L.) ²	Stalks.
Oswego bee balm (<i>Monarda didyma</i> L.) ^{2, 3}	Stalks, flower stems.
Pansy (<i>Viola tricolor</i> L.)	Stems.
Parsnip (<i>Pastinaca sativa</i> L.)	Stalks.
Peanut (<i>Arachis hypogaea</i> L.) ²	Stems.

¹ Two or more species or varieties are grouped under this common name. The names of these species will be furnished to interested persons.

² Plants occurring rarely or grown only in the experimental fields. These plants are classified according to their susceptibility rather than the frequency in which they are found infested.

³ Plants which apparently serve only as shelter for the larvae.

curled or yellow dock, green foxtail, lamb's quarters, bread grass, pigweed, common ragweed, smartweed, and common thistle.⁷ Here, occasional borers have also been found in the stems of soy bean, sorghum,⁸ Japanese millet,⁸ broom corn millet or proso, buckwheat, rhubarb,⁸ kidney or wax bean,⁸ milo⁸ tomato stem and fruit, potato, dahlia,⁸ and cosmos.⁸ During 1923 two fields (a total of 12 acres)

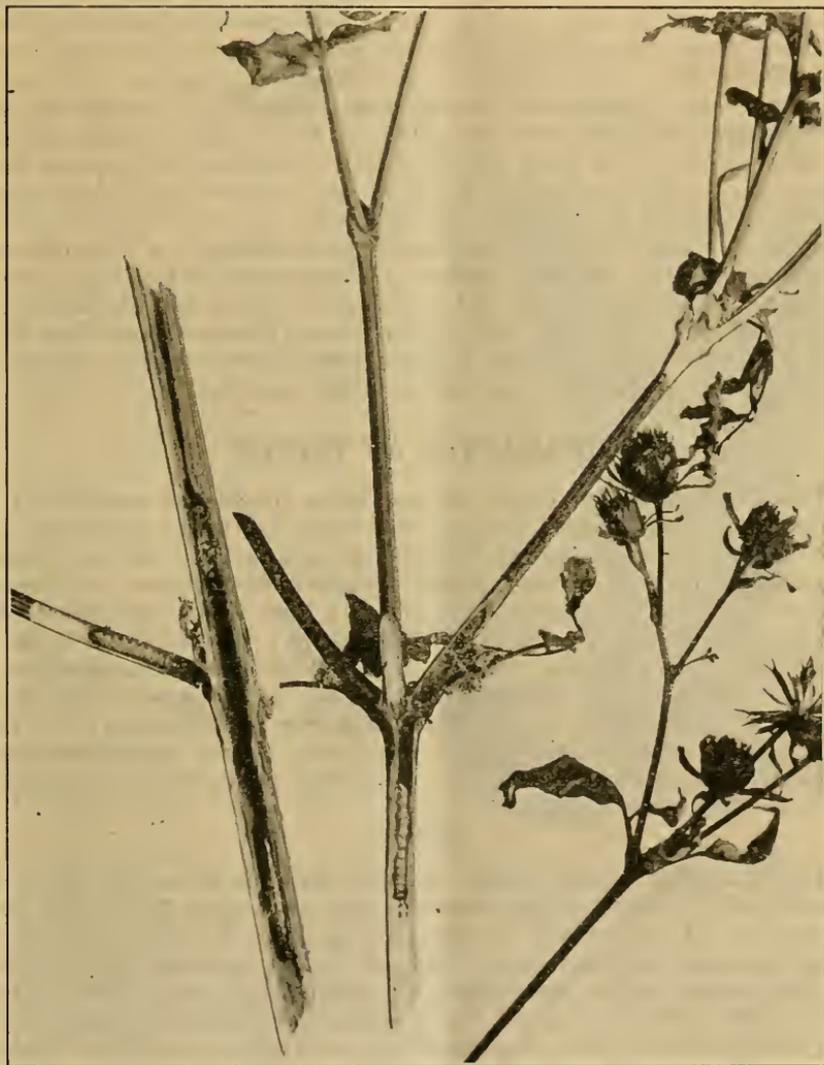


FIG. 5.—Beggar ticks (*Bidens* sp.) showing typical injury by the European corn borer

of broom corn grown at Irving, N. Y., showed stalk infestation of 12.7 and 15.8 per cent respectively. In Ohio, according to reports of F. W. Poos to December 31, 1924, occasional borers have been found in the following host plants in addition to corn: Smartweed, pigweed, cocklebur, ragweed, water hemp (*Acnida tuberculata* Moq.), beggar-ticks, old witch grass,⁷ and barley.

⁸ Found infested in experimental plats only.

CANADA

According to Crawford and Spencer (12, 60), the following cultivated crops and flowers, in addition to corn, were found to be infested in Ontario: Dahlia, geranium, aster, golden glow, beets, mangels, tomatoes (fruit), beans, oats, squash vines, broomcorn, Sudan grass, Early Amber sorghum, Hungarian grass, Mann's Wonder sorghum, white clover, and red raspberry. The following weed hosts are also recorded by the same investigators: Barnyard grass (*Echinochloa crus-galli* (L.) Beauv.), redroot pigweed (*Amaranthus retroflexus* L.), yellow foxtail (*Chaetochloa lutescens* (Weigel) Stuntz); lamb's quarters (*Chenopodium album* L.), Russian thistle (*Salsola pestifer* Nels., var. *tenuifolia* G. F. W. Mey.), green foxtail (*Chaetochloa viridis* (L.) Scribn.), lady's thumb (*Polygonum persicaria* L.), wild buckwheat (*Polygonum convolvulus* L.), ground cherry (*Physalis heterophylla* Nees), orchard grass (*Dactylis glomerata* L.), Canada thistle (*Cirsium arvense* Scop.), wild sunflower (*Helianthus* sp.), viper's bugloss (*Echium vulgare* L.), ragweed (*Ambrosia artemisiifolia* L.), mullein (*Verbascum thapsus* L.), goldenrod (*Solidago* sp.), old witch grass (*Panicum capillare* L.), yarrow (*Achillea millefolium* L.), burdock (*Arctium minus* Bernh.), and tumbling pigweed (*Amaranthus graecizans* L.).

CHARACTER OF INJURY

The European corn borer, as the name implies, is essentially a boring insect, and causes its most important injury by the tunneling and feeding of the larvae within the stems and fruits of the plants attacked. This injury, when severe, results in the collapse or deterioration of the parts of the plant affected, and when less severe the normal functioning of the injured parts may be interfered with if such injury occurs at a critical point. The larvae also feed to a slight extent upon the surface of plants, but such injury usually does not appear measurably to interfere with the normal growth of the host. The specific character of the injury varies somewhat with different groups of hosts and will, therefore, be discussed separately.

CORN

The character of the injury to corn depends upon the stage of growth of the plant when attacked, and also upon the habits and preference of individual larvae. In general, however, the most important and serious injury is caused by the tunneling and feeding of the larvae within the stalks, ear stems, and ears. The larvae also tunnel within the tassel, the midrib of the leaf, the brace roots, the stubble, and in fact all parts of the corn plant except the fibrous roots. They also feed to a slight extent upon the surface of the plant, particularly upon the tender leaf blades, tassel buds, husks, and silks of the ears, and between the leaf sheaths and stalks.

INJURY TO THE LEAVES

Attacks upon young corn plants are characterized by numerous small irregularly shaped feeding areas and the presence of very fine particles of frass. Minute punctures perforating the epidermis

appear upon the tender leaf blades surrounding the developing tassel. (Fig. 6.) Such injuries are caused by the feeding of the newly hatched larvae, and, while not economically important, this surface feeding affords a possible opportunity for attacking the larvae by insecticidal means. The midrib of the leaf blade sometimes is entered and tunneled, more particularly by the smaller borers, in the same manner and with the same result as will be described later for the stalk.

INJURY TO THE TASSEL

The tassel buds and the immature branches and main stem of the tassel are often entered and fed upon by the young borers (fig. 6) even before the tassel appears above the unfolding leaf blades. Often several adjoining tassel buds are webbed together with particles of frass and silk by the small larvae. In this condition the infested tassel is very conspicuous after it appears above the unfolding leaves. Frequently the injury to the immature tassel stem causes the breaking over of the tip of the tassel even before it begins to expand.

As the tassel expands and the buds begin to open the larvae continue to tunnel within the branches and the main stem. This injury usually causes the tassel, or the infested portion thereof, to collapse and break over. Such broken tassels (fig. 7), with masses of frass at the breaks, are very conspicuous and often afford the most noticeable sign of the presence of the insect. It does not necessarily follow, however, that because none of the tassels are broken over in a suspected field the insect is not present, as plants sometimes are attacked only at points lower down than the tassel or at a late stage in their development when the tassel or its stem does not attract the larvae.



FIG. 6.—Newly developed tassel of corn plant, showing injury by young larvae of the European corn borer. Note small gnawed areas on leaves at right caused by feeding of newly hatched larvae

INJURY TO THE STALK

Some of the newly hatched larvae, instead of tunneling within and feeding upon the tassel buds and tassel stems, habitually migrate to a point lower down on the same or near-by plants. Under these circumstances they commonly enter the plants at practically any point, but the favorite place of entrance is either between the leaf sheath and the stalk (fig. 8) or between the stalk and the base of the partly developed ear (fig. 9), providing the plant has advanced to that stage of growth.

After gaining entrance to the stalk the borer tunnels either upward or downward, usually the former, according to its individual preference. The character of this tunnel is subject to considerable variation, but usually the borer follows nearly a straight course for several inches through the path and generally lengthwise of the plant. The tunnels of 41 individual borers were found to average 8.6 inches in



FIG. 7.—Broken corn tassel, showing injury caused by larvae of the European corn borer

length. (See Table 14.) The tunnels made by fully grown larvae, when tunneling in green and succulent cornstalks, average 0.19 inch in diameter. In some instances the tunnel is more or less winding, and occasionally small cells are excavated along its course. There is a tendency for the larva to work in the internodes of the stalk, but when necessary it commonly pierces and apparently feeds upon the nodes. All parts of the stalk may be tunneled down to and in-

cluding the base or stubble. During this tunneling operation large quantities of yellowish-white frass, mixed with silken strands spun



FIG. 8.—Cornstalk, external view, showing extruded frass and entrance to burrow of larva of the European corn borer

by the larva, are pushed out of the entrance hole and suspended there by the silken strands or collected below in the axils of the leaf blades. (Fig. 8.) These masses of frass are very conspicuous and

serve to attract attention to infested plants at an early stage of the injury. Later in the season, or as the result of heavy rains, much of the frass becomes separated from the plant and falls to the ground.

The tunneling of one or two larvae in a stalk does not always cause appreciable damage; but where, as frequently occurs, several or many borers are tunneling and feeding within the same stalk, it



FIG. 9 — Longitudinal section of ear of sweet corn damaged by European corn borer, showing entrance of larva, the stem, and cob

becomes reduced to a mere shell filled with frass and particles of decayed and putrefied plant matter. Naturally the stalk is greatly weakened by this type of injury, and eventually it collapses and breaks over at one or more places. (Fig. 10.) Such breakage may also occur during wind or rain storms as a result of the tunneling of even one or two borers.

INJURY TO THE EAR

It is evident that the injury to the stalk may indirectly affect the ear by interfering with the supply of nutriment, such injury depending, of course, not only upon the stage of development of the ear during the maximum period of injury, but also upon the degree of injury to the stalk. The ear may be entered directly by the borers (fig. 11) at any stage of their development, at its tip, base, or side; or it may be entered indirectly through the short stem by



FIG. 10.—“Close-up” of hill of sweet corn ruined by European corn borer. Stalks sectioned to show extensive damage within. There were an average of 37 borers per plant in this field. Medford, Mass., September, 1922

which the ear is attached to the stalk. Ordinarily the ear is entered at its tip (fig. 9) by small borers which feed first upon the silk, or the tender portion of the husk, subsequently working their way down into the cob and grain. Ears entered in this manner do not always exhibit external evidences of infestation, as the small particles of frass made by the larvae in entering sometimes are very inconspicuous and the external evidences of feeding are small. It frequently is necessary to strip away the husk before evidence of

such infestation is disclosed. When once inside the ear, the larvae may tunnel through all parts of the grain and the cob, partially or totally destroying the kernels of grain which they attack. (Fig. 12.) The character of the actual feeding in the grain is subject to wide variation; it may consist of long irregular surface tunnels between the rows of the kernels, or it may consist of tunnels just underneath



Fig. 11.—External view of ear, showing extruded frass and numerous punctures caused by larvae of the European corn borer

the upper surface of the kernels, or again large irregular areas may be fed upon with no apparent regularity of procedure. Tunnels in the cob may extend either longitudinally or transversely through it (fig. 13), and when injury of this type occurs early in the development of the ear, it may seriously interfere with the normal formation of the grain. Where several borers are thus feeding upon the grain and the cob, the resulting damage usually is very severe, but when only one or two borers occur within the ear, the damage to the

grain may not be appreciable, particularly where this is confined to the tip of the ear or to the interior of the cob.

When the ear is entered from the side or the base the character of the damage is similar to that detailed in the preceding paragraph.

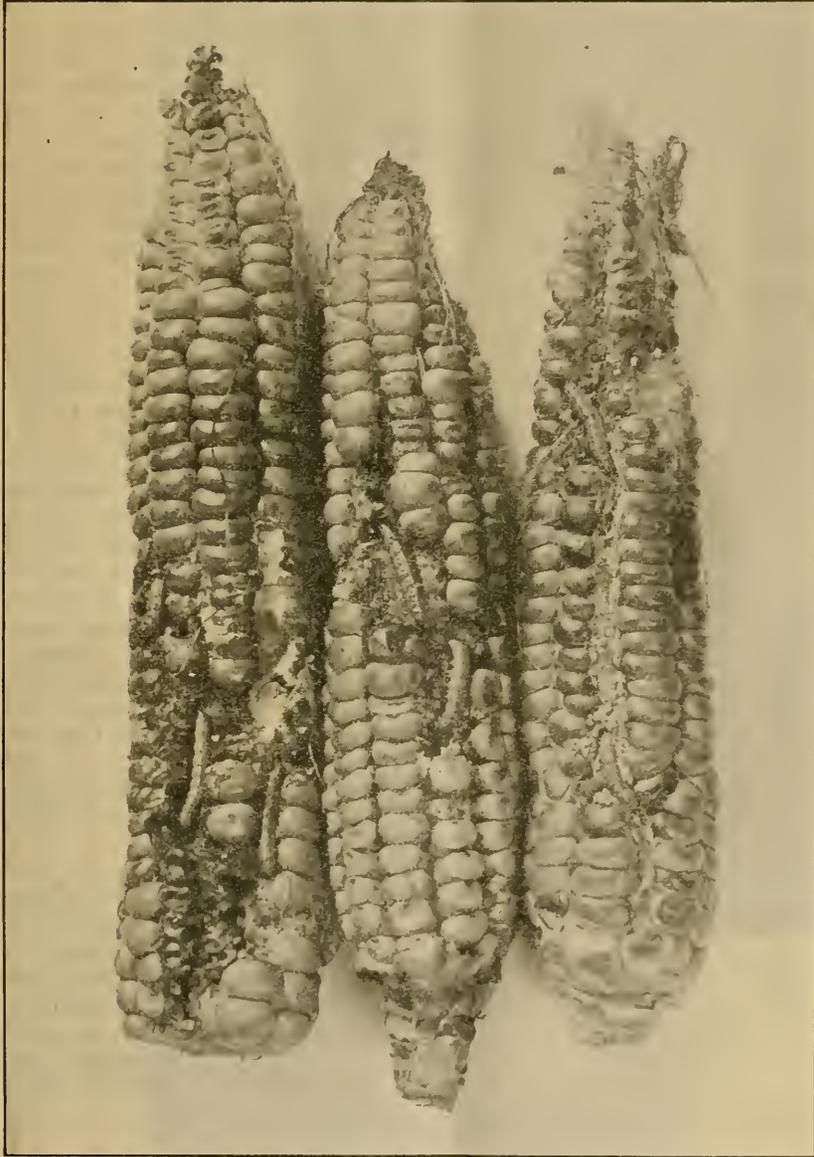


FIG. 12.—Typical injury by the European corn borer to the grain on the immature ears of flint (field) corn. Borers are shown feeding in natural position. The interior of the cobs was also badly tunneled by the borers.

The external evidence of infestation, however, usually is more conspicuous, as large masses of frass are thrown out of the entrance hole by the borer, and these become attached to the ear (fig. 11) or the lower part of the plant, as has been previously described.

Borers entering the ear by way of the ear stem (fig. 9) usually cause injury similar to that inflicted by the larvae entering the ear directly. The tunneling in the ear stem, when severe, and occurring



FIG. 13.—Typical injury by the European corn borer to stalks and ears of sweet corn at roasting-ear stage. Pupae of the first generation are shown in position. One hundred per cent of the stalks and 99 per cent of the ears were infested in this field by the first generation. Saugus, Mass., August 1, 1922.

early in the development of the ear, may interfere with its supply of nutriment. Furthermore, the ear stem is weakened by such injury and frequently breaks over (fig. 14) before the ear has completed its development. In instances where the injury to the ear stem is slight, or when such injury occurs after the ear is nearly mature, no appreciable damage to the grain results, even though the ear breaks over. Many ears thus affected, however, fall to the ground long before harvest and are subject to deterioration by rots and other destructive agencies. When, as sometimes occurs, a large proportion of the ears have fallen to the ground (fig. 15), the expense of harvesting is increased.

Injury to the ears, even where these remain attached to the plant, often is increased by the ingress of rots and molds as a result of the work of the borers, and

aids in reducing even slightly infested ears to a soft decaying condition, thus sometimes entirely destroying its food value.



FIG. 14.—“Close-up” of dent field corn ear and stalk, showing typical injury by the European corn borer. This experimental plat showed an average of 2.5 per cent grain injury, 62.2 per cent ears infested, 100 per cent stalks infested, with an average of 15.5 larvae per plant. Cambridge, Mass., October, 1920



FIG. 15.—Hill of flint field corn, showing severe European corn-borer infestation. Note broken-over stalks and ears lying on the ground. Cambridge, Mass., October, 1920

CHARACTER OF INJURY TO PLANTS OTHER THAN CORN

Injury to plants other than corn is of the same general character as that inflicted on corn, except that in some instances special parts of the plants appear to be habitually preferred as food or as shelter. (See Table 1.)

Although some of the infestation in plants other than corn results from the larvae which have migrated from susceptible plants growing in the vicinity, such as corn or weeds, the eggs are commonly deposited upon a variety of vegetables, field crops, flowering plants, and weeds. Many of the resulting larvae feed and complete their development therein, particularly in the two-generation area of New England.

VEGETABLES

In addition to sweet corn, the most important vegetable hosts of *P. nubilalis* (Table 2) are rhubarb, beets, mangels (fig. 16), celery, beans, spinach, peppers, tomatoes, potatoes (fig. 17), and Swiss chard. A summary of the more important observations relating to the character of injury to these plants is included in Table 2. With the exception of beans, which were slightly infested in the experimental plot at Silver Creek, N. Y., all of these observations are limited to the New England area.

TABLE 2.—Character of injury to vegetables by *Pyrausta nubilalis* larvae (New England, 1918 to 1922)

Name of plant	Parts of plant attacked	Appearance of infested plants	Remarks
Rhubarb.....	Leaf stalks, seed stalks, and main veins of leaves. Eggs deposited freely on leaves. Small larvae feed thereon.	Masses of dark-yellow frass, mixed with gum-like substance, exude from larval tunnels. Affected parts break over when injury is severe.	Most susceptible of vegetable crops. Much of the severe injury occurs after close of commercial season. Plant not seriously affected by this injury.
Beets.....	Leaf stalks, main veins of leaves. Rarely the fleshy portion of root. Eggs deposited freely on leaves. Small larvae feed thereon.	Black, granular frass ejected from larval tunnels. Affected parts break over when injury is severe.	Plants very susceptible. Injury to leaves or leaf stalks does not seriously affect plant. Injury to beet root renders it unsuitable for food.
Celery.....	Leaf stalks, main veins of leaves. Usually outer leaf stalks preferred, although frequent injury to heart of plant. Eggs deposited on leaves.	Wet, discolored frass ejected from larval tunnels. Unless badly infested the injured leaf stalk does not break over.	Plants very susceptible. Injury to leaf stalk renders it unfit for food. Usually the injured portion may be removed and remainder of plant used.
Beans.....	Primarily stalks, occasionally green beans and pods. Eggs deposited on leaves.	Masses of light-yellow frass extrude from larval tunnels. Affected parts break over when injury is severe.	Both low bush and pole beans attacked. Usually the severe injury occurs after beans have reached harvesting stage. Number of infested pods usually less than 1 per cent of total in field.
Spinach.....	Leaves fed upon by newly hatched larvae. Leaf stalks rarely tunneled. Eggs deposited on leaves.	Light-yellow frass ejected from larval tunnels. Injury very inconspicuous.	Infestation by eggs or larvae usually limited to less than 1 per cent of plants in field. Growth of plant not affected.
Pepper.....	Stalks and fruit.....	Light-yellow frass ejected from larval tunnels. Infested stalks break over. Seeds and pulp of fruit eaten.	Both sweet and hot varieties are attacked. Formation of fruit affected when stalks are attacked early. External signs of infested fruit not conspicuous.
Tomato.....	Stalks, and rarely the fruit.	do.....	do.
Potato.....	Stalks. Eggs freely deposited on leaves. Small larvae feed thereon.	Same as above. Tubers not infested.	Even severe breaking over of stalks does not appreciably affect formation of tubers.
Swiss chard.....	Leaf stalks. Eggs occasionally deposited on leaves. Small larvae feed thereon.	Black masses of frass ejected from larval tunnels. Usually the tunnel is discernible from surface of leaf stalk.	Growth of plant not appreciably affected. Injured parts unsuitable for food. Usually the affected parts do not break over.



FIG. 16.—Mangel severely injured by European corn borer. Note extensive decay following work of borers. As many as 60 borers were found in a single mangel. Winchester, Mass., November 1, 1922



FIG. 17.—Potato stalks sectioned to show typical work of European corn borer larvae therein and pupae in position. Fifty-four per cent of the plants in this field were infested. Winchester, Mass., July 27, 1922

FIELD CROPS

Practically none of the common field crops, with the exception of timothy and oats (fig. 18), are grown to any extent within the area where *P. nubilalis* has become well established in New England. It was necessary, therefore, to grow small experimental plats of the more important field crops at Medford, Saugus, Cambridge, Belmont, and Woburn, Mass., in order to ascertain the reaction of the insect to them. It seemed desirable to include such other important field crops as are normally grown in the South and West, with the object of obtaining advance information regarding the adaptability of the insect to these crops.



FIG. 18.—Oats showing European corn-borer larvae infesting stem

The experimental plats were duplicated at Scotia and Silver Creek, N. Y., but most of the information included herewith was obtained from the Massachusetts plats, where the insect is more numerous and habitually attacks a greater variety of plants under field conditions. The results obtained should be considered as merely indicative, because it does not seem possible definitely to forecast the reaction of *P. nubilalis* to some of these crops, under American conditions, if the insect should become well established where they are extensively grown. A summary of the observations relating to the character of injury to field crops is included in Table 3.

TABLE 3.—Character of injury to field crops by *Pyrausta nubilalis* larvae
(New England, 1919 to 1922)

Name of plant	Parts of plant attacked	Appearance of infested plants	Remarks
Millet.....	Stems (culms). Eggs rarely deposited on leaves.	Masses of light-yellow frass extrude from larval tunnels. Infested stems usually break over.	Japanese millet very susceptible. European millet to a lesser extent. Hungarian millet rarely attacked.
Hemp.....	Stalks, seed heads. Eggs freely deposited on leaves. Small larvae feed thereon.	Same as above. Plants break over only when severely injured.	Very susceptible. Found occasionally growing wild in Massachusetts area. Invariably infested when exposed to attack.
Grain sorghums.do.....	Red frass ejected from larval tunnels. Stalk breaks over just below seed head when severely injured. Resembles injury to tassel stem of corn.	Includes hegari, leterita, milo, and kafir. Hegari most susceptible and more severely injured than the others of this group.
Broomcorn.....do.....do.....	Appears to be able to withstand severe infestation without appreciable injury to the brush used in broom making.
Barley.....	Stems (culms).....	Masses of light-yellow frass ejected from larval tunnels. Infested stems usually break over.	Formation of grain seriously affected when stem is attacked early in its development. Late attack not seriously injurious.
Cotton.....	Stalks, bolls. Eggs freely deposited on leaves. Small larvae feed thereon.	Same as above. Bolls entered at base, under bracts, when nearly full grown. Dark-brown frass extrudes from entrance holes. Larvae tunnel through carpel, lint, and seed.	Quite susceptible. Development of bolls prevented when stalk breaks over early in its development. Bolls not affected by slight or late injury to stalk. Plants killed by frost before bolls opened.
Cowpea.....	Stalks, pods. Eggs occasionally deposited on leaves.	Masses of light-yellow frass extrude from larval tunnels. Infested stems usually break over. Injury to pods similar to beans.	Most of injury occurs late in the season. Growth of plant or yield of seed not appreciably affected.
Sorgo.....	Stalks, seed heads. Eggs freely deposited on leaves. Small larvae feed on leaves.	Appearance of injury similar to corn. Plants break over only when severely injured. Frass red in color.	Except when severely injured the growth of plants infested is not seriously affected.
Hop.....	Vine (stem) and leaf stems.	Light-yellow frass ejected from larval tunnels.	Only occasionally infested. ¹
Buckwheat.....	Stems.....	Masses of white frass extrude from larval tunnels. Infested stems usually break over.	Grains reduced in size or their formation prevented entirely when injury occurs before seed head develops.
Oats.....	Stems (culms). Eggs rarely deposited on leaves.do.....	Do.
Johnson grass.....do.....do.....	Yield of fodder or seed not appreciably affected.
Sudan grass.....do.....do.....	Do.
Soy bean.....	Stalks. Feeding injury to leaves. Eggs found on leaves.	Masses of light-yellow frass extrude from larval tunnels. Plants break over when severely injured.	Plants infested late in the season. Growth of infested plants not appreciably affected. Soy beans infested under field conditions in New York.
Rape.....	Leaf stalks.....do.....	Very slightly susceptible. No appreciable effect on plant.
Sweet clover (white).	Stems.....do.....	Same as above. White sweet clover grows wild in waste areas, in vicinity of Boston, Mass.
Timothy.....	Stems, seed heads.....do.....	Infested usually by smaller larvae. Full-grown larvae found rarely in larger stems.
Tobacco.....	Stalks.....	Masses of dark brown frass extrude from larval tunnels.	Infestation occurs during late season. No appreciable effect on plant. Larvae found in tobacco were dead, or died subsequently.

¹ Japanese hop (*Humulus japonicus*) is grown as an ornamental in Massachusetts and under these conditions it is frequently and severely infested.

FLOWERING PLANTS

Although a large number of flowering plants are known to be attacked by *P. nubilalis* (Table 1), the most important of this group, considering their susceptibility and economic importance, are dahlia, China aster, chrysanthemum, zinnia, calendula, canna, cosmos, geranium, gladiolus (fig. 19), golden glow, hollyhock, and salvia. A summary of the more important observations relating to these plants is included in Table 4. With the exception of cosmos and dahlia, which were slightly infested in the experimental plat at Silver Creek, N. Y., all of these observations are limited to the New England area.

WEEDS

The character of the injury to the weeds and wild grasses which are attacked by the European corn borer (Table 1) is essentially the same as has been described for corn and other economic hosts of the insect. Eggs are deposited upon some of these weeds and wild grasses, particularly in the New England area, and the resulting larvae may complete their development and pupate within, or may migrate to various other host plants in the vicinity. In addition, these plants frequently are infested by larvae migrating from near-by crops, notably corn. The injury to weeds and wild grasses is characterized by the collapse and breaking over of the stems or stalks which are severely infested. In weed infestation, such as occurs in barnyard grass, the larvae tunnel through the stalks and stems, even including the base of the stalk, or stubble, to a point below the surface of the ground. (Fig. 20.) The percentages of infestation in some of the more susceptible weed hosts are shown in Table 20.

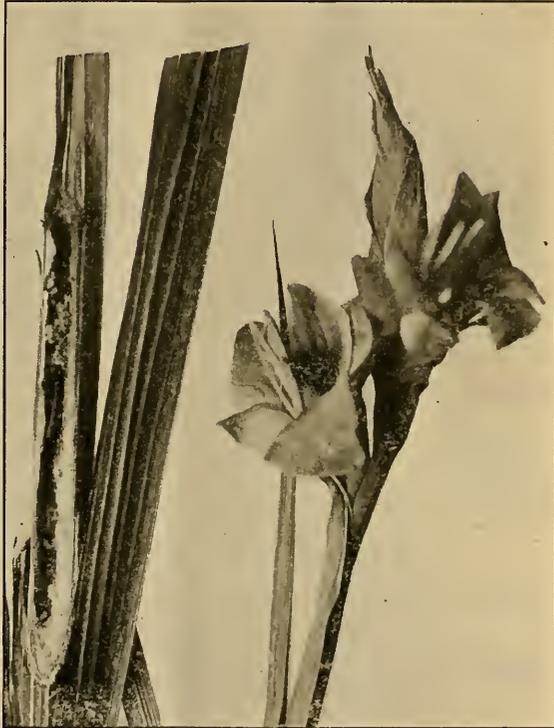


FIG. 19.—Gladiolus stem, showing European corn-borer infestation



FIG. 20.—European corn-borer larvae at base of barnyard-grass stubble

TABLE 4.—Character of injury to flowering plants by *Pyrausta nubilalis* larvae (New England, 1918 to 1922)

Name of plant	Parts of plant attacked	Appearance of infested plants	Remarks
Dahlia.....	Stalks, flower stems, and flowers. Eggs freely deposited on leaves. Small larvae feed thereon.	Large masses of light-yellow frass extrude from larval tunnels. Affected plants wilt and break over when severely injured.	Most susceptible of the flowering plants. Injury most severe at time of blooming. Entire planting frequently infested. Roots (tubers) not infested.
China aster...	Stalks and flowers. Eggs rarely deposited on leaves.	Same as above. Most of injury to middle part of stalk. Affected stalks usually break over.	Frequently infested in field and in greenhouse. Production of blooms usually reduced or prevented entirely.
Chrysanthemum.	Stalks, flower stems, and flowers. Feeding areas on leaves but no eggs found.do.....	Greenhouse and hardy varieties very susceptible. Size of blooms not affected by slight or late injury to stalks. Blooms reduced in size or prevented entirely by early breaking over of the stalk.
Zinnia.....	Stalks, flower stems, and flowers. Eggs rarely deposited on leaves.do.....	Same as above except not found infested in greenhouse. Rarely grown under glass.
Calendula....	Stalks, flowers.....do.....	Same as above. Rarely found infested in greenhouse.
Canna.....	Stalks, midrib of leaves and flowers. Feeding areas on leaves but no eggs found.	Light-brown frass extrudes from larval tunnels. Most of injury to midrib of leaf.	Seldom infested except when growing near other infested plants. No infestation found in roots.
Cosmos.....	Stalks. Rarely in flower stems.	Large masses of light-yellow frass extrude from larval tunnels. Affected parts break over when severely injured.	Most of injury to main stalks, late in season. Flower buds seldom open on part of plant broken over. Not found infested in greenhouse.
Salvia.....	Stalks, flower stems.....do.....	Do.
Geranium.....	Stalks.....do.....	Do.
Hollyhock....	Stalks, leaf stems.....do.....	Same as above. Leaf stems of young plants particularly susceptible.
Gladiolus....	Stalks and flowers. Eggs occasionally deposited on leaves. Small larvae feed thereon.do.....	Weakened or broken stems often render the spike unmarketable. Slight injury to flower stems, no appreciable effect on spike. Not infested in greenhouse.
Golden glow.	Stalks, flower stems. Eggs rarely deposited on leaves.do.....	Most of injury occurs late in season after flowers have formed. No appreciable injury to plant.

EXTENT OF INJURY AND ECONOMIC LOSS

CORN

Most of the direct injury and loss to corn, as a result of European corn-borer attack, is caused by the larvae feeding on the grain and in the cob of the ear. (Fig. 21.) In addition to this direct loss to the ear there is also an indeterminate amount of indirect loss, as previously described. The injury to the lower stalks and ear stem,

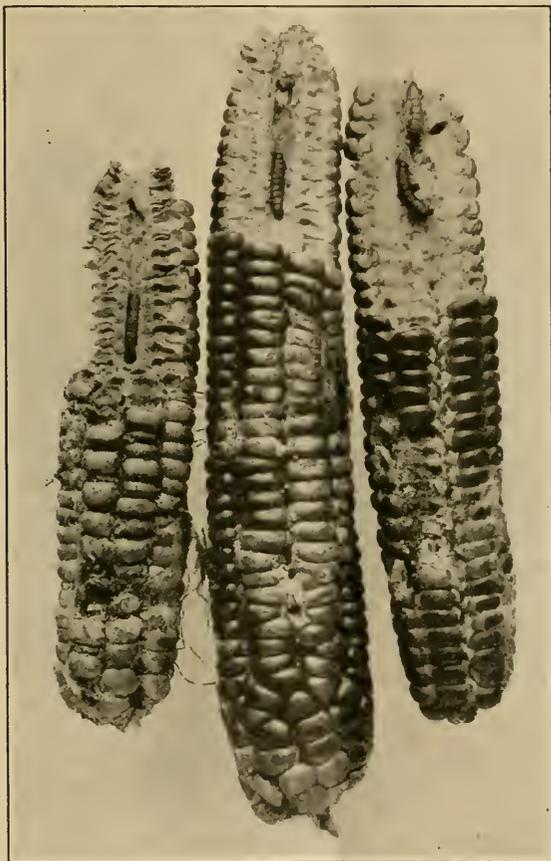


FIG. 21.—European corn-borer injury to grain and cob of flint field corn. Cobs sectioned to show borers within. One hundred per cent of the stalks and ears were infested and 17 per cent of the grain destroyed in the field from which these ears originated. Medford, Mass., October, 1922

if severe and occurring before the ear is nearly mature, frequently results in a small or poorly formed ear. The actual extent of injury and economic loss resulting from the indirect injury to the ear and the stalk is difficult to estimate definitely, as it varies greatly in different fields and depends upon several factors, the most important of which are (1) percentage of plants infested, (2) the number of borers per plant, (3) the stage of development of the plant when attacked, (4) the part of the plant selected for attack, and (5) the

The experimental fields were located where the corn borer has become well established, and the infestation and injury to the corn in these fields represented ordinary conditions. Moreover, the fact that these varieties were grown in adjacent plats under the same cultural conditions provides an indicative basis for comparison of relative susceptibility of varieties and types. The fields wherein these plats were located received a thorough clean-up and plowing during the preceding fall, or in the spring, so that the conditions of infestation prior to planting were much better than those existing in commercial fields of the vicinity. Most of the subsequent infestation in these plats, particularly that by the first generation,

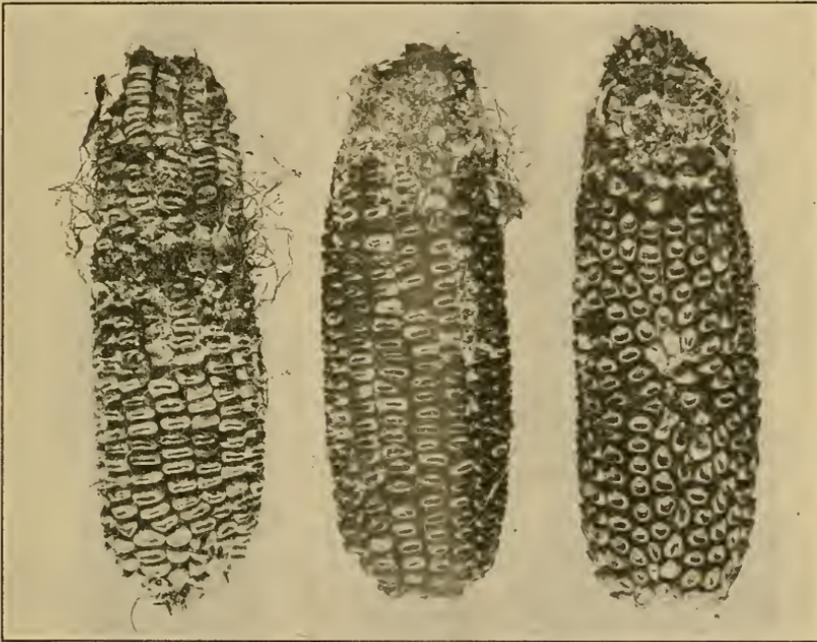


FIG. 22.—European corn-borer injury to grain of dent field corn. The cobs and ear stems were also badly tunneled by the borers. The experimental plat from which these ears originated showed 28.7 per cent grain injury, with 100 per cent of ears and stalks infested. Medford, Mass., October, 1922

is believed to have been caused by the flight of moths from adjoining fields. The results of the examinations of the experimental plats are shown in Table 5.

The counts shown in Table 5 were made at the time of harvest; 50 ears were selected at random from each plat of field corn when mature and 100 ears selected in the same manner from each plat of sweet corn at the roasting-ear stage. The stalk infestation was based upon an examination of 100 stalks from each plat. The actual grain injury to sweet corn is not indicative of the real loss, as many ears which suffered only slight damage to the grain at the roasting-ear stage were rendered unfit for market purposes or for canning. The grain injury to dent corn in comparison with flint corn is somewhat affected by the fact that in the 1920 series 4 of the varieties of dent corn did not mature under Boston conditions. According to experi-

mental evidence obtained in Massachusetts during 1922 (Table 5), under conditions of severe infestation, the ears (fig. 22) and stalks of the early-maturing or short-season varieties of dent corn are as susceptible to severe injury by *P. nubilalis* as the ordinary sweet or flint corn varieties. In general, however, the infestation

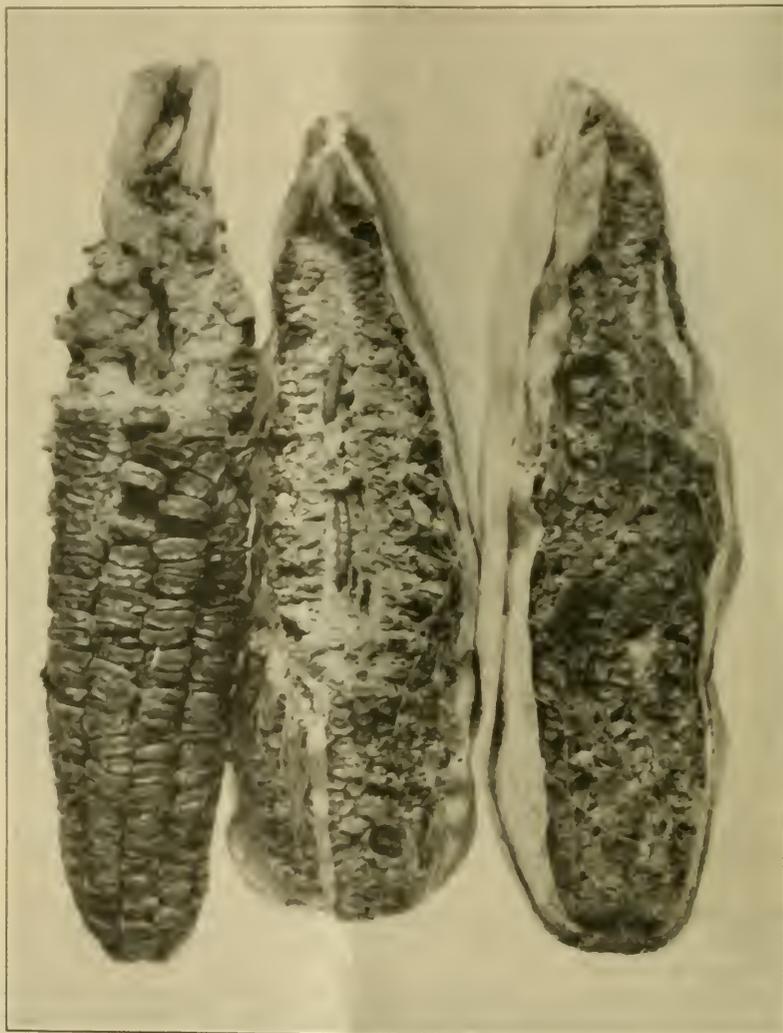


FIG. 23.—Ears of sweet corn left to ripen for seed, showing severe injury to grain and cob by European corn borer. Two cobs cut open to show borers within. Also note severe injury to ear stem. Medford, Mass., September, 1922

and injury to dent corn, particularly the large-stalked and late-maturing varieties, has been less severe than to the earlier maturing and smaller-stalked varieties of flint corn. It is a matter of speculation whether this relative susceptibility and injury would be retained in regions where the duration of the growing season permitted the maturity of large dent corn varieties. Flint and sweet

corn appear to be about equally susceptible to infestation and injury, although the commercial injury to the ears and grain of sweet corn is limited to the development of the ear to the roasting-ear stage, unless grown for seed (fig. 23), and therefore does not serve as a real comparison of susceptibility with flint corn grown for grain.

Table 6 gives data relative to the injury and loss to ears, grain, and stalks of flint field corn and sweet corn during the period 1920 to 1922 in representative commercial fields in that portion of the New England area where the insect has become well established. All of the flint cornfields grown within this area are included. Since dent field corn is seldom grown commercially for grain in that part of the New England area now infested by the corn borer, there were no fields of this type available for examination. The sweet corn fields included herein were selected on the basis of personal judgment of average conditions and not by the use of arithmetical methods. The injury and loss in certain small fields of sweet corn representing the maximum infestation (fig. 24) was greater than these figures indicate. No complete information is at hand relative to the clean-up measures employed in all of these fields during the preceding fall and spring, but judging from the usual practice in the section where these fields were located it is probable that all standing cornstalks were removed in the fall, and that the corn stubble, other crop refuse, and weeds were plowed under, either in the fall or spring. This type of field practice, however, usually results in leaving undisturbed large numbers of infested weeds along the field borders.

TABLE 6.—Extent of injury and loss caused by the European corn borer to ears, grain, and stalks of field and sweet corn in the New England area, 1920 to 1922

Locality (Massachusetts)	Acreage of fields examined			Ear examination						Per cent of grain injured or destroyed on ears examined			Stalk examination					
				Number examined			Per cent infested						Number examined			Per cent infested		
	1920	1921	1922	1920	1921	1922	1920	1921	1922	1920	1921	1922	1920	1921	1922			
Flint corn:																		
Medford	2.0			50			96.0			4.0			200			98.0		
Wakefield	4.0	7.0	2.0	50	50	100	24.0	70	39.0	.3	1.5	1.9	850	700	200	40.9	60	100.0
Arlington	1.5	1.0		50	100		80.0	96		10.4	7.3		300	200		100.0	100	
Stoneham	3.5	4.0		50	50		58.0	66		3.8	2.2		750	800		94.0	78	
Scituate			1.5			100			100.0			10.0			300			100.0
Sweet corn:¹																		
Arlington	2.5			100			64.0			3.1			500			88.0		
Watertown	3.5	4.5		100	100		44.0	72		4.1	2.8		200	300		100.0	89	
Medford		6.0	5.0		100	100		46	37.0		.5	.2		500	100		98	100.0
Melrose			6.0			300			57.6			.3		300				72.7
Saugus			5.0			200			82.5			3.9		300				100.0
Winchester			4.25			400			42.5			.4		300				63.0
Woburn			7.5			500			10.0			.02		500				24.0
																Flint	Sweet	
Three-year average (per cent):																		
Ear infestation																71.9		43.2
Grain injury																5.1		1.1
Stalk infestation																76.6		77.5

¹ At roasting-ear stage of growth.

The figures in Table 6 show an important amount of direct loss from ear infestation and grain injury to both flint and sweet corn. The susceptibility to infestation of flint field corn and sweet corn was nearly equal in these fields as shown by the average percentages of stalk infestation of 76.6 and 77.5 for the flint and sweet types, respectively. The difference between the percentages of ear infestation and grain injury of the two types is due to the fact that the sweet-corn ears are harvested before maturity, and therefore are exposed to injury for a shorter period than the flint corn.

During 1922 a series of examinations were made throughout the season in 50 fields of sweet corn, aggregating 63.5 acres, taken at random in 20 towns of the New England area. These examinations were made at harvest (roasting-ear stage) and on a basis of 100 ears and 100 stalks to each field. In 9 of these fields none of the ears were infested. In the remaining 41 fields the percentage of ears infested ranged from 1 to 100, the average for the entire 50 fields (5,000 ears) being 20.4 per cent. The stalk infestation for the 50 fields averaged 56.5 per cent. The majority of the ears found to be infested were unfit for market. A similar examination conducted in 66 fields of the New England area during 1923 gave an average ear infestation of 10.6 per cent, and during 1924 an average of only 1.2 per cent of the sweet-corn ears were found infested in 52 fields of the same area.

As a part of the investigation to determine the progress of annual increase or decrease of infestation, careful counts were made in 1921 and 1922 in the cornfields of 40 townships of New England, representing all conditions of infestation from the center of the area to the lightly infested townships near the border of the area. In these field counts 10 fields (or garden patches in residential districts) were selected in each town, such selections being made on the basis of the personal judgment of the field worker as to what constituted fields which were representative of the entire town. In figuring the averages the results from all fields, whether infested or noninfested, were included.

The majority of these fields were, of necessity, sweet corn. These counts show that in 1921 an average of 29.93 per cent of the stalks were infested in these 40 towns, including noninfested as well as infested fields, with an average of 4.44 larvae per infested stalk (132.9 larvae per 100 stalks); while in 1922 an average of 53.29 per cent of the stalks were infested in these same towns, with an average of 8.75 larvae per infested stalk (466.3 larvae per 100 stalks). These figures are believed to represent accurately the average conditions throughout the New England area for this two-year period. Comparable figures for the 1923 field survey show that in the 222 fields examined in 22 of the same towns included in the 1921 and 1922 surveys there were an average of 30.1 per cent of the stalks infested, containing an average of 3.8 larvae per infested stalk (114.5 larvae per 100 stalks); while in 1924 there were an average of 18.2 per cent of the stalks infested in the 178 fields examined in 35 of the same towns included in the 1923 survey, containing an average of 2.2 larvae per infested stalk (40 larvae per 100 infested stalks).

The annual surveys have shown a very significant decrease in the acreage planted to corn each year, especially in that portion of the

territory where the insect has become numerous. The decrease in aggregate acreage in 1922, as compared to 1921, was approximately 50 per cent in the 40 towns.

NEW YORK

The extent of injury and economic loss caused by the corn borer in New York State has been comparatively slight to date. Except in a very few fields the infestation has not approached that existing in New England.

EASTERN NEW YORK

Table 7 gives data relative to the injury and loss to ears, grain, and stalks of flint, dent, and sweet corn, during the period from 1920 to 1922, in that portion of the eastern New York area where the corn borer is known to have been present for at least four years and where it has become fairly well established, although it is probably not now as numerous in this area as may be expected in the future. Some of the smaller fields representing the maximum infestation in this area are not included in the table.

TABLE 7.—Extent of injury and loss caused by the European corn borer to ears, grain, and stalks of field and sweet corn in eastern New York, 1920 to 1922

Locality (eastern New York)	Acreage of fields examined			Ear examination						Per cent of grain injured or destroyed on ears examined			Stalk examination								
				Number examined			Per cent infested						Number examined			Per cent infested					
	1920	1921	1922	1920	1921	1922	1920	1921	1922	1920	1921	1922	1920	1921	1922	1920	1921	1922			
Flint corn:																					
Glenville.....	1.63		14.0	1,572			300	0.86		0.33	0.05		0.00	1,000		4,166	6.9	3.9			
Do.....			3.0				823			1.90			.03			1,086		7.9			
Dent corn:																					
Glenville.....	1.75	6		2,588	100			.62	9.00		.01	0.75		1,000	678		4.3	11.8			
Do.....	12.00	5		8,409	200			1.10	6.00		.09	.33		8,409	1,000		8.8	6.5			
Do.....			1.1				157			.64			.02			1,000		.9			
Sweet corn: ²																					
Glenville.....	2.00	4		100	100			5.00	9.00		.41	1.27		400	1,360		11.7	10.1			
Do.....	1.75	6		100	250			3.00	8.00		.12	1.08		200	500		2.5	7.4			
Do.....	2.50			100				2.00			.10			300			1.7				
Do.....	4.00			100				2.00			.11			5,074			7.5				
													Flint			Dent			Sweet		
Three-year average (per cent):																					
Ear infestation.....													0.98			1.03			5.46		
Grain injury.....													.044			.081			.628		
Stalk infestation.....													5.09			7.75			7.79		

¹ Experimental plat records.

² At roasting-ear stage of growth.

An examination of Table 7 shows that in eastern New York the corn borer as yet has caused but a very slight crop loss. Such infestation and loss as have occurred, however, indicate that in this area the three types of corn (flint, dent, and sweet) are equally susceptible. In the majority of the infested fields of this area the infestation is very sparse at present, and in many of these fields it is difficult to detect the presence of the insect.

Comparative counts of stalk infestation which were made during 1921 and 1922 in 12 average fields located within that portion of this area where the corn borer has become well established

showed 9.3 per cent of stalk infestation in 1921, with an average of 2.51 larvae per infested stalk (23.3 larvae per 100 stalks); while in 1922 in the same fields 7.9 per cent of the stalks were infested, with an average of 2.38 larvae per stalk (18.8 larvae per 100 stalks). Figures are not available for the 1923 field survey in this area. A comparable survey in 30 of the same or near-by fields in 1924 showed an average stalk infestation of 15.1 per cent, containing an average of 1.6 larvae per infested stalk (24.2 larvae per 100 stalks). Examinations of the ear infestation in 8 of these sweet-corn fields, included above, showed that an average of 5.3 per cent of the ears contained the borer in these fields at the time of harvest.

WESTERN NEW YORK

The injury and loss as well as the degree of infestation have been greater in the western than in the eastern area of New York State. Table 8 gives data for the period 1920 to 1922 regarding infestation and injury to field and sweet-corn fields, selected on the basis of personal judgment of average conditions, within the area where the corn borer has become well established in western New York. Some of the smaller fields which represented the maximum infestation of the area are not included in this table.

TABLE 8.—Extent of injury and loss caused by the European corn borer to ears, grain, and stalks of field and sweet corn in western New York, 1920 to 1922

Locality (western New York)	Acreage of fields examined			Ear examination						Per cent of grain injured or destroyed on ears examined			Stalk examination								
				Number examined			Per cent infested						Number examined			Per cent infested					
	1920	1921	1922	1920	1921	1922	1920	1921	1922	1920	1921	1922	1920	1921	1922	1920	1921	1922			
Flint corn:																					
Silver Creek			6.5			500			4.4			1.20			500			31.2			
Dent corn:																					
Hanover	4.00			200			12.0			0.37			300		71						
Silver Creek	3.50	10.0	200			500	1.5	1.4	.04	.07			300	1,000	19		19.7				
Indian reservation		22.0				1,000		1.9		.06				1,000				22.6			
Silver Creek		1.5				200		1.0		.11				200				15.5			
Do.		6.0				500		.4		.06				500				13.0			
Do.		5.0				500		.8		.04				500				13.6			
Do.		5.0				500		1.2		.12				500				13.2			
Do.		2.0				500		1.4		.09				500				9.6			
Do.		8.0				500		.2		.01				500				1.4			
Do.		2.0				500		.2		.00				500				3.6			
Do.		2.0				500		.6		.01				500				4.2			
Do.		4.0				500		.4		.01				1,000				3.5			
Sweet corn: ¹																					
Hanover	.25			100			22.0		1.14				100		45						
Silver Creek		1.0	.1			150		100		16.0	3.0	2.32	.14		150	100		78 16.0			
Do.		5.0				500		500		4.2		1.01			500			37.2			
Do.		2.0				500		500		1.4		.71			500			27.4			
Do.		4.0				1,000		1,000		2.6		.46			1,000			29.1			
Do.		1.0				500		500		3.2		1.02			500			16.4			
Do.		3.0				1,000		1,000		2.7		.89			1,000			22.7			
Do.		1.0				200		200		.5		.09			200			8.0			
Do.		5.0				1,000		1,000		5.2		1.64			1,000			44.9			
Do.		6.0				1,000		1,000		.7		.04			1,000			8.9			
Do.		3.0				500		500		.4		.07			1,000			3.5			
													Flint			Dent			Sweet		
Three-year average (per cent):																					
Ear infestation													4.4			1.33			3.18		
Grain injury													1.2			.06			.75		
Stalk infestation													31.2			14.40			23.90		

¹ At roasting-ear stage of growth.

An examination of Table 8 shows that in western New York the corn borer is now causing appreciable injury to all types of corn, and that while the present severity of the infestation is not comparable to that existing in New England, the degree of infestation is such that serious losses may develop in the near future, unless measures are taken to keep the insect in check.

The comparative field counts of stalk infestation which were made in 1921 and 1922 in 8 fields, selected on the basis of personal judgment of average conditions, within the worst infested portion of the western New York area, showed that 26.2 per cent of the stalks were infested in 1921, with an average of 3.33 larvae per infested stalk (87.2 larvae per 100 stalks), while in 1922 in the same fields 18.9 per cent of the stalks were infested, with an average of 1.76 larvae per infested stalk (33.3 larvae per 100 stalks.) Comparable figures for the 1923 field survey show that in 30 fields, in the same area where the 1921 and 1922 surveys were conducted, there were an average of 15.2 per cent of the stalks infested, containing an average of 1.3 larvae per infested stalk (19.8 larvae per 100 stalks), while in 1924 there were an average of 27.8 per cent of the stalks infested, in 36 of the same or near-by fields surveyed in 1923, containing an average of 2.7 larvae per infested stalk (75.1 larvae per 100 stalks). Examinations for ear infestation in field and sweet corn in this area during 1923 showed that an average of 5.5 per cent of the ears were infested in 19 of the fields mentioned previously and also including sample examinations of the sweet-corn ears brought to two canning factories. A similar examination of the ears from the 36 fields surveyed in 1924, and from three canning factories, revealed that 9 per cent of the ears, on an average, contained the borer. Sample examinations of 2,700 sweet-corn ears delivered to a canning factory at Silver Creek, N. Y., during 1924 revealed that 11.9 per cent of the ears examined contained the borer.

The unusual abundance of the corn ear worm in both the eastern and western New York areas during 1921 rendered it difficult to obtain accurate records of grain injury which could be attributed solely to the corn borer.

OHIO AND MICHIGAN

In Ohio and Michigan there has been very little economic loss caused by the corn borer to the close of 1924. There was, however, a widespread dispersion of the pest in this area during 1924, accompanied by an increase in intensity which amounted to 258 per cent when compared to conditions existing in 1923. Should the rate of annual increase which prevailed during 1923 and 1924 be continued, it appears reasonable to forecast that appreciable losses will become general in this area in the near future, especially since similar developments in the older area of infestation across Lake Erie in Ontario have led to severe losses to all types of corn under similar cultural conditions to those prevailing in Ohio and Michigan. During 1923 a survey of 133 fields of Ohio and Michigan revealed an average stalk infestation of 1.83 per cent, with an average of 1.41 larvae per infested stalk or 2.58 larvae per 100 stalks. These fields were selected throughout the area as representing average conditions according to the personal judgment of the field worker. A similar field survey in 241 fields of this area during 1924 showed an average stalk infesta-

tion of 5.28 per cent, with an average of 1.75 larvae per infested talk, or 9.24 larvae per 100 talks. Maximum were recorded of 52 per cent in stalk infestation of sweet corn and 33 per cent stalk infestation in dent field corn during 1924, as compared to a maximum of 17 per cent in 1923.

DISTRIBUTION OF GRAIN INJURY ON INFESTED EARS

In making detailed counts of the grain injury on ears damaged by *P. nubilalis*, it was noted that while in general the greater proportion of this injury occurred to the kernels on the tip of the ear, the injury was also well distributed on the side and butt of the ear. In the majority of the lots of ears examined the total injury to the butt and side kernels nearly equaled, and sometimes exceeded, the injury suffered by the tip kernels, as will be seen in Tables 9 and 10. The tip is here considered to be the upper third of the ear, the side is considered to be the middle third, and the base the lower third. Table 9 shows the distribution of the grain injury on the infested ears of flint, dent, and sweet corn which have been previously mentioned under Table 5.

TABLE 9.—Distribution of grain injury caused by European corn borer on infested ears (three-year average from experimental plats)

Type of corn	Total ears examined	Per cent of ears infested	Distribution of grain injury on infested ears (per cent) ¹		
			Butt	Side	Tip
Flint.....	900	86.7	17.58	29.67	52.75
Dent.....	1,250	74.6	19.05	19.05	61.90
Sweet.....	5,500	57.1	13.89	22.22	63.89
Average.....			15.48	22.80	61.72

¹ These percentages do not refer to the total per cent of grain injury on the butt, side, and tip; they show only the relative proportions of injury to these three parts of the ears.

That the distribution of grain injury on the ears is influenced by the severity of the infestation, was demonstrated during 1922 in the presence of a more severe infestation than during the preceding two years. Table 10 shows data on this point as taken from records of ear examinations in the 1922 experimental plats of flint, dent, sweet, and pop corn in New England.

TABLE 10.—Distribution of grain injury caused by the European corn borer on infested ears from experimental plats of 1922

Type of corn	Total ears examined	Per cent of ears infested	Distribution of grain injury on infested ears (per cent) ¹		
			Butt	Side	Tip
Flint.....	50	100	31.00	22.89	46.10
Dent.....	100	100	20.79	30.81	48.40
Sweet.....	1,300	74	23.46	29.18	47.36
Pop.....	50	100	24.34	26.46	49.20
Average.....			23.58	28.93	47.47

¹ These percentages do not refer to the total per cent of grain injury on the butt, side, and tip; they show only the relative proportions of injury to these three parts of the ears.

EFFECT OF INJURY TO CORN INTENDED FOR SEED

It has been shown by Brown (9) that the mutilation of corn kernels does not necessarily prevent the production of normal plants by these mutilated kernels when used for seed, although the growth and yield of plants produced by such kernels may be less than from uninjured seed. The proportion of "injured" kernels shown in Tables 5 to 10 which could be used as seed, or as food, was very small, however, and was more than counterbalanced by the rotting of adjacent uninjured kernels on the cob, caused by infection from the injured kernels (not shown on the records of grain injury). Moreover, the mutilation of the kernels by *P. nubilalis*, when such kernels were not completely destroyed, was usually confined to the seed coats and endosperms. According to Brown (9) the injury to these portions of the kernels has a greater effect on the reduction of yield than injury to the germ.

EFFECT OF STALK INJURY

With respect to the stalk infestation and the consequent indirect injury and loss which such infestation causes to the ears and grain, it is difficult to assign any definite and uniform degree of economic importance to the figures pertaining to this factor as shown in the preceding tables, since the percentage of stalks infested, or broken over, does not in every instance have a distinct bearing upon the reduction in yield of grain or fodder. A high percentage of infested or broken-over stalks does not always mean severe damage to the ears and grain, because the principal injury and breaking over may occur late in the development of the plant, so that the grain may reach practically normal maturity in the case of field corn, or the ears of sweet corn may reach the roasting-ear stage before being seriously injured by the larvae.

Definite relation between the percentage of infested stalks and the percentage of broken-over stalks seldom was found because the amount of breaking over, except in instances of very severe infestation, depends to a considerable extent upon the size of the stalks of the variety attacked, and upon the occurrence of heavy wind or rainstorms after the injury takes place. Large heavy-stalked varieties will sometimes withstand considerable infestation without breaking over or showing an appreciable effect upon the ears or grain, whereas small-stalked varieties are much more susceptible to such injury as a result of the tunneling of the borers, and if severely attacked early in their development, extensive curtailment of grain production may result.

EFFECT OF INJURY TO STALKS UPON THE NUMBER AND WEIGHT OF EARS

In attempting to obtain information regarding the effect of stalk injury upon the number and weight of ears produced by such stalks, an important handicap has been encountered because of the fact that in fields where stalk infestation was severe enough to exert an appreciable effect upon ear production, noninfested stalks which could be used as a means of comparison were wanting. It is obvious that for satisfactory information on this point the infested and non-infested plants should be of the same variety and type, planted at the same time, and grown under identical soil and other cultural conditions. Therefore, it became necessary to make a comparative

examination of this character in the same field, and to select a field for this purpose which showed a relatively light infestation in order to secure noninfested stalks.

Table 11 gives results from two fields of Longfellow flint field corn in which the ears and nubbins were removed and weighed from an equal number of severely infested and noninfested stalks. In field No. 1, located at Stoneham, Mass., 78 per cent of the stalks and 66 per cent of the ears were infested, with a total grain injury of 2.2 per cent. In field No. 2, located at Wakefield, Mass., practically 100 per cent of the stalks and 39 per cent of the ears were infested, with a total of 1.9 per cent grain injury. In this field it was possible to find a sufficient number of noninfested stalks to serve as a comparison.

TABLE 11.—*Effect of injury caused by the European corn borer to stalks upon the number and weight of field-corn ears*

Location (Mass.)	Total stalks examined in each lot	Infested stalks			Noninfested stalks			Loss in ears		Loss in weight	
		Number of ears	Number of nubbins	Weight of ears and nubbins (lbs.)	Number of ears	Number of nubbins	Weight of ears and nubbins (lbs.)	Number	Per cent	Pounds	Per cent
Stoneham.....	100	98	12	47.50	99	13	51.50	1	1.01	4.00	7.76
Wakefield.....	50	14	8	18.00	51	4	25.75	7	13.73	7.75	30.10
Total.....	150	142	20	65.50	150	17	77.25	8	11.75
Average.....	5.33	15.21

From Table 11 it appears that in the two fields examined the number of ears from the noninfested stalks exceeded those from the severely infested stalks by 5.33 per cent, while weight of the ears and nubbins from the noninfested stalks exceeded that of the infested stalks by 15.21 per cent. The "severely infested" stalks used as a basis of comparison were selected with a view to approximating average conditions in fields sustaining maximum infestation, and the losses shown in Table 11 may therefore be taken as indicative of actual loss occasioned by borer injury to the stalks. The percentage of loss due to prevention of ear production and reduced weight of ears and nubbins, as shown, undoubtedly is exceeded in fields sustaining maximum infestation, but in the absence of accurate means of calculating such losses no figures can be given. It is in this class and from this cause that the major portion of the gross damage by the corn borer occurs, as will be apparent by comparing the figures showing direct grain injury with the figures showing indirect grain loss through the prevention and reduction of ear (grain) formation.

EFFECT OF INJURY TO STALKS UPON NUMBER OF MARKETABLE EARS
PRODUCED BY SWEET CORN

A belief exists among growers of sweet corn in Massachusetts that severe injury to the plants by the corn borer results in a decrease in the number of marketable ears produced and an increase in the proportion of nubbins. In order to investigate this theory, a comparison

was made between the production of ears and nubbins by infested and noninfested plants growing in each of seven fields. Examinations were made in representative parts of each field, all the plants in a section of row being examined. The results are shown in Table 12.

TABLE 12.—Effect of injury to stalks of sweet corn upon the number of marketable ears produced

Town (Mass.)	Field No.	Variety	Per cent stalks infested	Per cent ears infested	Total plants examined in each lot	Infested plants		Noninfested plants		Loss in marketable ears	
						Number of marketable ears	Number of nubbins	Number of marketable ears	Number of nubbins	Number	Per cent
Saugus	1	Golden Bantam	58	18	25	41	32	49	26	8	16.33
Medford	2	Early Crosby	35	17	25	27	35	39	28	12	30.77
Do.	3	Quincy Market	47	11	25	47	35	47	40	0	0.00
Do.	4	Golden Bantam	100	52	200	190	130	263	129	73	27.76
Saugus	5	do.	86	66	200	110	92	193	52	83	43.01
Do.	6	Golden Giant	94	36	200	232	92	248	80	16	6.45
Do.	7	Golden Dawn	63	37	200	236	107	264	124	28	10.61
Total					875	883	1,523	1,103	479	220	
Average											19.94

¹ Increase in nubbins of infested plants equals 9.1 per cent.

All of these fields were of the early plantings and the infestation consisted almost entirely of first-generation individuals. The data for fields 1 to 3 were obtained in 1921, and for fields 4 to 7 in 1922. In field 4 it was necessary to include a number of slightly infested plants among the "noninfested" group owing to the difficulty of finding strictly noninfested plants.

Table 12 indicates that in the fields under consideration there was a reduction of 19.94 per cent in the number of marketable ears produced by infested plants as compared with the noninfested plants in the same fields. An increase of 9.19 per cent of nubbins was noted as a result of corn-borer injury to the plants.

In fields of sweet corn showing maximum infestation (figs. 24 and 25) the reduction in marketable ears was much more pronounced than these figures indicate. In such areas, however, practically 100 per cent of the plants were badly infested, which fact did not permit an accurate comparison between ear production of infested and noninfested plants.

PERCENTAGE OF BROKEN-OVER STALKS AND EAR STEMS DUE TO LARVAL INJURY

Reference has previously been made to the breaking over of stalks and ear stems as a result of the tunneling of corn-borer larvae. Although the effect upon grain formation of such breaking over is exceedingly variable, and no definite economic importance can be assigned to this type of injury, it was thought desirable to present figures showing the extent of its occurrence. The counts shown in Table 13 were obtained from examinations of average stalks and ears in the experimental plats of flint and dent corn at Medford, Mass., during 1920.



FIG. 24.—General view of a field of sweet corn ruined by European corn borer. No marketable ears were obtained from this field. Medford, Mass., September, 1922

TABLE 13.—Per cent of broken-over stalks and ear stems due to larval injury by the European corn borer

Type of corn	Number of plots	Total stalks	Per cent stalks infested	Per cent stalks broken over at harvest		Total ears	Per cent ear stems infested	Per cent ear stems broken over at harvest
				Below ear	Above ear			
Flint.....	4	147	100	10.8	16.3	110	72.7	19.9
Dent.....	4	140	100	22.8	29.9	78	85.9	2.6
Total.....		287				188		
Average.....			100	16.7	22.9		78.2	12.8



FIG. 25.—“Close-up” of hill of sweet corn ruined by European corn borer. No marketable ears were produced in this hill. Medford, Mass., September, 1922

Table 13 shows that as a result of larval injury, when 100 per cent of the stalks were infested at harvest, an average of 16.7 per cent of these stalks were broken over below the ear and an average of 22.9 per cent were broken over above the ear, thus making a total average of 39.6 per cent of the stalks broken over at this time. The examination of 188 ears borne by the 287 plants examined revealed an average of 78.2 per cent with infested ear stems and an average of 12.8 per cent of the ear stems broken over before harvest.

LENGTH AND VOLUME OF TUNNEL IN STALK MADE BY EACH LARVA

In order to obtain information relative to the length and volume of each tunnel bored out or consumed by each larva, measurements were made of individual tunnels in 35 stalks of sweet corn and in 6 stalks of dent corn, each of which was inhabited by a single larva. Care was taken in the selection of these stalks to ascertain that each tunnel was made by the larva then inhabiting it. It was not possible in every instance, however, to determine whether the larva in its younger stages had or had not fed upon the exterior of the same or adjoining plants before starting its tunnel in the stalk. The results of these measurements are shown in Table 14.

TABLE 14.—*Length and volume of tunnel in stalk made by each European corn borer larva*

Type of corn	Number of stalks	Average length of each tunnel in inches	Average volume of each stalk (cubic inches)	Average volume of each tunnel (cubic inches)	Average per cent loss in volume to each stalk
Sweet.....	35	9.036	7.0441	0.2492	3.538
Dent.....	6	6.125	16.5263	.1690	1.022
Average.....		8.610			2.816

From Table 14 it is seen that the average length of the tunnel made by each larva under observation equaled 8.61 inches, and that there was an average of 3.489 per cent loss in volume caused by the boring and feeding of each larva.

EXTENT AND EFFECT OF BROKEN-OVER TASSELS

Counts made in badly infested cornfields have shown as many as 89.9 per cent of the tassels broken over. Many ears of corn from fields thus affected are abnormally small in size, or lacking in proper grain formation, even though they are not directly injured by the larvae, but it has been difficult definitely to assign the lack of proper fertilization as a reason for this condition, because such ears are usually borne by plants which have been otherwise seriously injured by the insect. When the tassel breaks over early in its development there results a loss of pollen, but this type of injury or mutilation has been considered by corn technologists as unimportant, even where a large proportion of the tassels are thus affected. The remaining uninjured tassels are said to furnish sufficient pollen for the proper fertilization of the plants in the vicinity. The percentage of tassels broken over as a result of European corn borer injury during 1920 and 1921 in certain fields of sweet, flint, dent, fodder, and pop corn, representing ordinary conditions in the heavily infested portion of New England, is shown in Table 15.

TABLE 15.—Per cent of tassels broken over as a result of European corn borer injury

Type of corn	Number of fields	Tassels counted	Tassels broken over	Per cent tassels broken over		
				Average	Maximum	Minimum
Sweet	30	11,913	3,584	30.1	89.9	1.3
Flint	16	5,428	1,412	26.0	35.4	2.7
Dent ¹	10	6,700	992	14.8	16.5	8.2
Fodder	2	7,258	1,204	16.6	22.1	9.9
Pop.	1	500	227	45.4	—	—
Total		31,779	7,419			
Average				23.3		

¹ Limited to experimental plot counts. No dent corn grown for grain within the Boston area.

Table 15 shows that the average of broken-over tassels as a result of larval injury ranged from 14.8 to 45.4 per cent in the different types of corn examined, with an average of 23.3 per cent of the tassels in the entire lot. In fields representing maximum infestation the percentage of broken-over tassels was much higher than these figures indicate.

EXTENT OF INJURY TO VEGETABLES, FLOWERS, AND FIELD CROPS

NEW ENGLAND

The extent of injury and loss to vegetables, flowers, and field crops in New England, caused by the corn borer, has not been severe in most instances, seldom exceeding 5 per cent of the total value of any crop. There has been, however, a very considerable increase each year in the infestation of these crops. In 1917, when the field investigations on the corn borer were started, it was difficult to find infestations in crops other than corn, although according to Vinal (70) certain of the flowers, notably dahlias, were occasionally attacked. Infestation has progressed to a point where in 1921 and 1922 most commercial fields of the more susceptible vegetable and flower crops, such as rhubarb, beets, celery, beans, peppers, dahlias, asters, and gladioli, were infested in localities in Massachusetts where the corn borer has become at all numerous. The infestation in some of the beet and celery fields during 1922 was especially pronounced and led the growers of these crops to view with apprehension the increased damage to these vegetables.

Formerly most of the infestations in vegetables and flowers were confined to weedy fields, and along field borders where the plants were growing among or in close proximity to infested weeds or corn, but during 1922 these crops were commonly subjected to appreciable infestation and injury even in fields that were kept free of weeds and isolated from areas of susceptible weeds or corn. The following discussion applies principally to conditions existing during 1921 and 1922 with respect to the more important and susceptible economic hosts of the corn borer. During 1923 and again in 1924 a marked reduction occurred in the extent of infestation and injury to vegetables, flowers, and field crops, a reflection of the general decrease in intensity which developed in the New England area during those two years.

RHUBARB

Rhubarb has been infested to a greater extent than any other vegetable or garden crop excepting sweet corn. The large leaves of this plant are particularly attractive to the adults as a place for concealment and subsequent deposition of eggs. Later the larvae infest the leafstalks and veins of the leaves. In two fields where detailed examinations were made during June, 1922, an average of 2.5 egg clusters per plant were found on the leaves, with occasional egg clusters on the leafstalks. The majority of the fields in the Boston area contained from 5 to 40 per cent of infested stalks during 1921 and 1922. In fields representing maximum infestation as high as 75 per cent of the stalks were infested. Most of the severe injury occurred after the close of the commercial season for harvesting rhubarb, and the growth of the injured plants did not appear to be seriously affected by it. The necessity of discarding infested stalks in preparation for market caused appreciable loss in fields severely infested early in the season.

BEETS

The extent of infestation in beets was very nearly equal to that mentioned for rhubarb. Most of the injury to beets was confined to the leafstalks (fig. 26), although during 1922, when the increase of infestation in this vegetable was most marked, a considerable number of the beet roots, amounting in some instances to 5 per cent of the total in the worst infested fields, were found to contain the borer. Except in instances where several of the leafstalks were entered by the borer, the injury did not appear seriously to interfere with the growth of the plant. The fact that the injured leafstalks must be removed in preparing for market as bunched beets, affected the appearance and consequently the price of the product from fields where a high percentage of the plants were affected. Table 16 gives results of examinations in average beet fields of the Boston area taken on various dates distributed throughout the season when the plants were ready for market.

TABLE 16.—Extent of injury and infestation by the European corn borer in beets, New England area, 1922

Field No.	Locality (Massachusetts)	Date examined (1922)	Number of plants	Plants showing injury		Plants containing larvae		Larvae per infested plant	
				Number	Per cent	Number	Per cent	Average	Maximum
1	Arlington.....	Sept. 20	100	10	10.0	8	8.0	1.00	1
12	Do.....	June 30	600	35	5.8	23	3.8	1.00	1
13	Medford.....	July 11	100	39	39.0	31	31.0	1.32	3
14	Do.....	do.....	200	64	32.0	49	24.5	1.59	8
15	Do.....	July 10	100	10	10.0	8	8.0	1.12	2
16	Saugus.....	July 13	100	25	25.0	18	18.0	1.00	1
7	Do.....	Oct. 4	100	61	61.0	57	57.0	1.98	4
18	Somerville.....	July 17	100	9	9.0	8	8.0	1.25	3
9	Do.....	Oct. 5	100	71	71.0	66	66.0	2.95	14
10	Watertown.....	July 17	500	126	25.2	113	22.6	1.24	4
11	Do.....	Sept. 30	200	0	0.0	0	0.0	0.00	0
112	Winchester.....	July 12	100	48	48.0	41	41.0	1.53	6
13	Woburn.....	Sept. 28	100	59	59.0	59	59.0	1.79	6
14	Do.....	July 11	100	34	34.0	27	27.0	1.96	7
Total.....			2,500	591		508			
Average.....					23.6		20.3	1.69	

¹ Infestation chiefly by first generation.

Table 16 shows that in the 14 fields under observation an average of 23.6 per cent of the beet plants were injured and 20.3 per cent of the plants actually contained the borer at the time of examination. The difference between the percentage of plants showing injury and the percentage actually containing the borer at the time of

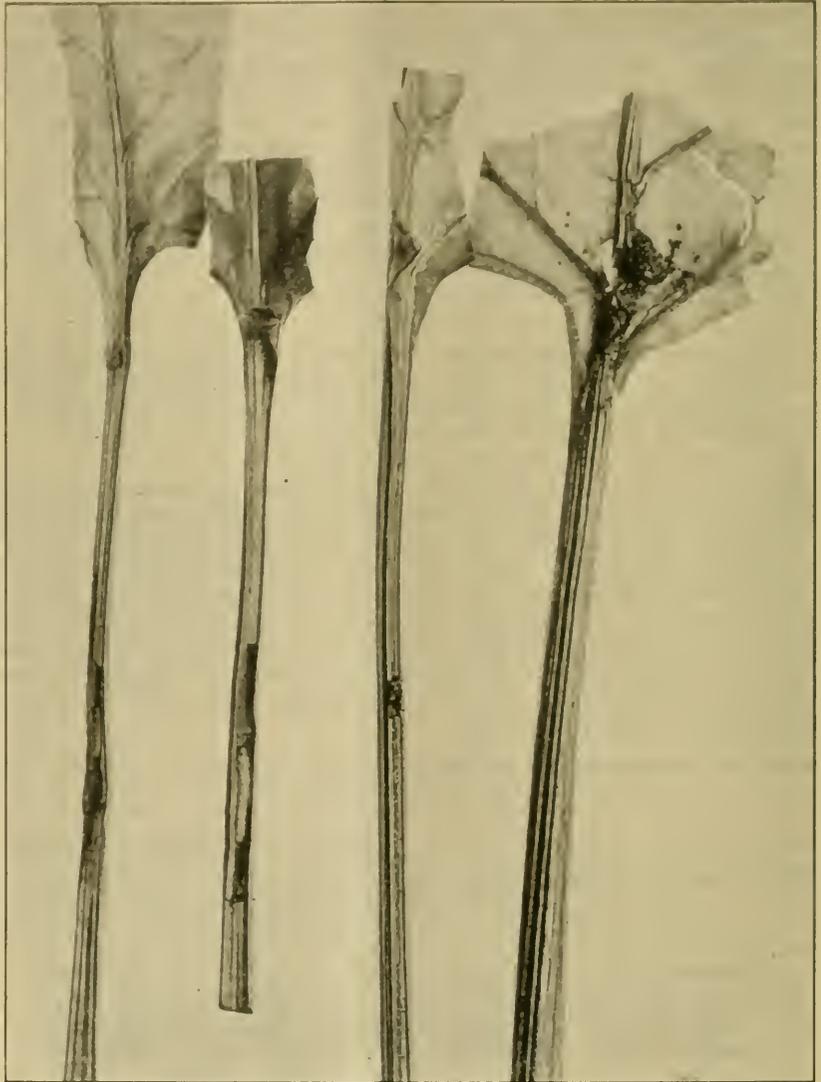


FIG. 26.—Beet stems injured by larvae of the European corn borer

examination is due to the migration of the borers from some of the badly injured plants to other plants furnishing a fresher food supply. There were on an average 1.69 borers per infested plant.

In some of the smaller fields and in home gardens representing maximum infestation the beet crop was abandoned, owing to the injury to the roots and leafstalks.

CELERY

The infestation in celery has been general for the last two years, and, although the injured portion of the plants could usually be removed with very little commercial injury to the remainder of the plant (fig. 27), there was an appreciable loss ranging from 5 to 10

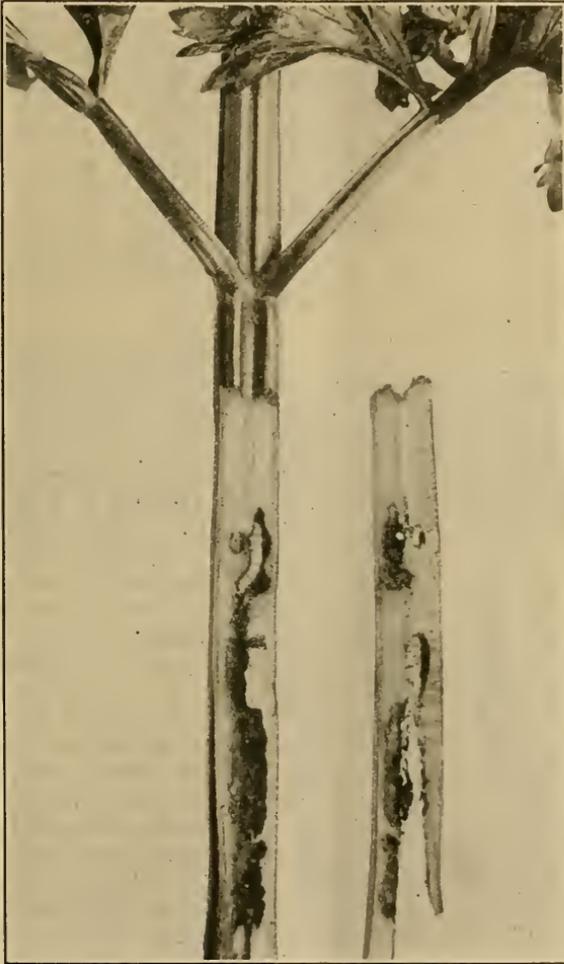


FIG. 27.—Stalks of celery sectioned to show injury by European corn borer

per cent of the total value of the crop in the worst infested fields, owing to the necessity of discarding severely injured plants. During 1922 the infestation in celery fields showed a considerable increase as compared with the previous year. Certain fields of celery, which were kept cleanly cultivated and isolated from corn or other susceptible plants, showed a severe and uniform infestation. In Table 17 are given figures relating to field examinations made in celery fields of the Boston area showing average infestation.

TABLE 17.—Extent of injury and infestation by the European corn borer in celery, New England area, 1922

Field No.	Locality (Maine)	Date examined (1922)	Plants showing injury		Plants containing larvae		Larvae per infested plant	
			Number ¹	Per cent	Number ²	Per cent	Average	Maximum
1	Arthington	Sept. 25	8	1.6	2	0.4	1.00	1
2	Do.	Sept. 26	22	4.4	17	2.6	1.00	1
3	Do.	Sept. 20	26	5.2	9	1.8	1.30	3
4	Do.	Oct. 5	131	30.2	42	8.4	3.92	8
5	Do.	Oct. 5	140	28.0	41	9.0	2.93	10
6	Belmont	Sept. 26	14	2.8	3	.6	1.00	1
7	Do.	Sept. 26	9	1.8	5	1.0	1.00	1
8	Madison	Sept. 26	78	15.6	32	6.4	1.37	3
9	Watersville	Oct. 5	38	7.6	16	3.2	1.50	4
10	Waterville	Sept. 30	3	.6	0	.0	.00	0
11	Do.	Sept. 30	8	1.6	2	.4	1.00	1
12	Woburn	Sept. 28	120	24.0	69	13.8	1.32	3
Total			627		238			
Average				10.4		3.96	2.00	

¹ 100 plants examined in each field.

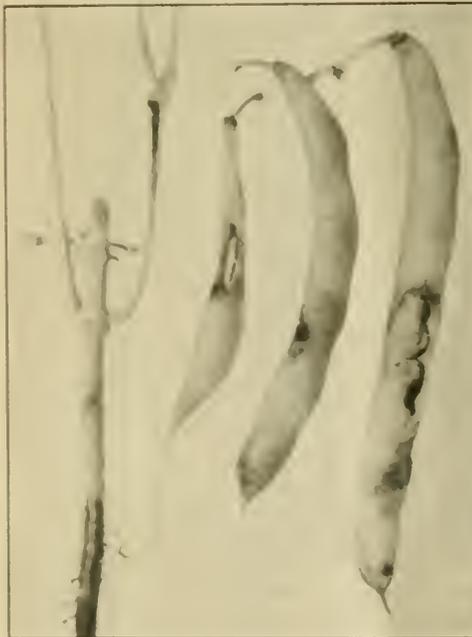


FIG. 28.—Green beans, showing the work of European corn-borer larvae

Table 17 shows that in the 12 fields under observation an average of 10.4 per cent of the celery plants showed injury and that an average of 3.96 per cent of the plants contained the borer at the time of the examination, with an average of two larvae per infested plant.

BEANS

Injury to beans (fig. 28) was confined principally to the stalks with an occasional infestation in the pods. Infested pods were usually unfit for sale, but less than 1 per cent of the total pods were affected in any of the commercial fields examined. In instances of severe injury to the stalks, the affected portions broke over and resulted in a decreased yield of pods. In some of the

small home gardens as high as 100 per cent of the plants and 22 per cent of the pods were infested. Field counts made in 10 bean fields of the Boston area, showing average infestation, are given in Table 18.

In the bean fields under observation (Table 18) an average of 3.55 per cent of the plants showed injury and 3.22 per cent contained larvae, with an average of 1.18 larvae per infested plant.

TABLE 18.—Extent of injury and infestation by the European corn borer in beans, New England area, 1922

Field No.	Locality (Mass.)	Date examined (1922)	Number of plants	Plants showing injury		Plants containing larvae		Larvae per infested plant	
				Number	Per cent	Number	Per cent	Average	Maximum
1	Medford.....	July 11	200	11	5.5	5	2.5	1.0	1
2	Do.....	July 12	500	20	4.0	19	3.8	1.3	4
3	Do.....	July 13	200	30	15.0	30	15.0	1.3	3
4	Do.....	July 13	200	15	7.5	14	7.0	1.2	2
5	Saugus.....	July 12	500	8	1.6	8	1.6	1.0	1
6	Somerville.....	July 17	200	7	3.5	7	3.5	1.0	1
7	Winchester.....	July 12	200	1	.5	1	.5	1.0	1
8	Do.....	July 12	300	4	1.3	3	1.0	1.0	1
9	Woburn.....	July 12	200	0	.0	0	.0	.0	0
10	Do.....	July 11	200	0	.0	0	.0	.0	0
Total.....			2,700	96	3.55	87	3.22	1.18	
Average.....									

SPINACH

The occurrence of corn-borer egg clusters on the leaves of spinach was very general during 1922-23 in the Boston area. In nearly every spinach field examined, egg clusters were found on the leaves, usually involving less than 1 per cent of all the plants. Usually the spinach was harvested before the larvae hatched or became large enough to injure the plants, but where harvesting was delayed, borers were occasionally found in the leaf stems. No commercial injury resulted to spinach in any instance under observation.

PEPPERS

The stalks and fruits of sweet and hot varieties of peppers are very susceptible to corn-borer attack. In the Boston area during September and October, 1922, every field of peppers examined showed conspicuous evidence of damage through the medium of broken-over plants. In three fields where detailed examinations were made, the percentage of plants injured ranged from 18 to 97, and 52 to 76 per cent of the fruits had been injured by the borer. In these pepper fields, in instances where the stalks became broken over before the fruit had fully developed, there occurred a cessation of growth to the fruit which caused a reduction in yield of marketable peppers. Much of the infested fruit was unfit for sale, but the proportion of actual loss from this cause varied according to the use for which the peppers were intended.

POTATO

The stalks of potato have commonly been found infested (fig. 17) in Massachusetts. In two fields where detailed examinations were made during late July, 1922, an average of 18 and 62 per cent respectively of the plants were found to contain the borer. Although such injury resulted in quite an extensive breaking over of the stalks in some fields, it did not appear to affect the successful formation of tubers. No economic loss resulted in any instance under observation.

TOMATO

The stalks and fruit of tomatoes have frequently been found infested each year since 1918. Usually less than 1 per cent of the stalks or fruit have been involved in the majority of the fields examined, but in some fields during the late summer of 1922 as high as 14 per cent of the stalks and 5 per cent of the fruit were found to contain the borer. When the stalks were severely attacked early in their development, they often collapsed and fruiting was greatly reduced, or even prevented. Otherwise the growth of injured plants was not appreciably affected. Infested fruits usually were rendered unfit for sale.

SWISS CHARD

The leaf stalks of Swiss chard were commonly infested by the corn borer, and although the injured portions usually were made unfit for food, the losses have been of but little commercial importance, as this plant is grown here mainly as a kitchen-garden vegetable. During 1922 an examination of one of the larger garden plots of Swiss chard showed that 23 per cent of the leaf stalks were injured by the corn borer.

DAHLIAS

Dahlias are the most susceptible of all the flower crops. During August and September of 1922 and 1923, 100 per cent of the dahlia plants were infested in many of the commercial gardens in the Boston area, causing an estimated loss in some instances amounting to 10 per cent of the crop. Many of these plants were ruined, and the susceptibility of dahlia plants to corn-borer injury caused certain of the commercial specialists in this flower to abandon its culture. The most careful scrutiny has failed to disclose any corn-borer infestation in the dahlia tubers, but all parts of the plant above ground are liable to injury. Egg clusters were commonly found on the dahlia blooms, as well as on the leaves, during July and August, 1922. In three commercial dahlia gardens the proportion of blooms bearing egg clusters ranged from 1.4 to 19.8 per cent.

ASTERS

China or garden asters very frequently have been found infested in home gardens and commercial establishments throughout the Boston area during the period from July to September. Infestation reached a maximum of 76 per cent of the plants in small home gardens, and in one commercial establishment 86 per cent of the plants were injured. The normal development of flowers was prevented in instances where plants were severely injured at an early stage of their growth, and during 1922 many of the flowers, involving in one instance 11 per cent of the total, were also entered by borers. The estimated loss in the most heavily infested aster plantings ranged from 10 to 15 per cent of the total value of the crop.

CHRYSANTHEMUMS

The injury to chrysanthemums (fig. 29) has been confined principally to plants grown under glass for the late fall trade. Infested plants have been found each year since 1919 in the majority of the greenhouses examined in the New England area. Usually less than

1 per cent of the plants were involved, but in extreme cases as high as 20 per cent of the plants contained the borer. In 1922 an inspection was made in 30 of the larger greenhouses in eastern Massachusetts, where a total of 353,500 chrysanthemums were grown.



FIG. 29.—Injury to stem and flower of greenhouse chrysanthemum by European corn borer. Stem sectioned to show borers within. Melrose, Mass., November 10, 1922

Infestations were found in 23 of these establishments, the number of plants involved ranging from less than 1 to 9.22 per cent, with an average of 1.08 per cent for the 30 houses, at the time of examination. Many of the injured plants had been removed and discarded

before examination occurred, so the percentages given represent minimum figures. When the injury occurred in the lower part of the stems and after the plants had become fully developed, the blooms were suitable for sale. The estimated loss amounted to 6 per cent of the value of the crop during 1922 in houses showing maximum infestation.

GLADIOLI

The flower stalks of gladiolus plants were infested by the corn borer (fig. 19), and egg clusters have occurred on the leaves, in a few fields each year since 1918. Usually this infestation has been very sparse, but in 1919 a maximum of 6 per cent of the flower stalks were injured by the borer in two fields grown in close proximity to other infested crops. In 1921 and 1922 a scattering infestation was found in the majority of fields examined, but less than 1 per cent of the plants were involved, and the economic loss in any instance was trivial. No infestation or injury to the bulbs has been observed to date.

ZINNIAS

The stalks and flowers of zinnias commonly are infested by the corn borer in home gardens and small commercial establishments. During the late summer of 1922 there was a decided increase in the injury to zinnias as compared with former years, but most of this injury occurred after the better blooms had been picked, and was, therefore, of little economic importance. In many of the home gardens of the Boston area practically 100 per cent of the plants were infested, and in one instance 90 per cent of the blooms contained the borer.

OATS

The stems (culms) of oats have occasionally been found infested (fig. 18) when growing as volunteer plants and in experimental areas. This crop rarely is grown commercially within the area where the European corn borer is numerous at present. In 1921 a small experimental plat of oats was grown in close proximity to infested corn and other susceptible plants. Only a fraction of 1 per cent of the stems were infested at the time of harvest. After being cured in the usual manner, part of the straw was baled and the remainder left loose. A detailed examination of about 58,000 straws from both lots revealed that living borers were present in the baled straw at a rate of 8 borers per 100 pounds, and in the loose straw at a rate of 11 borers per 100 pounds.

OTHER FIELD CROPS

In order to obtain information relative to the susceptibility and extent of injury by *P. nubilalis* to various field crops which normally are not grown to any extent in the Boston area, small plats of these crops were grown in the experimental fields at Medford, Saugus, Cambridge, Belmont, and Woburn, Mass., during the period from 1919 to 1922. Some of these crops, such as cotton and the grain sorghums, are seldom, if ever, grown in this section of the country. The more important information obtained from these plats is summarized in Table 19.

TABLE 19.—Susceptibility and extent of injury by *Pyrausta nubilalis* to various field crops in experimental fields (New England, 1919 to 1922)

Plant	Egg clusters			Larvae					
	Total plants examined	Total egg clusters found	Per cent plants bearing egg clusters	Total plants examined	Total plants found tunneled	Total plants containing larvae	Per cent plants containing larvae	Total larvae found	Average larvae per 100 plants
Millet (Japanese).....				200	64	27	13.5	38	19.0
Millet (European).....	50	1	2.0	200	52	17	8.5	27	13.5
Millet (Hungarian).....	50	0	0.0	200	6	1	.5	1	.5
Hemp.....				10	10	10	100.0	150	1,500.0
Hegari.....	66	15	21.2	84	77	70	83.3	218	259.5
Feterita.....	115	21	16.5	343	79	56	16.3	110	32.1
Milo.....	142	32	14.8	420	324	254	60.4	444	105.7
Kafir.....	174	16	9.2	400	29	8	2.0	8	2.0
Broomcorn.....	282	26	8.5	450	234	191	42.4	314	69.8
Barley.....	50		0.0	100	5	1	1.0	1	1.0
Cotton ¹	210	25	11.4	656	112	22	3.4	23	3.5
Cowpea.....	190	13	6.3	691	240	52	7.5	67	9.7
Sorgo.....	50	13	22.0	450	39	21	4.7	28	6.2
Hop (common).....	18	0	0.0	12	10	3	25.0	5	41.6
Buckwheat.....				200	11	11	5.5	11	5.5
Johnson grass.....	250	15	6.0	1,050	27	12	1.1	15	1.4
Sudan grass.....	25	3	12.0	50	7	5	10.0	7	14.0
Soy bean.....	441	2	.6	441	18	9	2.0	10	2.3
Peanut.....	82	1	1.2	114	11	3	2.6	3	2.6

¹ Bolls developed on plants in one plat during 1921. A count of 200 green bolls showed that 9 per cent were infested, one larva per boll. Plants killed by frost before bolls opened.

The experiments detailed in Table 19 were conducted under conditions of severe infestation, and due allowance should be made for this fact when interpreting the susceptibility of the plants listed. It is significant, however, that many of these plants which have been recorded in foreign literature as hosts of *P. nubilalis*, notably hemp (fig. 30), hops, millet (fig. 31), cotton (fig. 32), and the grain sorghums (fig. 33), were also infested by the insect in New England. This development is only indicative, of course, of the susceptibility of these plants if grown commercially in areas where two generations of *P. nubilalis* occur each year.

NEW YORK, PENNSYLVANIA, OHIO, AND MICHIGAN

There has been but very little loss or infestation to date from the work of the European corn borer in vegetables, flowers, or field crops, except corn and broomcorn, in the infested areas of New York, Pennsylvania, Ohio, and Michigan. During 1923 two fields of broomcorn, comprising a total of 12 acres, grown at Irving, N. Y., showed stalk infestations of 12.7 and 15.8 per cent, respectively. In western New York slight infestations have also been observed in commercial fields of soy beans, buckwheat, and potatoes, and in half-acre fields of European millet or proso, which was planted on two farms near Silver Creek, N. Y., to test its possible utility as a trap crop. Occasional infestations have also been observed in the stems and fruits of tomato. Occasional instances of infestation have also been observed in experimental plats of Japanese and European millet or proso, sorghum, rhubarb, kidney or wax beans, milo, soy beans, dahlias, and cosmos at Silver Creek, N. Y.



FIG. 30.—Hemp infested by European corn borer. A favorite host of the insect in the Old World

EXTENT OF INJURY AND INFESTATION IN WEEDS AND GRASSES

Injury to the weeds and wild grasses (figs. 3 to 5) serving as hosts of the European corn borer (Table 1) is not commercially important, but the infestation of such weeds and grasses affords abundant oppor-



FIG. 31.—Hungarian millet infested by European corn-borer larvae

tunity for the multiplication and spread of the pest in fields where corn or other economic plants are not grown or in cultivated fields where the borers are so numerous that they are compelled to feed upon these weeds or grasses in order to complete their growth. The infestation in such plants is most pronounced in the New England

area. In the other areas of the United States where the insect is present only a slight infestation in these plants as yet has occurred.

Table 20 details field counts of infestation in 17 of the more susceptible and widely dispersed weeds and wild grasses during 1920 and 1921 in cultivated fields and waste areas, showing average infestation in that portion of the New England area where the European



FIG. 32.—Typical injury to bolls of cotton by European corn borer. Cotton grown experimentally at Medford, Mass. Photo taken September, 1921

corn borer has become well established. It does not include small isolated patches of weeds which represented the maximum infestation. These counts were taken during the growing season at a time when the plants had reached full size, and while larvae contained in each plant examined apparently were feeding therein. It was not possible in every instance, however, to ascertain whether each individual was actually feeding or was using the plant as a shelter.



FIG. 33.—Typical injury to hegari by European corn borer. Woburn, Mass., September 29, 1921

TABLE 20.—Percentage of weeds infested by *Pyrausta nubilalis* larvae (New England, 1920-21)

Plant name	Number fields or waste areas	Total number plants examined	Total number found tunneled	Total number containing larvae	Per cent plants containing larvae	Total number larvae found	Average number larvae per 100 plants	Maximum number larvae per plant
Xanthium spp.....	4	170	168	162	95.3	1,067	627.6	35
Chenopodium ambrosioides.....	3	70	63	50	71.4	95	135.7	7
Polygonum spp.....	11	411	228	198	48.1	701	170.6	27
Ambrosia artemisiaefolia.....	6	205	(1)	91	44.3	135	65.8	6
Echinochloa crus-galli ²	5	325	153	136	41.8	175	53.8	2
Artemisia biennis.....	3	115	48	41	35.6	91	79.1	6
Arctium minus.....	5	115	81	40	34.8	123	106.9	17
Bidens frondosa.....	4	130	66	45	34.6	77	59.2	5
Iva xanthifolia.....	1	50	32	17	34.0	26	52.0	4
Rumex spp.....	4	260	88	84	32.3	129	49.6	3
Erechtites hieracifolia.....	2	35	13	9	25.7	9	25.7	1
Amaranthus retroflexus.....	10	636	189	135	21.2	172	27.0	7
Lactuca scariola var. integrata.....	1	50	11	9	18.0	17	34.0	3
Erigeron canadensis.....	2	80	5	5	6.3	7	8.8	2
Chenopodium album.....	2	100	6	6	6.0	6	6.0	1
Tanacetum vulgare ²	2	75	8	4	5.3	6	8.0	3
Galinsoga sp.....	1	200	10	3	1.5	3	1.5	1

¹ Not possible to discriminate between tunnels of *P. nubilalis* and those of other borers present in same plant.

² Each stem counted as a separate plant.

During the early spring some of the larger and more substantial weeds, such as *Xanthium*, *Arcium*, and *Polygonum*, frequently contain a greater number of larvae per plant than is shown in Table 20. Many of the larvae contained in large weeds at this time have migrated during the late autumn from more fragile weeds such as *Echinochloa*, or from the remnants of near-by cultivated plants. During the spring of 1922 a total of 203 larvae were taken from a single plant of *Xanthium* and 75 larvae from a single stalk of *Polygonum*.

The prevalence of the borer in weed growths has increased in intensity, especially since the abandonment of large-scale burning



FIG. 34.—Typical weed area in New England, severely infested by European corn borer. Similar weed areas contained over 400,000 borers per acre

and weed-control operations. This increased infestation may be partly due to the reduced acreage planted to corn in the badly infested districts, but in any event during the late summer of 1922 a series of detailed field counts showed that in three large typical weed areas (fig. 34) located at Cambridge, Watertown, and Arlington, Mass., and aggregating 85.3 acres in size, there were from 277,000 to 406,000 borers per acre. The predominating weeds in these areas were barnyard grass, pigweed, lamb's-quarters, cocklebur, beggar-ticks, broad grass, and Mexican tea. These neglected weed areas act as sources of infestation to the surrounding territory for many miles through the flight of the adults, and locally by the migration of larvae.

DESCRIPTION

THE EGG

Average length 0.97 millimeters, average width 0.74 millimeters; elliptico-ovate, sometimes nearly circular in contour, thin, more or less scalelike, slightly convex on its uppermost surface, flat on its undermost surface or conforming with the surface of the object upon which the egg is deposited. Chorion reticulated with fine elevated lines, which anastomose regularly and thereby inclose shallow pentagonal or polygonal foveae. Eggs when first laid greenish white, more or less translucent on the periphery, the opacity increasing centrally where the egg attains its greatest depth; ordinarily strongly iridescent. In 18 to 24 hours after deposition there appears in the egg a crecentiform clear area, slightly excentric in its position as viewed from above; the balance of the egg becoming strongly opaque. Two days before hatching the egg assumes a yellowish cast, and soon thereafter the head capsule of the inclosed larva is seen, its chitinization proceeding rapidly. Several hours before hatching the chorion collapses about the larva and its shape is plainly evident. At time of hatching the head and thoracic shield are black; the body segments are yellowish white.

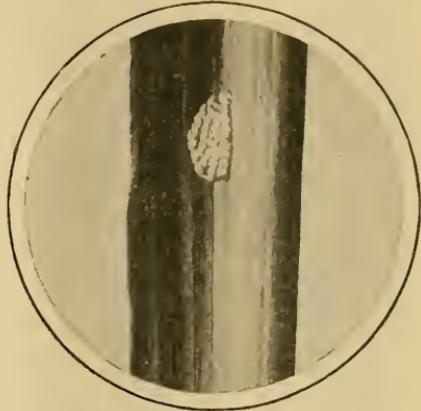


FIG. 35.—Egg mass of the European corn borer. Greatly enlarged



FIG. 36.—Larvae of the European corn borer. Slightly enlarged

which it is laid. The eggs in the mass are overlapped, shingle-like, with successive eggs deposited by the female. According to records obtained, they range from 1 to 162 in number, 15 to 20 eggs representing the average size of the mass.

THE LARVA

Full-grown larva (fig. 36), average length 20 to 23 millimeters, width 3 to 3.5 millimeters. Body cylindrical, abdominal segments, except 9 and 10, grooved transversely. Body dirty white, shading from light brown, or dark brown, to pink on the dorsum. Dorsum heavily granulated, skin granulations extending to the pleurae, heavily granulose along dorso-median line, taking the form of a band or

stripe. Chitinized areas of the body heavily pigmented, especially about the tubercles; thoracic shield yellowish brown, bordered or emarginated and more or less spotted with dark brown; anal shield yellowish; irregularly spotted with grayish brown. Chitinized areas of tubercles quite large, oval, and circular, yellowish and emarginated with brown. Thoracic legs yellowish, claws brown; crochets on planta of prolegs triordinal. Spiracles ovate.

Head polished brown to black, sometimes more or less blotched; mandibles strong, five-toothed, more or less square, distal tooth pointed. "Anterior setae A^1 and A^2 and puncture A^3 in a line or with A^4 a trifle postero-laterad of A^2 , not postero-dorsad; A^2 somewhat nearer to A^1 than to A^3 , A^1 , A^2 , and A^3 forming a decided obtuse angle" (24, p. 174).

The majority of the larvae in the field have five instars. In the rearing experiments shown in Tables 24 to 27 the majority of the larvae had four instars, a considerable number had five instars, and a few larvae had six instars; and in one series a few individuals had seven instars.

FIRST INSTAR

Prothoracic shield averaging 0.25 millimeter. A perceptible indentation present, but no division of the shield along medio-dorsal line. Indentation at cephalo-medio dorsal point.

SECOND INSTAR

Prothoracic shield averaging 0.41 millimeter in width. Indentation along dorso-median line increased but shield not divided.

THIRD INSTAR

Prothoracic shield averaging 0.71 millimeter in width. Division or indentation extended to half way between cephalic and caudal margins along dorso-median line.

FOURTH INSTAR

Prothoracic shield averaging 0.98 millimeter in width. Division of shield complete. Color of prothoracic shield black.

FIFTH INSTAR

Prothoracic shield averaging 1.72 millimeters in width, light yellow maculated with darker, smoky-fuscous areas. Larval body usually more robust than preceding.

THE PUPA

Average length of male pupa, 13 to 14 millimeters; female, 16 to 17 millimeters. Average width of male, 2 to 2.5 millimeters; female, 3.5 to 4 millimeters. (Fig. 37.)

Color yellowish brown; cephalic and caudal extremities brown to black; cremaster nearly black; dorsum of thorax darker than general body color, but not shining.

Moderately slender; abdominal segments tapering caudad; sterna smooth; terga of abdominal segments with transverse wrinkles and two rows of spines on segments 1-7; appendages compacted against the body. Wings, maxillae, and mesothoracic and metathoracic legs approximately equal in length, extending to the mesal part of the fourth abdominal segment ventrad; metathoracic legs lying directly

beneath the mesothoracic; prothoracic legs terminating half way between the head and the tips of the wings; prothoracic femora plainly indicated; antennae terminating short of the wings. Labrum and pillifers well developed; labial palpi small. Proleg scars visible on the sterna of abdominal segments 5 and 6; a pair on each segment. Dorsum of the thorax bearing a slightly elevated ridge extending along the dorso-median line; thorax only slightly humped. Abdominal spiracles small, oval, slightly produced, rings stoutly chitinized, blackish brown. Caudal segment terminating in a dark-brown or black cremaster, prominent, spatulate, stout, longer than broad, and armed at its extremity with a series of 5 to 8 recurved spines, which serve to fasten the pupa to its cocoon or to a pad of silk spun by the larva prior to pupation. The pupa ordinarily, but not always, is enveloped in a very thin cocoon. The anal and genital openings are slitlike in both sexes.

The sexes are readily separated by comparing the position of the genital opening with the seventh abdominal spiracles, which are constant or fixed in their position. In the female the genital opening is cephalad of the seventh abdominal spiracles, whereas in the male the genital opening is caudad thereto.

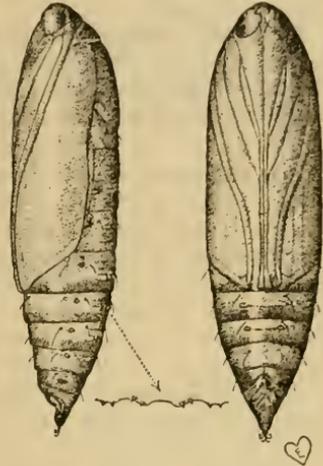


FIG. 37.—Pupa of the European corn borer, lateral and ventral views. About three times natural size

ADULTS

(Fig. 38)

MALE

Alar expanse 20 to 26 millimeters; length of body in both sexes 13 to 14 millimeters.

Head and thorax cinnamon brown on the thorax; white ventrad. Labial palpi porrect, snow white ventrad, otherwise grayish fuscous. Maxillary palpi erect, slightly dilated at apex. Proboscis long, covered with cream-colored scales, tightly coiled and almost hidden when viewed laterad. Antennae filiform in both sexes, terminal half curled in dried specimens, two-thirds the length of the cephalic wings.

Prothoracic legs snow white outwardly, slightly fuscous inwardly; mesothoracic and metathoracic legs white. Inner spurs on legs twice the size of the outer ones. Cephalic and caudal wings equal in width, costal margin gently curved toward the apex, anal angle rounded, inner margin straight. Cephalic wings reddish brown or grayish fuscous, with a bright ochreous discal spot and a like colored serrate band running the width of the outer third of the wing. This band is frequently cut into by extensions of the grayish fuscous coloration present on the outer third of the wing, so that at times the band tends to be broken up into series of lunate spots. Hind wings dark grayish fuscous, with a broad median fascia which does not attain the cephalic or caudal margins of the wing. Male speci-

mens reared at high temperatures are brilliant, the cephalic wings possessing a pleasing blue-gray hue. Likewise females reared at high incubator temperatures are highly colored and deviate to a large extent from the type specimen in the field. Abdomen dark grayish fuscous above, white beneath; caudal margin of segments on the dorsum with a fine line of white scales. Frenulum consisting of one long stout spine.

Genitalia strongly chitinized; anellus with two dorsal projecting lobes supported by two chitinous arms; face of clasper oval and spinose; tegumen trifurcate; sacculus of the harpe bearing one large and two smaller stout spines.

FEMALE

Alar expanse 25 to 34 millimeters.

Cephalic wing of the female dull yellow or sometimes sulphurous, the costa and inner two-thirds of the wing more or less streaked with brown; a serrate brown line is present on the outer third of the wing and extending its width, followed on the outside by a narrow yellow band more or less serrate on its outer margin. On the outside of the latter there is present a brown band interspersed with yellow. Caudal wing grayish brown with a rather broad light ochreous fascia beginning slightly caudad of the costa and terminating short of the caudal margin of the wing. In some specimens cephalic wings may be dull



FIG. 38.—Adults of the European corn borer; At left, male moth; at right, female moth. Not quite twice natural size

yellow and cinnamon brown tinged with ferruginous, and with the caudal wings very pale brown streaked irregularly with shades of darker color. Frenulum of the female consisting of two long spines and a shorter, more slender one.

Ovipositor terminating in a chitinous plate emarginated with long and shorter amber-colored setae; genital opening without strongly chitinized cephalic margin; chitinized plate caudad of the genital opening well developed.

SEASONAL HISTORY

The seasonal history of the corn borer in various localities is variable, as would naturally be expected of any widely dispersed insect; but a somewhat surprising feature is that in localities where the climatic complex is superficially the same, there is a variation in the number of generations annually. Between the areas of infestation in eastern Massachusetts and western New York, the early spring mean temperatures, the frost dates in spring and fall, and the length of the growing season are comparable. If there is any apparent difference in the two localities it is slightly cooler in

eastern Massachusetts than in the western New York area of infestation, yet in eastern Massachusetts there are normally two generations a year, or at least a preponderance of individuals which develop a second generation, whereas in western as well as in eastern New York but one generation occurs, judging from the observed behavior of the insect.

Table 21 gives a partial list of the localities where *Pyrausta nubilalis* is known to occur, with the corresponding number of generations annually. The data concerning the number of generations in the various localities have been taken from miscellaneous sources of information and, of course, represent only generalized conditions owing to the fact that in many of the foreign localities the field records of seasonal history, occurrence, and behavior are in many cases insufficient, and possibly inaccurate.

TABLE 21.—Number of generations (annually) of *Pyrausta nubilalis* in various localities from which data are available

Locality	Number of generations	Remarks
New England.....	2	1920, ¹ 1 complete and 70 per cent of a second generation; 1921, 2 complete and a small partial third; 1922, 1 complete and 86 per cent of a second generation; 1923, 1 complete and 60 per cent of a second generation; 1924, 1 complete and 78 per cent of a second generation.
Eastern New York.....	1	One complete and a small partial second generation in 1921.
Western New York.....	1	Do.
Pennsylvania.....	1	Do.
Ohio.....	1	Do.
Michigan.....	1	Do.
Ontario, Canada.....	1	Do.
Southern France.....	2	
Northern France.....	1	
Southwestern Russia.....	1	Probably a partial second generation during favorable seasons.
Transcaucasia.....	2	
Belgium.....	1	
Netherlands.....	1	
Hungary.....	1	
Italy.....	2	A third generation is reported from environs of Florence.

¹ Two complete generations and a small partial third generation were reared in the insectary during 1918, and two complete generations were reared under the same conditions in 1919, but extensive field studies to determine generation development were not initiated until 1920.

SEASONAL DEVELOPMENT

Since the corn borer appears to be more destructive and presents a more difficult problem in localities having two generations in this country than in those having one generation, obviously it is a matter of economic importance to ascertain, if possible, the factors that determine the number of generations in localities within its present distribution. This information is necessary in order that the probable seasonal history of the insect may be forecast for various sections of the United States, should the insect become widely distributed. The solution of this problem has been approached from various angles.

The possibility that distinct biological species inhabit the New York and Massachusetts areas, which are one and two generation localities, respectively: The results have shown that individuals taken from both areas, as well as individuals from various foreign localities, crossbreed and are capable of producing fertile eggs. The project of rearing these hybrids is still under way.

The possible presence of geographic races: The manner of conducting experiments to determine this point was the transfer of material from one locality to the other, that is, from a one-generation locality to a two-generation locality, and vice versa, subsequently breeding the offspring for several years to observe their reactions to change in environment.

During the winter of 1920-21 a series of overwintering larvae were transferred from western New York to the Massachusetts area, and the progeny of this material have been carried through their entire seasonal development since that time in large field cages. A similar cage was used as a check in which native Massachusetts material has been reared under similar conditions, and the results from each lot of material checked by insectary rearings. The results during the first four years are shown in Table 22.

TABLE 22.—Results of rearing *Pprausta nubilalis* material transferred from western New York to Massachusetts during winter of 1920-21

Source of material	Number of generations in original locality	Number of generations in Massachusetts			
		1921	1922	1923	1924
Silver Creek, N. Y. (environs).....	1	1	1	1	1
Medford, Mass. (check).....	2	2	2	(1)	2

¹ 1 complete, 2 partial.

² A second flight of moths was observed in this cage in 1924, but no dissections were made to determine the percentage of the second generation which developed.

Similar rearings were carried on at Silver Creek, N. Y., during the period 1921 to 1924 with two-generation material transferred from Massachusetts in the early spring of 1921. Under these conditions the Massachusetts material adhered to its two-generation seasonal development for this four-year period.

These experiments must be continued for a period of several years before any conclusions can be reached as to the effect that climatic factors may have in changing the number of generations through which the insect may pass in completing its seasonal development. The time of year when the material is transferred, and the method of handling after its arrival, as well as conditions under which the experiment is conducted, undoubtedly exert an influence during at least the first year or two of the experiment.

Climatic conditions: In the past, temperature, since it is conceded to be one of the most important stimuli for biological development, has been given great weight in the solution of many parallel problems.

A detailed study of the variation of climatic factors upon the seasonal history of this insect includes a course of experiments covering the study of the effects of the important climatic factors. The study of temperature consists of temperature work, carried on in incubators, where a constant temperature of great accuracy can be maintained, with the humidity conditions fairly uniform. The results of these experiments, in connection with important information obtained from the study of the behavior of the insect under field and insectary conditions, will be used when the data obtained

are sufficient to warrant doing so, in an attempt to evaluate the temperature influence upon seasonal development. As is noted further on in the discussion, the other factors are being carefully studied, but until experimental proof becomes stronger, it would be unwise to draw definite conclusions from the available data regarding the future behavior of the insect under widely different climatic conditions.

In nearly all investigations of important economic pests the necessity has arisen of attempting correlations with one or more climatic factors to aid in forecasting the time of appearance and duration of important phenological events. The most common correlation to be found is that involving the effects of accumulated degrees of temperature, above a threshold of development, with the seasonal-history features. It has been determined by experimentation that the methods of correlation commonly used to express the temperature effects upon development are not satisfactory for practical purposes, and until a more basic knowledge is obtained concerning the reactions of the insect to its environment, the usual temperature summations will be avoided.

All the climatic factors, not temperature alone, must be studied to obtain the solution of these physiological problems.

Experimental work carried on at Arlington, Mass., to date has revealed the following points:

1. Moisture conditions, i. e., precipitation, humidity, and evaporation, have an apparent effect upon development, and in the case of humidity and precipitation, an effect that can not safely be averaged out.

1. Individuals in New England which experienced the usual winter temperatures but were deprived of moisture up until time for normal spring pupation in the field were delayed in their seasonal occurrence beyond the normal time, and as a result of this treatment only 60 per cent of the progeny produced the normal two generations.

2. Individuals which experienced a mean temperature of approximately 75° F. and an average humidity of less than 45 per cent during the hibernation period failed to pupate and died in large numbers. A small percentage completed development under these conditions. Individuals having a similar history, placed under field conditions at the time for normal pupation in the field, were greatly delayed in their development, and the progeny completed their development—60 per cent one generation, and 40 per cent two generations.

3. Preliminary correlation work shows that humidity deficiency raises the threshold of development and decreases the point of maximum rate of development.

2. Temperature (humidity conditions approximately 75 to 85 per cent) :

	Egg	Larva	Pupa
1. The reciprocal of the curve of development is not a straight line, except within certain limits, which are.....	° F. 67-87.5	° F. 61-81	° F. 62.5-87
2. The maximum rate of development occurs at.....	92	94.5	92
3. The optimum for development (fastest rate with least mortality) is.....	70-75	70-75	82-86
4. Straight-line threshold, as used by other workers, is.....	58.7	49.7	55.4
5. Actual threshold of development is.....	44.3	36.5	41.2
6. Corrections must be made for the different velocities of development which exist outside of the straight-line limits.			
7. The points as here given will vary in accordance with the humidity fluctuations or change in any of the other climatic factors.			

The data given are only preliminary, since all of the experimental results have not as yet been carefully checked.

Although in the past the effect of humidity upon the development of an insect whose life habits prevent it from directly experiencing continued atmospheric humidity, has been somewhat discounted, it has been found that, in some manner, humidity does play an important rôle in the development of the corn borer. How the external humidity affects the borer within the stalk can, of course, only be conjectured; but the fact that it does affect it serves to illustrate the fallacy of attempting to derive a close correlation between development and a single factor of climate, which will apply and prove useful over a period of years.

In the investigations thus far the importance of fluctuation of temperature in lengthening or shortening a stage has been very marked, and in many instances where the temperature has been higher, humidity conditions the same, but fluctuation less, there has been a marked increase in the period required to complete a given stage.

The entire difference in duration of stages apparently produced by fluctuation is not due to the mere rise and fall of temperature. A study of recent constant temperature experiments shows that the lower temperatures, i. e., 10° or 15° above the actual threshold of development, have a much greater effect upon development than those temperatures 20° or 30° higher. Since during the spring months the daily temperatures are for a greater part of the time within these more influential limits, an accurate evaluation of the effects of these temperatures must be considered before any definite knowledge can be obtained concerning the possibilities of development at this time of year.

However, variation in temperature is more advantageous to development than is constant temperature, although the advantage seldom rises over 10 per cent in favor of the former, and in most cases can be figured at 2 or 3 per cent.

The results of the experiments in connection with this type of investigation will be advanced far enough in the near future to warrant a more detailed discussion of these physiological reactions. Although it is not expected that a definite mathematical interpretation can be evolved that will express the effects of climate in relation to development, it is hoped that certain definite facts may be learned which will give a much clearer appreciation of the possible reactions of the insect to its environment.

Precipitation, as a determinant of development in entomological research, has not, until very recently, been given the attention which, upon closer scrutiny, it seems to merit. That the distribution of precipitation during the winter and spring months is of immense importance biologically can not be denied, but in just what particular manner this factor affects the future seasonal activities of this insect can not at present be explained.

During the last three years a preponderance of precipitation in March, April, and May, followed by a dry June, induced an early start of the insect in New England, and so far under these conditions a complete second generation has occurred and evidences of a partial third generation were observed. On the other hand a deficiency of rain in March, April, and May, followed by a rainy

June, were unfavorable, and in those years in which such conditions have prevailed there has been a diminution in the number of individuals developing a second generation.

In order to present a picture of conditions in several representative localities where *P. nubilalis* is known to exist, a series of climographs for these localities have been constructed, following the methods of Taylor (66) and Shelford (57). These are shown in Figures 39 and 40. All data used in the construction of these climographs have been based upon normal means, and the graphs may be taken as representing mean conditions of typical localities in the areas indicated. Temperatures are plotted along the "Y" axis and tenths inches of precipitation along the "X" axis. The numerals along the lines composing the graphs refer to the months of the year. The 3-inch precipitation line has been made a heavy broken line to give an easier means of comparison and differentiation between the months. It must be understood that these graphs will not indicate definite conclusions; they serve rather to show the differences in climate existing in normal years. The comparative deficiency of precipitation which exists in the one-generation areas can be readily appreciated by a comparison of Figure 39, C and D, with Figure 39, B, which represents a two-generation area. In view of the uniform advantage of temperature which Hungary, represented by Figure 39, C, has over New England (fig. 40, A), the deficiency of precipitation in Hungary would lead one to believe that here was a potent factor in limiting the number of generations annually to one, whereas the New England climate (temperature and precipitation) has been favorable for two generations. Compare the localities in the United States known to be infested by *P. nubilalis*; New England (fig. 40, A) with eastern and western New York (fig. 40, B and C) and Ohio (fig. 40, D). Note the difference in the distribution of precipitation, particularly during the winter and early spring. Again the deficiency and distribution of precipitation appear to separate New England's two-generation area from the New York and Ohio one-generation conditions.

The graphs for the Corn Belt (fig. 39, A) have been inserted as a means of visualizing the normal conditions which exist in the 10 towns selected in comparison with the localities from which seasonal history information has been obtained. Note the dotted graph of Sioux City. Again, the comparative deficiency of precipitation during the critical winter and early spring months would lead one to believe that there would be a strong possibility of only one generation in that section of the United States.

The accompanying graphs representing the one and two generation localities are typical of similar graphs constructed for 111 single-generation and 52 two-generation localities in Europe, Asia Minor, and the United States, where *P. nubilalis* exists and from which seasonal-history data are available. It must be borne in mind, however, that such comparisons are certainly not proof of what might happen in similar areas not now infested, although useful in studying locality conditions and in formulating various hypotheses which must be tested experimentally. Prognostications founded upon empirical comparisons of this nature are extremely dangerous and should be used only as a key to avenues of experimentation.

Considering the inadequacy of the experiments here described definitely to establish the relation between climatic factors and the various phases of development, it would not be expedient to advance

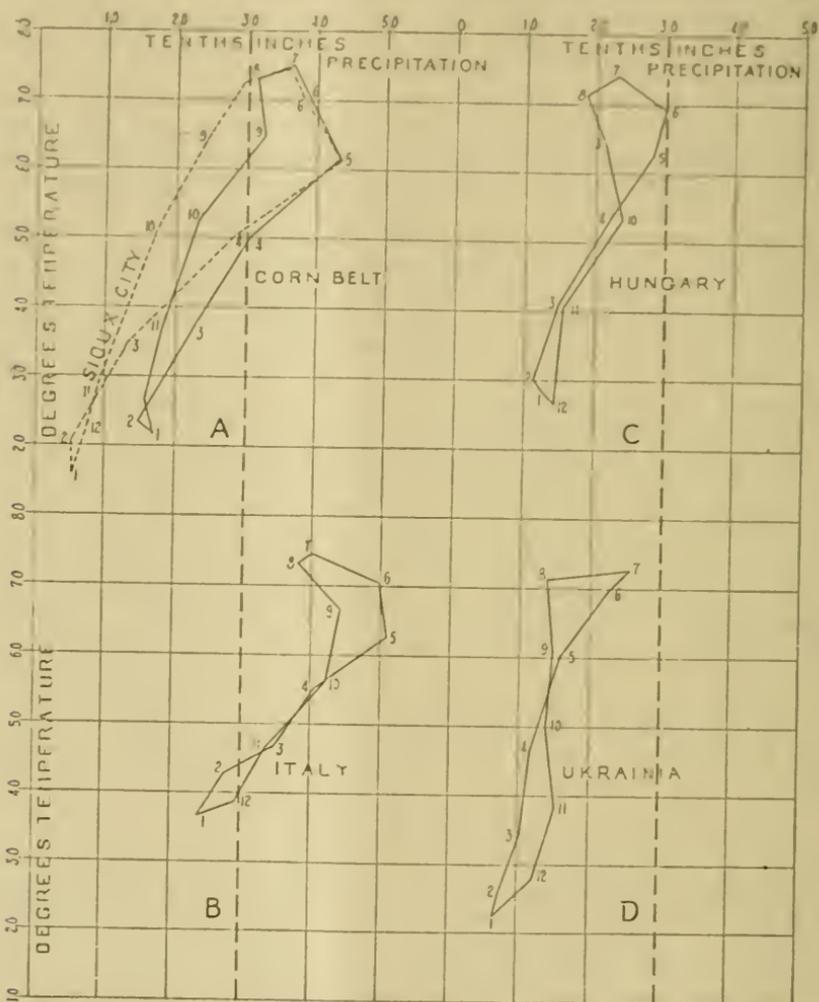


FIG. 39.—Climographs of typical localities in the Corn Belt, and of localities known to be infested in Italy, Hungary, and Ukraine. Constructed from the averaged normal means (Weather Bureau) of the towns listed under each locality.

A, Corn Belt: Sioux City, Iowa; Clarinda, Iowa; Webster City, Iowa; Waterloo, Iowa; Mount Pleasant, Iowa; Monmouth, Ill.; Pontiac, Ill.; Urbana, Ill.; La Fayette, Ind.; Bluffton, Ind.

B, Italy (two generations): Treviso, Oderzo, Conegliano.

C, Hungary (one generation): Bacsfoldvar (Yugoslavia), Hodmezo-Vasarhely, Mesohegyes.

D, Ukraine (one generation): Poltava, Odessa, Nikolaev, Kherson.

at this time a conclusive statement regarding the status of the insect in new localities to which it may spread.

K. W. Babcock began in 1924 a careful survey of the insect in its native home, with a view to obtaining accurate data concerning

the reactions of the insect to its environment in localities where there has been a good chance for a long period of adaptation. These data should give an accurate means not only of defining the best methods

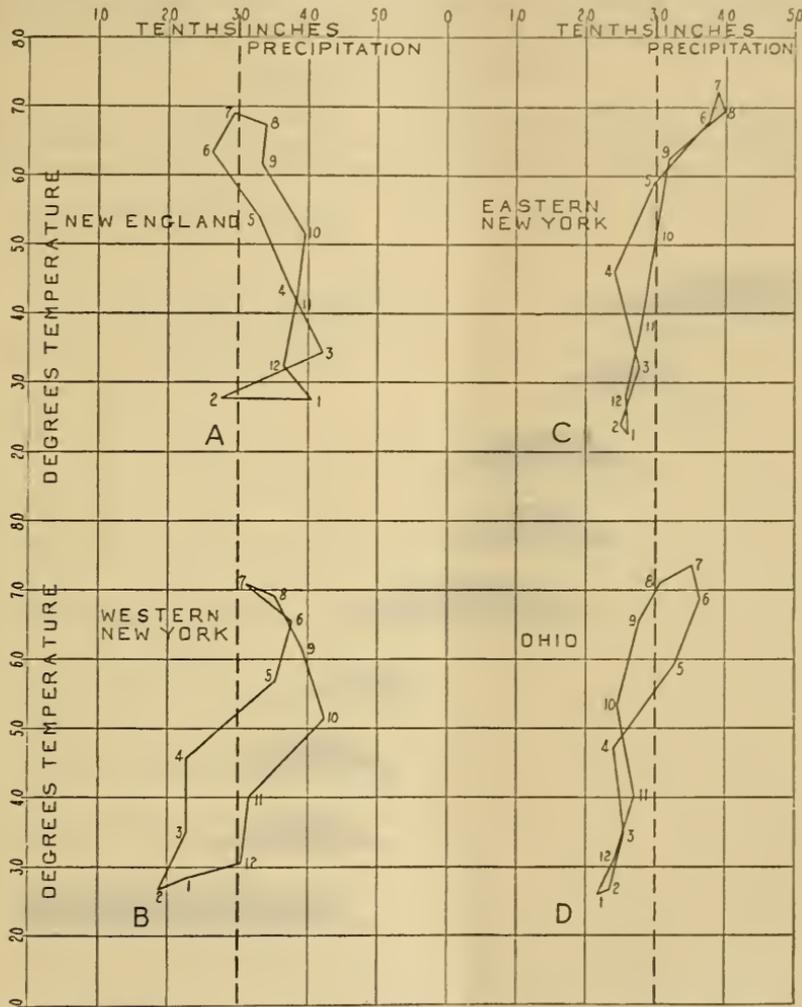


FIG. 40.—Climographs of typical localities infested in New England, western New York, eastern New York, and Ohio. Constructed from the averaged normal means (Weather Bureau) of the towns listed under each locality

- A, New England (two generations) : Boston, Mass. ; Rockport, Mass. ; Plymouth, Mass. ; Provincetown, Mass.
- B, Western New York (one generation) : Buffalo, Fredonia.
- C, Eastern New York (one generation) : Albany.
- D, Ohio (one generation) : Cleveland, Toledo, Sandusky.

of studying the insect experimentally but also should serve as a basis for more accurate knowledge concerning the possibilities of damage under particular environmental conditions.

SEASONAL OCCURRENCE

A knowledge of the date of appearance, the maximum occurrence, and last records of the different stages of any insect is indispensable and often of great practical importance in the application of control practices as well as in the selection of proper quarantine dates.

EASTERN NEW ENGLAND AREA

In order to present a general idea of the seasonal occurrence of *Pyrausta nubilalis* in New England, a graph has been constructed (fig. 41) based upon the average obtained from actual observations

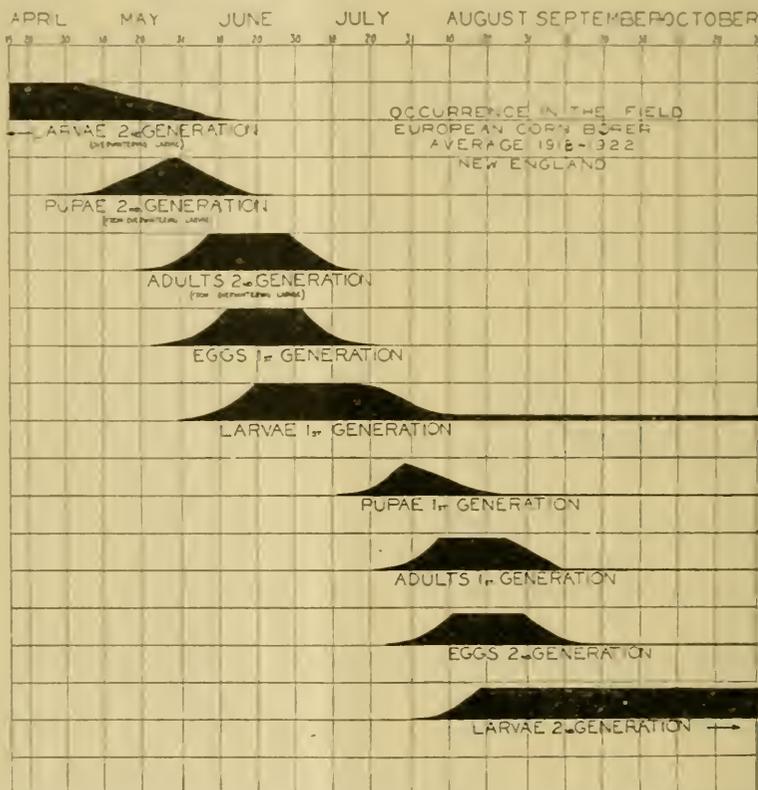


FIG. 41.—Seasonal occurrence of the European corn borer in New England. Averaged from data obtained during the period 1918 to 1922, inclusive

in the field and from insectary rearings during the five-year period from 1918 to 1922, inclusive.

Prior to 1922 no systematic field examinations were made with this particular object in view, consequently it was necessary in the instance of some of the stages, notably the first occurrence of eggs and larvae in certain years of the five-year period, to depend upon insectary records, or to compute the first occurrence from the known presence and duration of the preceding stage in the field. This procedure undoubtedly affected to a slight extent the computation of the five-year average shown in Figure 41, consequently the average date of the actual presence of eggs and larvae in the field during this

period may have occurred a few days earlier or later than is indicated. Since, however, the majority of these records were based upon averages of actual field observations, it is believed that the seasonal occurrence of the stages as shown in Figure 41 represent closely the average occurrence during this five-year period. A detailed explanation of the manner in which this chart and the three following charts were constructed is given in another publication (7).

During the season of 1922, beginning March 23 and extending to September 8, a systematic investigation was conducted to determine more accurately the occurrence of *P. nubilalis* in the field. Field examinations were made to ascertain the occurrence and progress of pupation and adult emergence in representative localities in the Massachusetts area, on practically every working day throughout the season when weather conditions permitted. The examinations occurred in corn and Xanthium, although some of the more widely distributed and susceptible weeds, such as Echinochloa, Bidens, Amaranthus, and Polygonum, were included. During the course of the season 559 separate examinations were made, involving a total of 71,528 individuals.

With the information concerning the occurrence and progress of pupation and adult emergence at hand, similar data relating to eggs and larvae were computed from the known duration of the adult stages and incubation period, as determined by contemporaneous insectary rearings, supplemented by observations in the field. The daily percentages of larvae, pupation, and adult emergence which were found at the time of examination, averaged for all localities and food plants, are shown graphically in Figure 42. The incidence of eggs and younger larvae, as well as the larvae entering hibernation, is indicated by dotted lines. The prevalence of first-generation larvae which hibernated in that stage, consisting of about 1.4 per cent of the total larvae present, is shown by a dotted extension.

The fact should be emphasized that the percentage of each stage designated in Figure 42 as being present in the field on a given date is an average for all localities and food plants. In general the incidence of egg deposition as well as the development of the larvae and subsequent pupation in the summer broods was earlier in the early corn than in the later corn. For this reason the percentage of larvae, pupae, and empty pupal cases (denoting adult emergence) often varied considerably on the same date in different corn plantings in the same field or farm, during the growing season. Since 1922 was in most respects a normal season it is believed that the progress of seasonal development during that season as represented in Figure 42 was very nearly typical, although it is realized that this procedure must be repeated for several years before definite, reliable information on this point can be secured.

For the purpose of illustrating more graphically the occurrence of each stage of *P. nubilalis* in the field during 1922, a graph (fig. 43) has been constructed based upon the field examinations discussed above. The black areas represent the actual field counts, while the areas inclosed by dotted lines are computed from the occurrence and the known duration of the preceding stages, as determined by contemporaneous insectary rearings, supplemented by observations in the field.

NEW YORK AREAS

The seasonal occurrence of each stage of the corn borer is usually from three to four weeks later in the New York areas than in New England.

Figure 44 represents graphically a general idea of the seasonal occurrence of *P. nubilalis* in New York during the period from 1920 to 1922, based upon the averages obtained from actual field observations in the environs of Scotia and Silver Creek, as well as from contemporaneous insectary rearings. Owing to the sparse

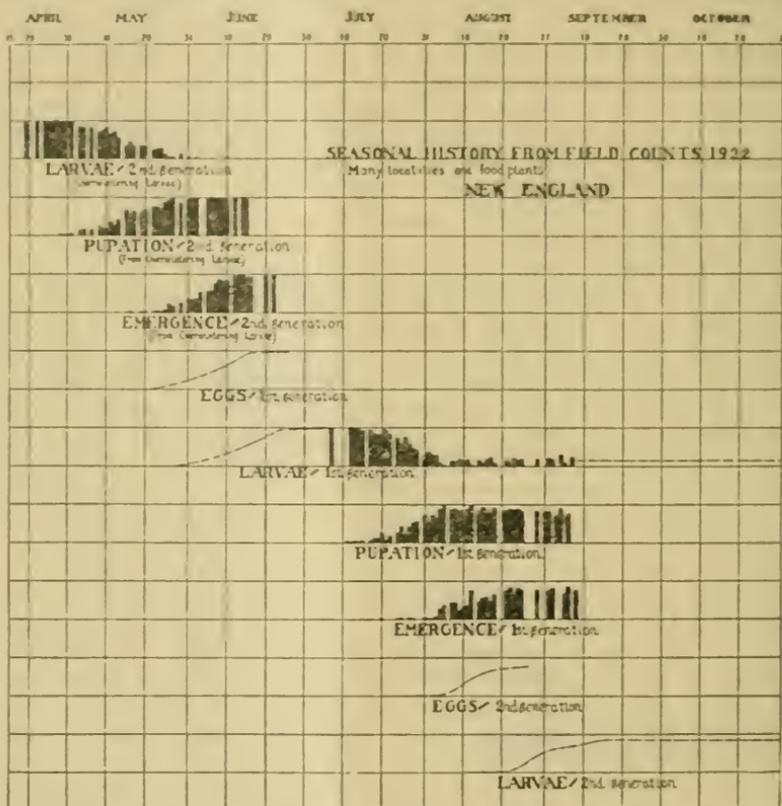


FIG. 42.—Seasonal history of the European corn borer in New England during 1922. Black areas denote per cent of each stage in the field, as determined by field counts. Dotted lines show the probable occurrence (in per cent) of eggs and young larvae, as determined by plotting rearing records. Dotted line following the graph of first-generation larvae indicates the per cent of single-generation individuals.

infestation and the consequent difficulty in making field examinations during the early season, it is believed that the records pertaining to the beginning of pupation, adult emergence, and egg deposition are a few days later than the actual appearance of these stages in the field.

The records for 1920 were obtained principally from Scotia, and for 1922 from Silver Creek, whereas during 1921 complete records were obtained from both localities. During 1921 the seasonal occurrence of each stage of the corn borer at Scotia coincided very closely with the occurrence of the same stage at Silver Creek.

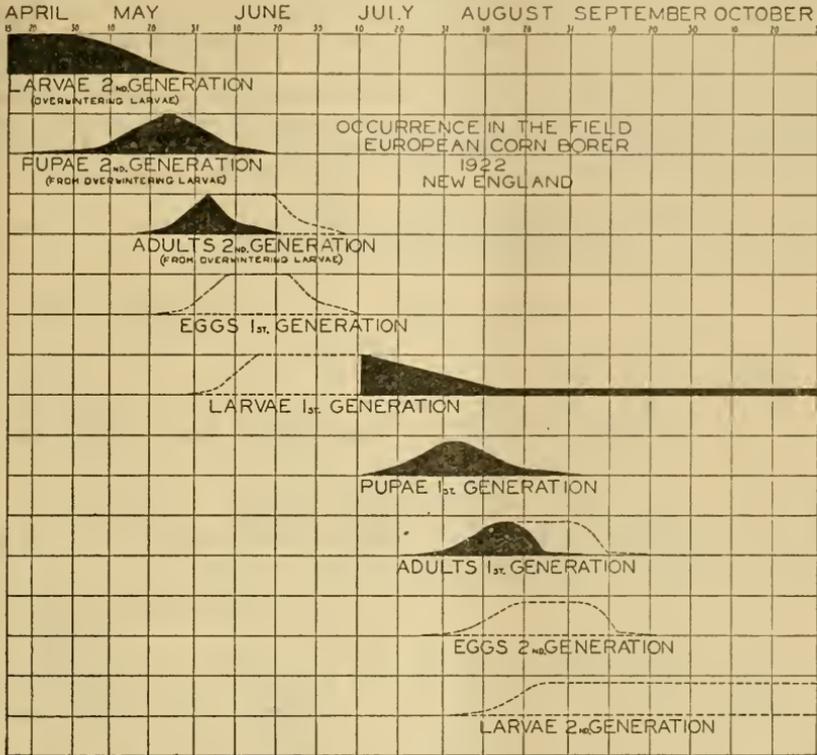


Fig. 43.—Seasonal history in New England during 1922. Black areas denote actual field counts. Areas inclosed by dotted lines show the probable occurrence of eggs and immature larvae, and the length of life of adults, as determined by plotting rearing records and from field observations

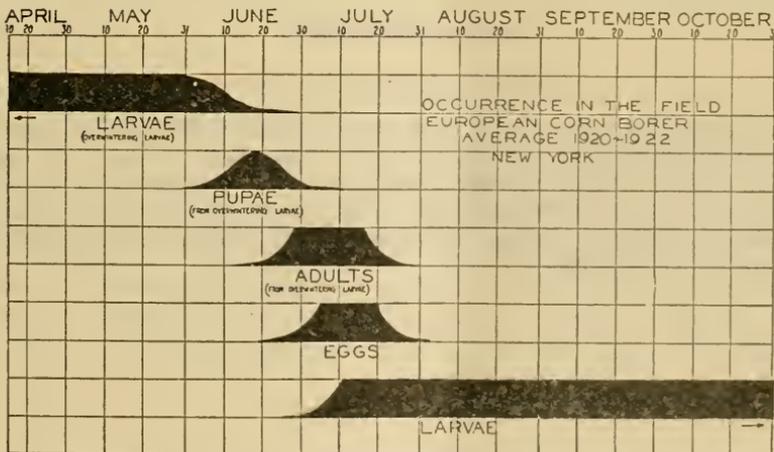


Fig. 44.—Seasonal occurrence of European corn borer in the infested areas of New York. Averaged from data obtained during the period 1920 to 1922, inclusive

OHIO

Owing to the comparatively sparse infestation existing in Ohio, it has not been possible to conduct extensive or detailed field studies to determine dates of seasonal occurrence. During 1923 and 1924, however, some preliminary data were accumulated upon this point by F. W. Poos and L. H. Patch, a summary of which appears in Table 23, showing the seasonal occurrence of each stage. Most of these observations were made in the vicinity of Sandusky, Ohio.

TABLE 23.—Summary of seasonal-occurrence notes on the European corn borer at Sandusky, Ohio, for 1923 and 1924

Stage	Date of first record				Date of greatest abundance (approximate)			
	1923		1924		1923		1924	
	Laboratory	Field	Laboratory	Field	Laboratory	Field	Laboratory	Field
Pupa.....	June 15	June 20	June 23	June 28	July 10
Adult.....	June 26	July 1	July 2	July 16	July 25
Egg.....	July 2	July 10	July 5	July 9	July 18
Larva.....	July 9	July 11	July 11	Aug. 5-10	Aug. 20

Stage	Date of last observed record			
	1923		1924	
	Laboratory	Field	Laboratory	Field
Pupa.....	July 2	Aug. 12
Adult.....	Aug. 8	Sept. 2
Egg.....	July 31	Aug. 3
Larva.....	(¹)	(¹)

¹ Overwintered

LIFE HISTORY

EASTERN NEW ENGLAND

The seasonal occurrence of each stage of the corn borer in eastern New England for the period 1918 to 1922 has been given in Figures 41, 42, and 43. The average duration of the stages of *Pyrausta nubilalis* in eastern New England, as obtained from insectary records at Arlington, Mass., during the period from 1919 to 1921, inclusive, are shown in Table 24.

TABLE 24.—Duration of stages of *Pyrausta nubilalis* in New England (Arlington, Mass.), 1919 to 1921, inclusive

	1919				1920				1921			
	First generation		Second generation		First generation		Second generation		First generation		Second generation	
	Average days	Number of specimens	Average days	Number of specimens	Average days	Number of specimens						
Egg stage.....	7.14	2,990	7.84	6,087	7.16	4,600	6.25	4,992	7.00	4,053	7.31	20,727
Larval period:												
First instar.....	4.98	154	6.76	30	4.50	59	5.00	18	5.54	24	4.00	87
Second instar.....	4.70	152	5.44	30	4.70	59	5.90	18	5.40	24	5.20	87
Third instar.....	4.84	151	7.86	30	4.00	59	9.30	18	5.48	23	5.20	87
Fourth instar.....	7.50	147	8.83	130	6.90	59	12.10	18	4.18	22	6.49	87
Fifth instar.....	13.10	113	15.30	7	13.80	156	14.40	7	9.50	21		
Sixth instar.....	12.70	40	25.00	2	12.20	5	16.00	1				
Seventh instar.....	11.00	8										
Total larval period ²	{ 35.12 to 58.82 }		{ 28.89 to 69.19 }		{ 33.90 to 46.10 }		{ 32.90 to 63.30 }		30.10		120.89	
Pupal period:												
♀.....	10.94	197	18.76	103	11.04	91	19.14	28	9.86	61	18.12	114
♂.....	12.61	214	20.41	118	11.92	71	20.71	23	9.24	54	19.04	126
Adult stages:												
Preoviposition.....	4.30	109	5.10	120	3.20	93	4.10	17	2.60	42	4.60	21
Oviposition.....	11.80	109	14.10	120	9.50	93	10.60	17	13.00	42	6.80	21
Postoviposition.....	3.20	109	1.50	120	1.70	93	3.80	17	2.60	42	4.50	21
Longevity ♀.....	19.30	109	20.70	120	14.40	93	18.50	17	18.20	42	15.90	21
Longevity ♂.....	20.20	102	19.50	110	15.20	83	21.10	16	17.10	46	16.00	21
Total period from egg to egg.....	{ 57.60 to 81.20 }				{ 55.30 to 67.70 }				49.56			

¹The duration of the total larval period varied because a majority of individuals pupated (in the first generation) at the end of the fourth or fifth instar, whereas other individuals had additional instars. Similarly, in the second generation the length of larval life to the last molt prior to entrance to period of winter inactivity varied because a majority of the larvae entered this period at the end of the fourth instar, whereas others developed fifth and sixth instars.

²To last molt in second generation; not including indefinite duration of last instar and winter period of inactivity.

From Table 24 it is seen that during the three-year period the average duration of the egg stage each year varied from 7 to 7.16 days for the first generation and from 6.25 to 7.84 days for the second generation. The average duration of the larval period each year, for the majority of the individuals under observation, varied from 30.1 to 35.12 days for the first generation and from 20.89 to 32.9 days for the second generation to the last molt. This does not include, of course, the indefinite duration of the last instar and its winter period of inactivity. Under insectary conditions four instars were developed by the majority of the individuals in both genera-

tions, although six and seven molts before pupation were recorded by a few individuals of the first generation, and a few of the reared larvae of the second generation recorded five and six molts before reaching full growth preceding the period of winter inactivity. The average duration of the pupal period each year varied from 9.86 to 11.04 days for the females, and from 9.24 to 12.61 days for the males of the first generation, and averaged from 18.12 to 19.14 days for the females, and from 19.04 to 20.71 days for the males of the second generation. The average duration of the preoviposition period each year varied from 2.6 to 4.3 days for the first generation, and from 4.1 to 5.1 days for the second generation. The average total life cycle of the first generation, from the egg to the termination of the preoviposition period of the female, varied each year from 49.56 to 57.6 days for the majority of the individuals under observation. The duration of the total life cycle of the second generation includes the winter period of inactivity and can not, therefore, be accurately expressed.

The duration of the egg stage was obtained by isolating individual egg clusters in small salve-box and plaster-of-Paris cages as soon as deposited by females in confinement.

The duration of the larval instars was determined by isolating newly hatched larvae in cages containing stems and leaves of corn and other favored food plants (*Rumex* and *Amaranthus*). After the larvae entered these plant portions it became necessary to make daily dissections in order to determine molts. This procedure resulted in a heavy mortality of the larvae under observation, and undoubtedly prolonged the duration of the instars of the surviving larvae. No satisfactory rearing cage or rearing method has yet been devised which will permit frequent examinations of *P. nubilalis* larvae for molts without disturbing the feeding larvae to such an extent as to affect their normal development. Therefore, for this reason alone, the average for the total period of larval development in each generation shown in Table 24 probably varies to a considerable extent from the actual duration of the larval period in the field, in the case of individuals exposed to comparable conditions of temperature, humidity, etc.

The duration of the pupal period was obtained by isolating full-grown larvae in individual glass-tube cases and noting the pupal formation and adult emergence.

The duration of the adult stages was determined by confining pairs of newly emerged adults in individual lantern-globe cages placed over flowerpots filled with soil and containing a branch of *Rumex* or *Amaranthus* inserted in a tube of water buried in the soil. In this type of cage the females deposited eggs freely upon the leaves of the plant, and in many instances upon the sides of the lantern globe, as well as upon the cheesecloth with which the top of the cage was covered. The soil in the flowerpots was kept moist, and small wads of cotton soaked with water were also placed in the cage, thus providing necessary moisture for the confined adults.

NEW YORK

Table 25 gives a rather incomplete record of the average duration of *P. nubilalis* stages at Silver Creek, N. Y., as obtained from insectary rearings during the period from 1922 to 1924, inclusive.

TABLE 25.—Duration of stages of *Pyrausta nubilalis* at Silver Creek, N. Y.

	1922		1923		1924	
	Average in days	Number of specimens	Average in days	Number of specimens	Average in days	Number of specimens
Incubation period.....			6.3	10,383	6.4	15,307
Larval period:						
First instar.....	6.18	64				
Second instar.....	3.76	64				
Third instar.....	5.16	63				
Fourth instar.....	¹ 13.47	58				
Fifth instar.....	16.92	13				
Sixth instar.....	12.00	1				
Total days to last molt ²	² 28.6 to 57.5					
Pupal period:						
Female.....	13.34	29				
Male.....	14.00	26				
Adult stages:						
Prooviposition.....			9.5	39	5.8	42
Oviposition.....			12.5	39	11.3	42
Postoviposition.....			4.1	39	5.5	42
Longevity ♀.....			24.8	50	22.3	50
Longevity ♂.....			22.7	50	17.5	50

¹A majority of the larvae entered the period of winter inactivity at the end of the fourth instar, but certain of them developed fifth and sixth instars.

²Not including indefinite duration of last instar.

In the 1923 and 1924 records pertaining to incubation and adult stages, shown in Table 25, 50 pairs of adults were used in separate cages. In the 1923 series 11 females and in the 1924 series 8 females did not deposit eggs. The averages for adult stages, except longevity, are based upon the number of females which deposited eggs.

TABLE 26.—Duration of *Pyrausta nubilalis* stages at Scotia, N. Y.

	1920		1921	
	Average in days	Number of specimens	Average in days	Number of specimens
Incubation.....	5.20	3,567	6.30	806
Larval period:				
First instar.....	9.00	15	4.39	97
Second instar.....	7.80	15	4.30	94
Third instar.....	6.00	15	4.61	86
Fourth instar.....	¹ 8.80	15	¹ 5.85	81
Fifth instar.....	8.50	6	8.50	38
Sixth instar.....	12.30	3	9.00	2
Total days to last molt ²	² 31.6 to 52.4		² 27.7 to 35.7	
Pupal period:				
Female.....	12.22	40	11.80	30
Male.....	13.17	40	12.40	30
Adult stages:				
Prooviposition.....	6.90	122	7.90	30
Oviposition.....	11.80	122	11.40	30
Postoviposition.....	3.20	122	2.80	30
Longevity ♀.....	21.00	122	22.10	30
Longevity ♂.....	14.20	120	15.70	30

²Not including indefinite duration of last instar.

¹See footnote 1, Table 25.

In the spring of 1921 a total of 100 overwintering larvae were caged at Silver Creek, N. Y., for pupation records. From this material a total of 14 females and 19 males were reared, the pupal period of the females averaging 10.93 days and for the males 11.26 days.

Table 26 gives the available records of the duration of life-history stages which were taken at Scotia, N. Y., during the seasons of 1920 and 1921.

OHIO

Table 27 gives a summary of the available records relative to the duration of life-history stages at Sandusky, Ohio, during 1923 and 1924.

TABLE 27.—Duration of *Ppyrausta nubilalis* stages at Sandusky, Ohio

	1923		1924	
	Average in days	Number of specimens	Average in days	Number of specimens
Incubation period.....	5.01	4,801	5.58	17,693
Larval period:				
First instar.....			4.32	100
Second instar.....			4.56	100
Third instar.....			4.80	100
Fourth instar.....			7.94	100
Fifth instar.....			8.83	24
Total days to last molt ¹			² 21.6 (630.5)	
Pupal period:				
Female.....	12.41	39	12.12	16
Male.....	12.39	46	13.25	20
Adult stages:				
Preoviposition.....	2.79	24	3.68	47
Oviposition.....	6.46	24	14.85	47
Postoviposition.....	1.50	24	2.59	47
Longevity ♀.....	9.60	25	19.70	50
Longevity ♂.....	12.40	34	22.50	78

¹ See footnote 1, Table 25.

² Not including indefinite duration of last instar.

The records pertaining to incubation and adult stages which appear in Table 27 were obtained by confining 25 pairs of adults in the 1923 series and 50 pairs of adults in the 1924 series, together with extra males in some of the cages. In the 1923 series one female and in the 1924 series three females did not deposit eggs. The averages for adult stages, except longevity, are based upon the number of females which deposited eggs.

LARVAL HABITS

HATCHING

About a day before hatching takes place the black eye spots and reddish mandible tips of the developing larva become discernible through the semitransparent chorion of the egg. A few hours before hatching the head and thoracic shield become black and assume a central position in the egg. The body segmentation and the black spines on the body of the larva are also plainly discernible before

hatching. At this time the developing larva is curled up inside the egg with its mandibles resting upon the next to the last abdominal segment. These mandibles soon begin to move laterally, and the larva straightens itself out in such a manner that the mandibles are brought into contact with the eggshell. A slit in this is soon made and the larva crawls forth. After hatching, the larva feeds to some extent upon the empty eggshell, but has not been observed to entirely devour it.

FERTILITY AND HATCHING

The greater proportion of eggs deposited in the field and in the insectary were found to be fertile. Table 28 gives data relating to the percentages of fertile eggs, as observed during the progress of life-history studies at Arlington, Mass. The percentages of fertile eggs which hatched, excluding parasitism, are also shown.

TABLE 28.—Fertility and hatching of *Pyrausta nubilalis* eggs (New England)

Generation	In insectary			In field		
	Eggs under observation	Fertile eggs	Fertile eggs hatching	Eggs under observation	Fertile eggs	Fertile eggs hatching
	Number	Per cent	Per cent	Number	Per cent	Per cent
First, 1919	13, 893	87. 2				
Second, 1919	27, 285	94. 3		2, 245	98. 1	98. 9
First, 1920	14, 886	89. 5	95. 7			
Second, 1920	19, 646	85. 7	96. 4			
First, 1921	4, 053	96. 1				
Second, 1921	20, 727	97. 2				
Second, 1923				5, 232	94. 3	
Average		91. 5	96. 0		95. 4	98. 9

From Table 28 it may be noted that an average of 91.5 per cent of the eggs deposited in the insectary were fertile, and 95.4 per cent of the eggs observed in the field were fertile. An average of 96 per cent of the fertile eggs deposited in the insectary hatched, and 98.9 per cent of those hatched upon which observations were made in the field.

An average of 97.2 per cent of the eggs hatched under insectary conditions at Sandusky, Ohio, during 1923 and 1924. A total of 22,494 eggs were under observation in these experiments. At Silver Creek, N. Y., an average of 73.6 per cent of the eggs hatched under insectary conditions during this same period. A total of 25,690 eggs were under observation in this series. In a total of 11,320 eggs collected in the field in Ohio during 1924 an average of 99.3 per cent were fertile.

EFFECT OF DIRECT SUNLIGHT ON HATCHING

Direct sunlight appears to prevent the hatching of the eggs of *P. nubilalis*. During July, 1920, several leaves bearing clusters of fertile eggs were removed from life-history cages and inverted in such a manner as to expose the eggs to direct sunlight. Under these conditions none hatched. In the field the eggs usually are deposited upon the undersides of the leaves and are not directly exposed to the sun, although they have been found infrequently on the upper sides of the leaves and upon the stems of plants, as well as upon the husks of ears of corn.

EFFECT OF COVERING EGGS WITH SOIL.

During the operation of cultivating small corn plants, some of the lower leaf blades bearing egg clusters often are covered lightly with soil. This treatment does not prevent the eggs from hatching, and, unless covered to a depth of at least 4 inches, most of the newly hatched larvae are able to make their way to the surface of the soil. In June and July, 1920, a total of 56 clusters of fertile eggs of the first generation were buried in damp sand-loam soil at depths varying from 1 to 4 inches. All of these eggs hatched. At a depth of 1 inch all of the resulting larvae came to the surface of the soil, at 2 inches 57 per cent, at 3 inches 57 per cent, while at a depth of 4 inches none of the larvae were able to reach the surface of the soil.

EFFECT OF TOTAL IMMERSION IN WATER ON HATCHING

During August, 1920, experiments were conducted to determine the effect of total immersion in fresh water upon the hatching of the eggs. The results of these experiments showed that fertile eggs did not hatch after a period exceeding 6.5 hours of total immersion. This fact may be of importance when treating plants or plant products bearing *P. nubilalis* egg clusters.

FEEDING HABITS OF LARVAE

The general feeding habits of *P. nubilalis* larvae have been previously discussed with relation to the character of injury to corn and to other plants.

METHOD OF FEEDING

The method of feeding by *P. nubilalis* larvae, as distinguished from their boring habits, is subject to a wide variation in accordance with the habits of individual larvae and with the stage of development of the plant, as well as with the part of the plant attacked.

When the eggs are deposited upon young corn plants of which the tassel has not yet appeared, the newly hatched larvae feed at first upon the upper and lower surfaces of the tender leaf blades, thus excavating small irregular-shaped areas in the epidermis. Some of the small larvae may also perforate the leaf blades surrounding the tassel, or work their way between the leaf blades and feed upon the developing tassel within. Once inside the tassel cavity, they feed upon and within the tassel buds. As the tassel expands and the larvae become larger, they enter the tassel stem or its branches and feed within. Instead of feeding upon and within the tender leaf blades and tassel, some of the newly hatched larvae habitually migrate to points lower down on the same or near-by plants, where they may enter the plant at practically any point, although their favorite place of entrance is between the leaf sheath and the stalk. Later in the development of the plant many of the larvae also enter between the stalk and the base of the ear, or they may enter the ear directly.

When the eggs are deposited upon corn plants which have reached the tassel stage, the newly hatched larvae usually do not attack the tassel, nor do they feed to any extent upon the surface of the leaf blades; under these circumstances they enter the stalk directly, or the thick midrib of the more tender leaf blades. If the plant has developed an ear, the newly hatched larvae frequently feed upon the

tender tips of the husks and upon the silk, or work their way down between the silks into the ear and feed upon the grain and cob.

After the larva has entered the stalk it tunnels upward or downward. The character of the tunnel is subject to great variation, but typically the larva follows a nearly straight course through the pith and generally lengthwise of the plant. In some instances the tunnel is more or less winding and occasionally small cells are excavated along its course. Sometimes the larva also excavates a large horizontal chamber either just above or just below the entrance hole and starts its tunnel from this chamber. Stalks bearing this type of tunnel are greatly weakened and soon break over. All parts of the stalk may be tunneled down to and including the base or stubble. There is a tendency for the larvae to work in the internodes of the stalk, but many of the nodes are also perforated, especially where several larvae are present in the same stalk.

Even during the period of active growth of the larva it is apparent that not all of the plant substance removed by the larva during the process of tunneling within the stalk is actually devoured. The larva appears to prefer as food the portions of the interior of the stalk which are most succulent and rich in sugar. The harder and less nutritious portions of the stalk are merely bored out and cast aside. This discarded material, together with the excrement of the larva, is pushed out of the entrance hole in the form of yellowish-white frass, which later becomes darker in color. Much of this frass is held together in masses by silken threads spun by the larva and usually hangs suspended below the entrance hole or collects below in the axils of the leaf blades and upon the ground. Some of the frass, instead of being ejected from the tunnel, is packed by the larva into the cells or chambers of the tunnel.

When the larva bores an ear of corn it may enter directly at the tip, base, or side of the ear, or indirectly through the short stem by which the ear is attached to the stalk. Once inside the ear the larva tunnels through all parts of the grain and cob. The actual feeding areas on the grain may consist of long irregular surface furrows between the rows of kernels, or tunnels just underneath the upper surface of the kernels; or large irregular areas may be fed upon with no apparent regularity of procedure. The larvae tunnel the cob in a similar manner to that described for the stalk, the tunnels extending either longitudinally or transversely through the cob.

The feeding habits of the larvae when attacking plants other than corn are essentially the same as described for corn.

LARVAL ESTABLISHMENT AND SURVIVAL

In view of the known fecundity of the *P. nubilalis* female, as exhibited in confinement, and the number of eggs present in fields under close observation compared to the relatively small number of fully grown larvae which develop subsequently in such fields, it has been apparent that there must be a very high egg and larval mortality from natural causes, since the wide discrepancy between the number of eggs present and the number of fully grown larvae developing from such eggs could not, in most instances under observation, be accounted for by nonfertility, nonhatch, parasitism, disease, predators, or other assignable causes.

Cage experiments which were conducted at Sandusky, Ohio, during 1924 to obtain information upon the percentage of larval establishment and survival, and the causes contributing thereto, showed that an average of only 5.87 per cent of the eggs developed into larvae which became established in their host plant and survived to at least the third instar, in cases where such eggs were deposited upon growing corn plants (dent, flint, and sweet corn) by females temporarily confined in large cages while the eggs were being deposited. These cages were removed immediately after the deposition of the eggs to allow for the subsequent development of the insect and its host plant under natural conditions. Based upon the total larvae hatching in this series, an average of 8.36 per cent of the larvae became established in their host plant, as shown in Table 29, and reached at least the third instar before they were dissected from the plant.

TABLE 29.—Summary of experiments of larval establishment and survival of the European corn borer at Sandusky, Ohio, 1924

Type	Variety	Larvae under observation		Total larvae recovered		Per cent of recovery for type
		Date hatched (1924)	Number	Number	Per cent	
Flint.....	No data.....	July 17 to July 30..	1,195	82	6.86	7.77
Do.....	do.....	Aug. 8 to Aug. 12..	658	62	9.42	
Dent.....	Claridge.....	July 17 to Aug. 1..	1,361	108	7.94	10.80
Do.....	Claridge, high per cent grain..	Aug. 5 to Aug. 6..	576	86	14.93	
Do.....	Claridge, low per cent grain..	Aug. 5 to Aug. 7..	784	100	12.76	6.09
Sweet.....	Golden Bantam.....	July 17 to July 30..	1,169	96	8.21	
Do.....	Evergreen.....	July 17 to July 30..	1,276	53	4.15	
	Total.....		7,019	587		8.36
	Average.....					

Of the total of 587 larvae shown as recovered in Table 29, definite records are available concerning the instars of 474 individuals in this group as follows: Thirteen larvae were in the third instar, 219 larvae in the fourth instar, 132 larvae in the fifth instar, and 110 larvae were mature. The remaining larvae recovered, 113 in number, had migrated to adjacent corn plants, and no records are available concerning the instars they represented. Close observation of the young larvae used in this experiment showed that the greatest mortality occurred during the first and second instars and was attributable to a variety of causes, the most important of which appeared to be desiccation, starvation, and drowning.

Complete records are not available pertaining to the number and percentage of eggs used in this experiment which failed to hatch or produce larvae. This information is available, however, for a portion of the eggs, 3,181 in number, and in this group 23.76 per cent were missed during their incubation period, presumably blown from the plants by the wind, 3.83 per cent failed to hatch, and 2.33 per cent dried up—a total egg mortality of 29.92 per cent. Assuming that the same rate of egg mortality was sustained by all the eggs used in this experiment, the total establishment and survival to at least the third instar, based upon the number of eggs in the experiment, equaled 5.87 per cent.

That the percentage of larval establishment and survival in the field is higher than that obtained in the experiment previously described is indicated by an analysis of 236 isolated infestations found in Ohio cornfields during 1924, wherein an average of 1.88 larvae were collected per infestation. Since each of 731 egg clusters collected in the field earlier in the season contained 15.5 eggs, on an average, the survival of 1.88 borers per infestation shows that 12.13 per cent of the eggs involved developed into larvae which became established, assuming that each of these isolated infestations developed from a single egg cluster.

VOLUME OF PLANT TISSUE CONSUMED OR REMOVED BY LARVAE

The tunnels of 41 fully grown larvae which had spent practically their entire feeding period in isolated sweet corn and dent field cornstalks, were measured and found to average 8.6 inches in length. (See Table 14.) The tunnels of 35 of these larvae in sweet corn were found to average 0.2492 cubic inches in volume, and the tunnels of the 6 larvae in dent field corn averaged 0.1690 cubic inches in volume. It was not possible to determine the relative proportion of plant tissue which had actually been consumed by the larvae in comparison with the proportion of the tissue which had been bored out and cast aside during the excavation of the tunnel.

DISTRIBUTION OF LARVAE IN THE PLANT

While the host plant is green and succulent, it may be entered and tunneled by the feeding larvae at practically any point, but as the plant nears maturity and begins to dry out in its upper portions, or breaks over as a result of larval injury, the larvae exhibit a tendency to migrate to the lower and more succulent portions.

On September 27, 1921, 78 per cent of the stalks were found to be infested in a 4-acre field of flint field corn at Stoneham, Mass., averaging 5.3 larvae per infested stalk. A total of 65.4 per cent of the larvae were distributed in the lower third of the infested stalks and the remaining 34.6 per cent in the upper two-thirds of the stalks. In this same field and on this same date a record was made of the relative distribution of the larvae in the stalks, ears, and ear stems of 10 plants showing average infestation. In these 10 plants 63.3 per cent of the larvae were distributed in the stalks, 23.3 per cent in the ears, and 13.3 per cent in the ear stems. An analysis of the larval distribution in partly matured plants of dent, flint, and sweet corn which were dissected at Sandusky, Ohio, during the period from August 12 to September 1, 1924, showed that in a total of 474 larvae involved in these dissections 17.29 per cent were distributed in the lower quarter of the stalks, 18.77 per cent in the lower middle quarter of the stalks, 16.66 per cent in the upper middle quarter, 16.45 per cent in the upper quarter, 10.97 per cent in the tassel, and 19.82 per cent in the ears.

The relative distribution of the larvae in the stalks and stubble is subject to considerable variation in accordance with the height of the stubble left after cutting, the date stalks were cut, and the stage of development of the plant when cut. There is also a certain amount of larval migration to stubble from corn which is cut and

stacked in the field, and from infested weeds or other plants growing near by. For this reason the percentage of the infested stubble (fig. 45) in certain fields sometimes exceeds the percentage of infested plants determined before cutting. During the late summer of 1921 counts were made of larval infestation in the stubble of 15 fields of sweet and field corn in New England soon after the plants were cut. Field counts in these same fields previous to cutting showed that an average of 68.4 per cent of the stalks were infested.

An examination of the stubble after cutting showed that 31.7 per cent contained living larvae. The stubble in these fields ranged from 5 to 12 inches in height.

In western New York an examination of the stubble in 30 fields of dent and sweet corn during the period from August 8 to November 11, 1923, showed that 6.63 per cent of the stubble was infested, containing on an average 7.78 larvae per 100 stubble. Field counts in these same fields previous to cutting demonstrated that an average of 15.16 per cent of the stalks were infested, containing an average of 19.75 larvae per 100 stalks.

Comparing the average number of larvae left per 100 stubble with the average number of larvae per 100 stalks, it will be noted that 39.39 per cent of the total larval population was left in the stubble. In these 30 fields the stubble ranged from 2 to 18 inches high, with an average height of about 7 inches. A similar comparison between the larval population in the stalks and in the stubble of 36 dent and sweet cornfields in western New York during 1924 showed that 16.12 per cent of the total larval population



FIG. 45.—European corn-borer larva at base of corn stubble; entrance hole just above

was left in the stubble. In these 36 fields the stubble ranged from 2 to 10 inches high, with an average height of about 6.2 inches.

Examinations made of standing cornstalks in Ohio during the period from September 10 to November 3, 1924, showed a pronounced movement of the borers to the lower part of the stalks, as detailed in Table 30.

TABLE 30.—Distribution of larvae of the European corn borer in cornstalks in Ohio during period from September 10 to November 3, 1924

Date of observation (1924)	Total larvae		Larvae 3 inches and below		Larvae 6 inches and below		Larvae 9 inches and below		Larvae 12 inches and below		Larvae 15 inches and below		Larvae 18 inches and below		Larvae 21 inches and below		Larvae 24 inches and below		Larvae 27 inches and below		
	Number	Per cent	Number	Per cent	Number	Per cent	Number	Per cent	Number	Per cent	Number	Per cent	Number	Per cent	Number	Per cent	Number	Per cent	Number	Per cent	
Sept. 10 to 16.....	547	16	2.9	40	7.3	61	11.1	91	16.6	108	19.7	124	22.7	140	25.6	168	30.7	185	33.8	8	
Sept. 17 to 25.....	226	10	4.4	23	10.2	26	11.5	46	20.4	53	23.5	67	29.6	68	30.1	85	37.6	95	42.0		
Oct. 1 to 8.....	173	7	4.0	15	8.7	25	14.5	41	23.7	46	26.6	61	35.3	67	38.7	78	45.1	95	54.9		
Oct. 23.....	135	7	5.2	23	17.0	36	26.7	52	38.5	67	49.6	81	60.0	85	63.0	92	68.2				
Nov. 3.....	110	11	10.0	25	22.7	36	32.7	46	41.8	63	57.2	73	66.4	78	70.9	82	74.6				

In general the percentage of total larval population present in the stalks up to and including 18 inches from the ground increased approximately threefold between September 10 and November 3, and similar increases in larval population occurred in that portion of the stalks situated from 18 to 24 inches of the ground during this same period. (Table 30.) The high percentage of larvae present in that portion of the stalk up to and including 6 inches from the ground late in the season is also very impressive and serves to emphasize the necessity of cutting stalks low and as early in the season as possible. The greater proportion of the corn stubble in the machine-cut fields of Ohio and Michigan is at least 6 inches in height, while 24 inches is about the maximum height in fields cut by hand methods.

POSSIBILITY OF SPRING FEEDING BY OVERWINTERING LARVAE

In a previous publication (71) dealing with the habits of *Pyrausta nubilalis* larvae, reference has been made to the spring "feeding" of overwintering larvae. After a more detailed observation of the spring activities of the overwintering larvae, it appears that no real feeding occurs at this period and that the frass ejected from the larval burrows is composed of material which has been gnawed and cast aside during the process of preparing quarters for pupation. This frass is composed of rough angular particles, in contrast to the smooth, rounded pellets predominating in the normal excrement of actively feeding larvae. A histological study of the internal tract of overwintering larvae reveals an entire absence of solid food, and, furthermore, that important structural changes have occurred in the digestive tract of the larvae after active feeding ceased in the fall. The most important modification occurs in the ventriculus and rectum of the larva, and is of such a nature as to render these organs much more simple and less specialized in structure, the rectum losing for the most part its musculature. According to present knowledge, it appears improbable that overwintering larvae could successfully digest food or evacuate unassimilable matter in the spring. This conjecture is confirmed in a measure by inability to find larvae feeding on new growth in the spring, after they have passed through the winter. A spring examination of the digestive tracts of over-

wintering larvae found in the field revealed an entire absence of solid food, and when these larvae were isolated from any boring medium whatever and supplied with proper moisture conditions, they pupated and emerged as normal adults.

Repeated experiments have been performed in which overwintering larvae were confined during April and May in small cages with green succulent stalks of rhubarb, celery, Rumex, and Polygonum. None of these individuals fed upon or entered these plants, although rhubarb, celery, Rumex, and Polygonum are preferred hosts of the active feeding larvae during the summer.

Field examinations during April and May of rhubarb, spinach, and early spring weeds growing closely adjacent to plant remnants containing overwintering larvae failed to show any infestation in these plants by such larvae.

DURATION OF LARVAL LIFE WITHOUT FOOD

The larvae of *P. nubilalis* are capable of maintaining life without food for a considerable period of time during their active development. This is especially true of larvae in the later instars. By isolating, in individual cages, a large series of first-generation larvae of each instar, it was determined that the average duration of life without food for the first instar was 1.95 days, second instar 5.5 days, third instar 6.7 days, fourth instar 8.1 days, fifth instar 22.8 days, and for the sixth instar 31.3 days. In this series newly hatched larvae were used for the first instar and newly molted larvae for each of the subsequent instars. Pieces of damp blotting paper provided suitable moisture conditions in each cage.

MOLTING

When tunneling inside its host plant, the larva molts within its tunnel near the last feeding place. Where the larva is feeding upon or close to the surface of its host plant, as frequently occurs during the early instars, molting usually takes place inside a thin silken web with which the larva surrounds itself for protection or concealment. Certain individuals in all instars have also been observed molting on the outside of the host plant without any other protection than that afforded by fragments of frass or a few strands of silk spun by the larva previous to molting.

LARVAL MIGRATION

The migration of *Pyrausta nubilalis* larvae from one part of the host plant to another part of the same plant, or to near-by plants, has already been discussed. In addition to this very localized migration, the larvae, especially in their later instars, frequently leave their host plants when such plants are disturbed, or when such hosts become unsuitable for food or shelter through decay or as a result of the drying out of the plant tissues. This migration is especially likely to occur (1) where infested cornstalks are being collected in the fields; (2) where such stalks are left in piles of "stacks" in the field, in the barnyard or under shelter, with the consequent decay through excessive moisture, or the drying out of the plants when protected from rain and snow; (3) when badly infested plants col-

lapse and break over in the field; (4) after infested plants with comparatively small stems, such as oats and some of the weeds, are cut while in a green condition, with the consequent rapid withering or shriveling of the stems; (5) during the handling and shipment to market of infested plant products such as sweet corn ears or beets with tops; (6) from certain plant products, such as celery, after they are placed in underground pits; (7) from infested material which has been buried in the soil. This last is especially likely to occur where such material is buried or plowed under in the spring, or in the early fall to about November 1. Much of this migration is nocturnal, an interesting habit which the species may have developed in an endeavor to escape natural enemies which are more active during the daylight hours. Observations conducted at night in

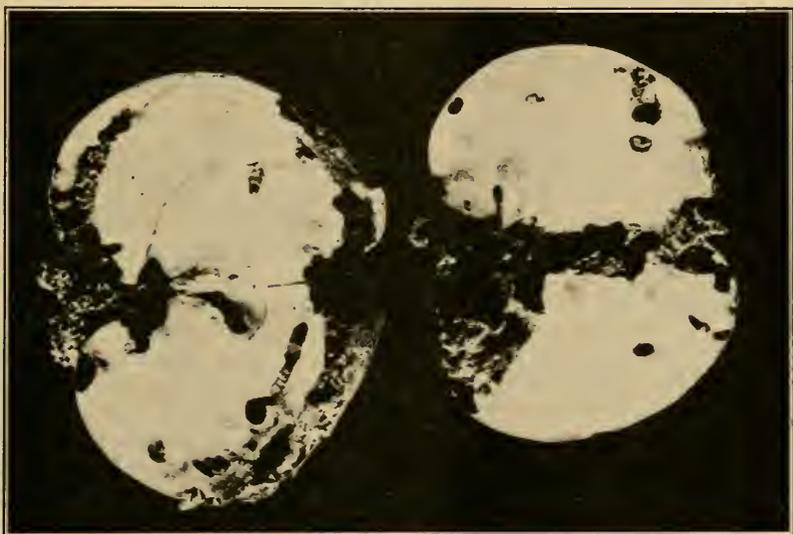


FIG. 46.—Windfall Baldwin apple infested by migrating European corn-borer larvae. A common occurrence in areas of severe infestation. Medford, Mass., September 15, 1922

severely infested fields of corn have revealed great activity on the part of the larvae at this time. Where infested cornstalks or other plant remnants are cut and gathered in large piles during the fall and left in this condition in the field all winter, many of the contained larvae migrate to the outer and drier layers of the pile, or to adjoining shelter, in order to escape the excessive moisture prevailing in the interior of the pile. These outer layers usually are dry enough to be burned easily during late April or early May and thus destroy a large percentage of the borers contained therein.

When the migrating larvae are only partially grown they may enter and feed upon any of the host plants of the species, providing such plants are in a green and succulent condition. When, however, the migrating larvae are fully grown and have ceased feeding, they may enter almost any plant material (fig. 46) which affords suitable shelter, or they may seek shelter in various locations, as will be subsequently shown.

The actual distance traversed by migrating larvae in the field has not been determined with accuracy, although infested cornstalks have been found at a distance of about 15 feet from the location of the nearest known original egg cluster in a very lightly infested corn plot. In a series of controlled experiments wherein crawling larvae of each instar except the second were restricted to sheets of paper from 5 to 6 feet in length, without food, until death resulted, the average distance covered by larvae in the first instar was 31 feet 3 inches; third instar, 118 feet 1 inch; fourth instar, 79 feet 8 inches; fifth instar, 170 feet; and sixth instar, 97 feet 1 inch. These experiments, of course, do not give reliable information relative to the probable migrating ability of the larvae in the field and are only indicative as showing their power of locomotion.

HIBERNATION

The European corn borer normally passes the winter as a full-grown larva within the tunnel made in its host plant during the previous summer and fall. If, however, the host-plant material is unduly disturbed during the progress of field work, or if for any other reason the plants containing the larvae do not afford suitable quarters for winter shelter, many of the larvae migrate from their hosts and enter other plants. Under conditions of severe infestation the larvae have entered such woody stemmed plants as blackberry, raspberry, sumac, elderberry, and grape. If suitable plants are not available for winter shelter, the larvae often burrow into such objects as the walls and crevices of buildings, fences, and posts. Here they form short tunnels in which to pass the winter. When more suitable winter quarters are lacking, the larvae sometimes secrete themselves in loose leaves, under the loose bark of trees or fence posts, and underneath rubbish, clods of soil, loose stones, and similar objects. Here they may, or may not, inclose themselves entirely or partially with a rough silken web. Many of these larvae which seek shelter in locations other than plants, as mentioned above, have been found by experimentation to pass the winter successfully and subsequently to pupate and emerge as moths; providing that the moisture conditions of their habitat were suitable for normal hibernation and pupation.

In every instance under observation all of the hibernating larvae were in the last instar. No case of molting in the spring has been observed.

LARVAL MORTALITY DURING HIBERNATION

Dissection of *Pyrausta nubilalis* larvae during their period of hibernation has revealed that the vital organs are surrounded with a layer of tissue resembling fat. Apparently this fatty material greatly aids the hibernating larvae not only in surviving the adverse natural conditions to which they are exposed during this period but also supplies available means for carrying on the metabolism which occurs during this long period of comparative inactivity. It may also aid the hibernating larvae in resisting such artificial influences as fumigation and heat.

The normal percentage of winter mortality in plants left in natural position in the field is comparatively low. Table 31 gives data relative to the winter mortality for a five-year period in represen-

tative localities of the New England area. These counts, with exceptions noted, were taken during the spring of each year in corn and weeds left in their natural position in the field. Less than 1 per cent of the overwintering larvae were parasitized, so this factor may be practically ignored.

TABLE 31.—Winter mortality of *Pyrausta nubilalis* larvae in New England

Winter period	Total larvae counted	Total larvae dead	Per cent of larval mortality
1919-20.....	1,231	110	8.9
1920-21.....	1,776	133	7.5
1921-22.....	2,478	233	9.4
1922-23.....	10,100	835	8.3
1923-24 ¹	10,989	440	4.0
Total.....	26,574	1,754
Five-year average.....	6.6

¹ Limited to counts in experimental plats of corn.

Table 31 shows that the average winter mortality for the period was 6.6 per cent. This figure applies to plants which were in a natural position; that is, plants which were standing erect, broken over, or lying upon the surface of the soil. When infested cornstalks or other plant remnants are cut and gathered and placed in large piles during the fall and left in this condition all winter, a considerable proportion of larval mortality sometimes occurs in the interior of such piles when they are exposed to conditions of excessive moisture. It is not possible, however, definitely to attribute this killing to true winter mortality, because other influences, such as mechanical injury during handling or fermentation of the plant material may contribute to this result. In a recent publication (5) Barber discusses the importance of winter mortality in the natural control of the European corn borer in New England.

COMPARATIVE WINTER MORTALITY ACCORDING TO POSITION OF HOST

In the course of experiments carried on during the winter of 1920-21, with the object of ascertaining the comparative winter mortality of larvae in cornstalks standing erect and cornstalks lying upon the surface of the soil, it was found that in the former the winter mortality was 1.5 per cent and in the latter 4.3 per cent. In cornstalks standing erect there was no appreciable difference in the percentage of mortality between larvae inhabiting the lower and upper portions of the stalks.

COMPARATIVE WINTER MORTALITY ACCORDING TO TOPOGRAPHIC LOCATION OF HOST

During the spring of 1921 counts for winter mortality were made in localities representing typical conditions of lowland areas, highland areas, and coastal areas. These counts were all made in cornstalks left in the field of the New England area under natural conditions. According to the figures obtained in these counts, the percentages of winter mortality on lowland areas, highland areas, and coastal areas were 19.9, 16, and 12.8 per cent, respectively. The average winter mortality for the New England area, including larvae from cornstalks and weeds, was 7.5 per cent during this period.

COMPARATIVE WINTER MORTALITY IN PROTECTED SITUATIONS

Reference has previously been made to the habits of certain of the migrating larvae in seeking winter shelter by boring into various wooden objects and by secreting themselves underneath rubbish, clods of soil, loose bark of trees, and similar situations. In order to obtain information concerning the probable percentage of winter mortality among such larvae, a series of experiments were started during the late fall of 1919 in which large larvae were confined in cages containing soil, sawdust, dry manure, dry leaves, dry grass, moss, and wooden objects. Larvae were also confined in an empty wooden box. These cages were kept under a shelter, but otherwise they were exposed to winter conditions. A similar cage of infested cornstalks, kept under the same conditions, was used as a check. The average winter mortality in the test cages was 13.3 per cent and in the check cage 7.6 per cent.

COMPARATIVE WINTER MORTALITY IN DIFFERENT SPECIES OF HOST PLANTS

Table 32 shows the comparative winter mortality of the larvae in different species of host plants left in a natural position in the field during the winter of 1921-22 in the New England area.

TABLE 32.—Comparative winter mortality of larvae of the European corn borer in different species of host plants during winter of 1921-22 in New England

Host plant	Number of localities	Number of larvae counted	Total larvae dead	Per cent winter mortality
Corn.....	9	901	100	11.0
Xanthium.....	5	644	33	5.1
Echinochloa.....	4	273	30	10.9
Polygonum.....	2	150	4	2.6
Bidens.....	2	210	16	7.6
Amaranthus.....	2	200	42	21.0
Chenopodium.....	1	100	8	8.0
Total.....		2,478	233	
Average.....				9.4

According to the data shown in Table 32, there was some variation in the percentage of mortality in different host plants. No explanation can be given for the cause of this apparent variation. The mortality in the weeds in this series of experiments was 8.4 per cent, in comparison to a mortality of 11 per cent in corn.

LARVAL MORTALITY WHEN FROZEN IN ICE

In order to determine the mortality of *P. nubilalis* larvae contained in material frozen in ice, several series of experiments were performed in which infested cornstalks were placed in bodies of water during the late fall in such a position that they were subsequently frozen in the ice. Examinations of the larvae contained in these stalks were made once a month during the period from December to April, and it was found that the mortality for the first three months was practically equal to that of the check material left in a natural position. Beginning from about the 1st of March, however, the mortality of the larvae contained within the frozen-in stalks

increased very rapidly. When the last series were examined during the first week of April less than 1 per cent of the larvae were alive. The heavy mortality occurred, therefore, during the period when the larvae would normally have become active preparatory to pupation.

WINTER MORTALITY OF LARVAE IN STORED MATERIAL⁹

Jablonowski⁹ has recommended, as a possible means of control to be applied to overwintering larvae, the storing of cornstalks in a comparatively weather-tight shed or barn until after the normal time for emergence of the moths the following spring. His idea is that the larvae contained in such stored material would be unable to complete their development when deprived, during the winter and early spring, of the moisture which is available to those larvae overwintering in the normal locations and which is so essential for the completion of histolysis.

The experiments which have been carried out up to the present time to determine the advisability of such a recommendation have shown that when larvae in stalks are stored in the insectary, or even more thoroughly inclosed structures for the winter season, a reduced percentage of them, ranging from 4 to 30 per cent, were able to complete their development, and that these were considerably retarded beyond the normal seasonal development that would be expected in the field.

The percentage of larvae able to pupate and successfully emerge as adults was decreased when stored material was kept under heated, low-humidity conditions, such as those prevailing in a room of the laboratory. As will be discussed in a paper dealing with experiments upon the hibernation period, the cumulative effect of these various conditions of storing not only induces an immediate reaction reflected by increased mortality and delayed pupation but also has the effect of delaying seasonal development during the subsequent growing season. In fact, only 9 per cent of the individuals which for two consecutive seasons had been denied the normal precipitation conditions during hibernation were able to develop the two generations normally occurring in this area.

Larvae without protection of cornstalks, ears, or similar covering seem unable to withstand either of the two conditions just discussed, and usually shrivel and dry up after the long exposure from fall to the following spring.

PUPATION

Pupation normally occurs within the tunnel made by the larva in its host plant. The larvae of the overwintering brood pupate in the tunnels which they have occupied during the winter, unless the condition of the host material in the spring is such that they are forced to migrate and seek similar but more suitable quarters free from extremes of moisture or desiccation. The summer-brood larvae normally pupate not far from the last feeding place in their tunnels. Larvae of both broods may also pupate in protected places on the exterior of their host plant, such as between the silks on the ears of corn, between the leaf sheaths and the stalks, or between overlapping leaf blades of corn or other plants. Full-grown larvae which

⁹ See footnote 1.

migrate to situations removed from the plant and bore into wood or similar material for shelter usually pupate within these shelter tunnels, provided that the moisture conditions of the shelter medium are suitable for pupation. The same statement applies to full-grown larvae which migrate from the plant and secrete themselves in the cracks and crevices of lumber or underneath rubbish of various kinds.

COCOON FORMATION AND LARVAL CHANGES

When preparing for normal pupation the larva first closes the entrance to its tunnel with a thin silken partition and then retreats into the tunnel, where it forms a thin silken cocoon. Larvae which pupate in situations lacking the protection of a tunnel partly or entirely inclose themselves with similar cocoons. Some of the larvae spin such a meager quantity of silk that it is an exaggeration to describe the fabrication thus formed as a real cocoon.

When the cocoon is completed, the larva attaches itself thereto by means of the crochets on the anal legs, and then passes into a short semiquiescent stage preparatory to pupation. During this stage the head becomes inflexed and the use of the thoracic and abdominal legs is lost, while the abdominal segments become greatly swollen and show distinctly the outlines of the pupal abdomen.

PROCESS OF PUPATION

As a result of pressure exerted from within, the larval skin splits along the dorsal line of the head and thoracic segments, and also down each side of the front, thus liberating the emerging pupa. As soon as it is freed from the larval skin the newly formed pupa revolves on its longitudinal axis two or three times, in this manner firmly attaching its cremaster to the cocoon at the point formerly occupied by the anal feet of the larva. Out of a total of 141 pupae under observation in vertical tunnels, 118 individuals formed with the head pointing upward, and the remaining 23 individuals with the head downward. The newly formed pupa is nearly white in color with a longitudinal pink line down the dorsum. Permanent coloration proceeds very rapidly after emergence and in five or six hours the pupa is fully colored. Mature pupae vary from light brown to dark brown in color.

ADULT HABITS

EMERGENCE

The emerging moth pushes off the head of the pupal skin until its head, thorax, and bases of the wing pads are visible. Here it rests for a short period before struggling completely out of the pupal skin. Ten individuals under observation required an average of two minutes for complete emergence. After emergence the moth escapes from its cocoon and crawls to the surface of the plant, provided pupation occurred within a tunnel. After reaching the surface the moth clings to some convenient object until the wings become fully expanded and dried. Within a period of from two to three hours after emergence it is prepared for flight.

PROPORTION OF SEXES

Table 33 gives data relative to the proportion of sexes as recorded from insectary reared material at Arlington, Mass., during the period from 1918 to 1921.

TABLE 33.—*Proportion of sexes of Pyrausta nubilalis at Arlington, Mass. (two generations)*

Generation	Number of individuals	Per cent females	Per cent males
Second generation, 1917-18.....	342	49.5	50.5
First generation, 1918.....	366	57.6	42.4
Second generation, 1919-20.....	221	37.0	63.0
First generation, 1920.....	134	45.5	54.5
Second generation, 1920-21.....	933	48.0	52.0
First generation, 1921.....	45	51.2	48.8
Total.....	2,041		
Average.....		48.7	51.3

Table 33 shows that of the individuals under observation during a three-year period at Arlington, Mass., the sexes occurred in about equal proportions, although in the spring brood the preponderance of males is marked. In each group under observation the males greatly outnumbered the females during the first part of the seasonal emergence period.

Relative to the proportion of sexes in the one-generation areas, the adult emergence from 234 pupae collected at Scotia, N. Y., during the spring of 1920 consisted of 114 females, or 48.7 per cent; and 120 males, or 51.3 per cent. At Silver Creek, N. Y., notes were made upon the sex of 690 adults which emerged during the experimental work throughout the period 1921 to 1924. Of this number 350, or 50.7 per cent, were females and 340, or 49.3 per cent, were males. At Sandusky, Ohio, 53.3 per cent of the adults emerging from experimental material during 1924 were females and 46.7 per cent were males. A total of 809 adults were included in this group. In each group under observation in these areas the males emerged sooner than the females in the proportion of nearly two to one, but as the emergence period advanced the females predominated in numbers.

COPULATION

Copulation usually occurs within a period of 12 hours after emergence from the pupa. During this act the male assumes a position to one side of the female and turns his abdomen at right angles with the body, meanwhile thrusting out the genital organs. When coition is successful, the male assumes a position directly to the rear of the female, the long axis of each being in a straight line. Three pairs of moths under observation remained in copula for an average period of 2 hours and 23 minutes. The moths have been observed in copula at nearly all hours of the day, but this usually occurs during the late afternoon and evening, at which time they are most active.

MATINGS NECESSARY TO FERTILIZE TOTAL COMPLEMENT OF EGGS

A single mating was found to be sufficient to insure the normal percentage of fertility of the total complement of eggs deposited by each female in a series of experiments wherein single pairs of newly emerged moths were confined in separate lantern-globe oviposition cages. Each of these cages contained a virgin female, which had emerged from an individual glass vial cage, and a male which had emerged from similar cage. These cages were kept under observation and as soon as copulation occurred the male was removed. It is not known whether more than one mating normally occurs in the field, but in confinement several matings have been observed in instances where pairs of moths were retained in cages throughout their period of life. The fact that a single mating appears to be sufficient to insure the fertility of the eggs apparently would enable gravid and fertilized females to perpetuate the species if dispersed for a long distance by flight or by carriage.

NUMBER OF FEMALES FERTILIZED BY EACH MALE

In order to determine the number of females fertilized by each male, a vigorous newly emerged male was placed in an oviposition cage with a newly emerged female. As soon as copulation occurred, the male was transferred to a similar cage also containing a virgin female. This process was repeated until the death of the male 19 days from the start of the experiment. During this period the male had mated with nine different females. The total complement of eggs deposited by the second, third, fourth, and sixth females used were fertile, whereas the eggs deposited by the first, fifth, seventh, and ninth females used were infertile. The eighth female died without depositing eggs. The other females in this series deposited a normal number of eggs. It will be noted, therefore, that the *Pyrausta nubilalis* male used in this experiment fertilized a total of four females. Even allowing for cage conditions, it seems probable that under natural conditions each male would fertilize several females.

OVIPOSITION

The average preoviposition period of *P. nubilalis* females in confinement varied from 2.6 to 5.1 days in Massachusetts, as shown in Table 24. Among the females under observation in confinement and in the field, oviposition was greatest during the period between dusk and midnight, and rarely occurred during the daylight hours. The eggs usually are deposited upon the undersides of the leaves of the host plant, although they have been found infrequently on the upper sides of the leaves and upon the stems of plants such as corn, rhubarb, and cocklebur, as well as upon the husks of ears of corn.

During the act of oviposition the female extrudes the ovipositor until its tip comes in contact with the leaf blade at the spot selected for egg deposition. She then stands still and vibrates the abdomen until the spherical egg appears at its tip. The egg is then quickly pushed against the leaf and tamped into place with the ovipositor. This operation changes the egg from its original spherical shape into a more flattened one. The remaining eggs of the cluster are then

deposited in irregular rows, each egg overlapping the adjoining egg in the manner of shingles. The female rarely changes her position during the deposition of an egg cluster, as the flexibility of the abdomen allows quite a radius of movement.

PLANTS PREFERRED FOR OVIPOSITION

Although corn usually is preferred for oviposition, the eggs have been commonly found in the New England area on a variety of other plants, particularly rhubarb, spinach, beets, beans, potatoes, celery, dahlias, hemp, dock, smartweed, barnyard grass, pigweed, and cocklebur. Eggs have also been found occasionally upon most of the other host plants listed in the first three classes shown in Table 1. It has been observed that the moths usually prefer to deposit eggs upon plants bearing relatively large leaves or dense foliage. Doubtless this choice is somewhat influenced by the fact that plants of this character afford protection to moths from the sun and wind during the day. Preference is also shown for that portion of the plant on the lee or opposite side from the prevailing winds. Oviposition is not confined to plants affording shelter during the day, however, as eggs are sometimes found upon young corn plants not more than 6 inches in height. During late May and early June in New England, dock, smartweed, rhubarb, and spinach are the most favored plants for egg deposition by the early emerging females. At this time corn and other preferred host plants are just starting their development.

In the one-generation areas of eastern New York and the Lake Erie region, egg clusters rarely have been found on plants other than corn.

In New England a few egg clusters have been found on plants in which the larvae are not known to feed under natural conditions, namely, dandelion (*Leontodon* spp.), horseradish (*Radicula armoracia*), lettuce (*Lactuca sativa*), plantain (*Plantago* spp.), oxalis (*Oxalis* spp.), and rye (*Secale cereale*).

OVIPOSITION HABITS OF FEMALES IN CONFINEMENT

In confinement the moths frequently deposited eggs upon the interior of lantern-globe cages as well as upon the leaves of susceptible host plants which were provided for egg deposition. When the moths were confined in cages constructed of transparent paper and lacking any vegetation, but which were adequately supplied with moisture, they readily deposited their egg clusters upon the paper walls of these cages. This habit of the moths was utilized to advantage when large numbers of egg clusters were needed for egg-parasite and other studies.

TOTAL NUMBER OF EGGS DEPOSITED BY EACH FEMALE

Judging from oviposition records obtained in confinement, *Pyrausta nubilalis* is very prolific. Tables 34 and 35 show the average, maximum, and minimum number of eggs which were deposited by the females of the first and second generations when confined in lantern-globe cages at Arlington, Mass., for each year during the period from 1918 to 1921, inclusive.

TABLE 31.—Total number of eggs deposited by first-generation *Pyrausta nubilalis* females in New England

	Number of females under observation	Average total eggs per female	Maximum total eggs per female	Minimum total eggs per female
First generation of—				
1918	17	430	901	53
1919	109	378	828	72
1920	50	487	874	72
1921	37	562	1,994	44
Total	213			
Average		448		

TABLE 35.—Total number of eggs deposited by second-generation *Pyrausta nubilalis* females in New England

	Number of females under observation	Average total eggs per female	Maximum total eggs per female	Minimum total eggs per female
Second generation of—				
1917-18	11	344	724	107
1918-19	69	335	1,192	43
1919-20	121	358	895	55
1920-21	17	271	465	4
Total	218			
Average		344		

The average, maximum, and minimum number of eggs which were deposited by the females of *P. nubilalis* in the one-generation areas when confined in lantern-globe cages at Silver Creek, N. Y., and Sandusky, Ohio, during 1923 and 1924, are shown in Table 36.

TABLE 36.—Total number of eggs deposited by *Pyrausta nubilalis* females at Silver Creek, N. Y., and Sandusky, Ohio (one generation)

Place	Year	Total females in experiment	Total eggs deposited	Average total eggs per female	Maximum total eggs per female	Minimum total eggs per female
Silver Creek, N. Y.	1923	50	10,900	218	1,000	12
Do.	1924	50	17,714	354	1,061	12
Sandusky, Ohio	1923	25	8,056	322	661	26
Do.	1924	50	29,250	585	1,075	2

The averages shown in Table 36 were computed from the number of females in the experiment. In the Silver Creek experiments 11 females in the 1923 series and 8 females in the 1924 series did not deposit eggs. In the Sandusky experiments 1 female in the 1923 series and 3 females in the 1924 series did not deposit eggs.

NUMBER OF EGGS PER CLUSTER

The majority of the egg clusters collected in the field in New England have contained from 15 to 20 eggs, although the number of

eggs per cluster is subject to considerable variation. From 1 to 162 eggs have been found in individual clusters. Jablonowski¹⁰, quoting from observations made by his assistant, Gabriel Bako, states that in Hungary "each cluster contained a minimum of from 22 to 35 eggs." Table 37 gives data relative to the average number of eggs per cluster deposited by females in confinement at Arlington, Mass.

TABLE 37.—Average number of eggs of *Pyrausta nubilalis* per cluster, New England, 1918 to 1921

Generation	Number of clusters counted	Average number of eggs per cluster	Average maximum number of eggs per cluster per female
Second generation, 1917-18.....	172	20.0	34.0
First generation, 1918.....	431	17.3	31.6
Second generation, 1918-19.....	1,666	13.9	31.2
First generation, 1919.....	2,884	14.0	33.0
Second generation, 1919-20.....	3,539	12.2	40.0
First generation, 1920.....	3,255	13.0	30.8
Second generation, 1920-21.....	260	19.2	38.7
First generation, 1921.....	1,127	23.4	35.2
Total.....	13,334		
Average.....		14.6	

Table 37 shows that the average number of eggs per cluster varied from 12.2 to 23.4 in the different generations of females under observation, with an average of 14.6 eggs per cluster for the entire series. The last column in this table pertains to the average maximum number of eggs per cluster deposited by any one female in the generation.

At Silver Creek, N. Y., there were an average of 14.5 eggs per cluster in 747 egg clusters deposited in confinement during 1923, and an average of 16.7 eggs per cluster in 1,060 egg clusters deposited under the same conditions in 1924. Comparative figures for Sandusky, Ohio, observations show an average of 14 eggs per cluster in 575 egg clusters during 1923, and an average of 16.8 eggs per cluster in the 1,746 egg clusters upon which observations were made in 1924. A total of 731 egg clusters collected in the field in Ohio during 1924 contained 15.5 eggs per cluster on an average. The average number of eggs per cluster in the one-generation areas of New York and Ohio compares very closely with the average for the two-generation area of New England.

DAILY RATE OF OVIPOSITION

In confinement the daily rate of oviposition varied with different females and according to the temperature conditions. In some instances a single female deposited several egg clusters within a 24-hour period, whereas in other instances a period of several days elapsed between the deposition of successive egg clusters. Table 38 gives data relative to the daily rate of oviposition of females confined in individual lantern-globe cages at Arlington, Mass.

¹⁰ See footnote 1.

TABLE 38.—Daily rate of oviposition of *P. nubilalis* females, New England, 1918 to 1921

Generation	Number of females under observation	Average oviposition period in days	Average number of days during oviposition on which no eggs were deposited		Average number of eggs per day during oviposition period	Maximum eggs deposited on any one day (average)	
			Number	Per cent		Number	Per cent
Second generation, 1917-18.....	11	12.1	3.8	31.4	28.4	87.0	25.3
First generation, 1918.....	17	13.4	4.5	33.6	32.7	119.9	27.3
Second generation, 1918-19.....	68	12.7	4.8	37.8	26.4	96.0	28.6
First generation, 1919.....	109	11.8	4.0	33.9	31.6	123.0	32.5
Second generation, 1919-20.....	121	14.1	4.6	32.7	25.4	80.8	22.6
First generation, 1920.....	92	9.5	1.6	16.8	51.3	153.3	31.5
Second generation, 1920-21.....	17	10.6	4.6	43.4	27.4	68.2	23.5
First generation, 1921.....	42	13.0	3.4	26.1	52.3	142.4	20.9
Total.....	477						
Average.....		12.2	3.7	30.3	34.7	113.1	26.3

The data given in this table show that for approximately one-third of the days of the oviposition period the moths under observation did not deposit any eggs and that an average of from 22.6 to 32.5 per cent of the eggs were deposited in one day by moths of the different generations.

Approximately 23.7 per cent of the moths of the second generation 1919-20 series, shown in the table, deposited the greatest number of eggs per day during the first day of their oviposition period, whereas 55.1 per cent of such moths deposited the greatest number of eggs per day during the first five days of their oviposition period. One individual of this series deposited 330 of her total complement of 517 eggs on the first day of her oviposition period, and the remaining eggs were deposited throughout a period of 14 days. The average duration of the oviposition period of this series of moths was 14.1 days. In the 1920 series of first-generation moths 42.4 per cent deposited the greatest number of eggs per day during the first day of their oviposition period, whereas 81.5 per cent of these deposited the greatest number of eggs per day during the first five days of their oviposition period. The average oviposition period of this series of moths was 9.5 days.

The long period of fertility of the moth is important because it results in larvae of several instars being present in the same field, and often on the same plant simultaneously, thus causing a difficulty in evolving control measures having for their objective the destruction of the young larvae before they enter the plant. This fact also increases the opportunity of dispersion by flight or carriage of the gravid females.

FLIGHT

The moths are essentially nocturnal in habit, although individuals have been observed taking short flights during daylight. Normally, however, they seek shelter during the day underneath the leaves of weeds, grasses, and cultivated crops. They are often found lurking in the grass headlands adjacent to fields of corn and other crops. When disturbed during the day, they make short flights, close to the ground, for distances of from 10 to 20 feet, and eventually seek cover again.

The moths are most active during warm nights and comparatively inactive on cool or cold nights or during heavy winds. The daily period of greatest flight activity begins shortly after dusk and does not materially decrease until after three or four hours of darkness. Only a few moths have been observed in flight during the later hours of the night, although this observation may have been influenced by the difficulty of observing the moths at this period. During the month of June the moths were most active in laboratory cages from 9 p. m. until about 11 p. m. and more or less active until 4.30 a. m.

The flight of the sexes is somewhat different in character. Since the female is heavier her flight is direct, while that of the male is more rapid and of an erratic zig-zag character.

DISTANCE OF FLIGHT

In the course of experiments to determine the flight abilities of the moths it was found that both sexes possess the power of sustained flight for considerable distances either in single flights or in a series of flights. Flight usually occurs in the direction of the prevailing wind, although moths have been observed flying against a light wind.

Previously it has been stated that when dislodged during the day the moths usually fly only a few feet before seeking shelter. During their daily period of active crepuscular flight, however, certain of the moths fly much longer distances, although it was not possible accurately to gauge the distance of such flights because of the dim light. In order, therefore, to obtain indicative information regarding the flight capabilities of moths in single flights it was necessary to liberate moths during the day in situations where shelter was absent. For this purpose a stretch of low, wide, sandy beach was selected, which was devoid of shelter within 200 yards, and moths of both sexes were liberated at the edge of the water during low tide at a time when a light breeze was blowing off the water. Under these conditions individual moths were traced in single flights in the direction of the prevailing breeze for a maximum distance of 258 yards and to an elevation of approximately 50 feet before they were lost to view. All of the moths used in this experiment took flight directly after liberation and flew rapidly with the prevailing breeze, gradually ascending to elevations of from 15 to 50 feet before being lost to view. At this point they were flying strongly, and it seems probable that they covered at least 300 yards from the point of liberation before alighting.

In these and in similar experiments, little difference was observed between the flight capabilities of the sexes. The males as a rule took flight quicker than the females after liberation and flew more rapidly, but the females were more direct in their flight and appeared to cover at least an equal distance. All of the females used in these experiments were gravid.

FLIGHT EXPERIMENT ON CAPE COD

Prior to the summer of 1921 several experiments, having for their object the recovery of artificially stained moths liberated from a central point, had shown that the moths were capable of a total

flight of at least three-fourths of a mile. It was believed, however, that these experiments did not indicate the real limits of dispersion of the moths by flight, keeping in mind their relatively long period of life and the distance which they have been observed to fly in single flights. In order, therefore, to obtain additional information upon this point, a total of 8,650 moths stained with an aqueous solution of carbol fuchsin (acid) were liberated from a central point at Truro, Mass., on Cape Cod, during August, 1921. This region was selected for the experiment on account of the open nature of the country and the fact that areas of corn and other favorite host plants were few and far between. Although there is no evidence at present to indicate that high hills, large bodies of water, or densely wooded areas are barriers to the flight of the moths, yet it seemed advisable to select a region having as few of these potentially limiting factors as possible. The selection of Truro as the point of liberation was also influenced by the fact that the prevailing winds during August are from the southwest, which fact probably would influence the flight of the moths toward the open country to the northward, between Truro and Provincetown, 9 miles distant.

Recovery of the stained moths was attempted by systematically sweeping all susceptible plants and other vegetation likely to be frequented by the moths, in the surrounding country. The territory examined included that portion of Cape Cod lying north of Wellfleet. From the point of liberation it extended 10 miles northwest to the tip of the cape, 2 miles east to the ocean, 5 miles south, and 1 mile west to the ocean. As previous experiments had resulted in the recovery of the moths at a maximum distance of nearly a mile from the point of liberation, no examinations were made within this limit.

Table 39 gives the results of this experiment.

TABLE 39.—*Result of experiment in sweeping stained Pyrausta nubilalis moths on Cape Cod, Mass.*

Direction	Maximum distance of examinations from point of liberation	Recoveries			Remarks
		Number of moths	Sex	Distance from point of liberation	
North.....	Miles 3.5	1	Female	Miles 3.0	Gravid. Swept territory to ocean beach.
Do.....	3.5	1	do	2.4	Not gravid.
Do.....	3.5	1	do	2.6	Gravid.
Northwest.....	10.0	1	Male	2.7	
Do.....	10.0	1	do	2.8	
Do.....	10.0	1	Female	4.7	Do.
Do.....	10.0	1	Male	5.0	
Northeast.....	2.0	None.			Swept territory to ocean beach.
East.....	2.0	None.			Do.
Southeast.....	5.7	None.			Do.
South.....	5.0	None.			
Southwest.....	2.3	None.			Do.
West.....	1.0	None.			

From this table it will be noted that, under the conditions of the experiment, moths of both sexes were recovered at a maximum distance of about 5 miles from the point of liberation, and that three

of the moths recovered were gravid. During the period when this experiment was in progress the direction of the prevailing wind at the point of liberation was from the south and the southwest. This is believed to have influenced the flight of the moths in a general northerly direction, and may explain the failure to recover moths beyond the 1-mile limit at any other points of the compass.

Although 5 miles was the maximum distance at which a stained moth was recovered in this experiment, it is believed that they are capable of dispersing to greater distances during a single flight, or in a series of flights, under favorable wind conditions. In the summer of 1922 a similar experiment indicated that adults were capable of flights of at least 20 miles over water.

EFFECT OF NATURAL BARRIERS ON FLIGHT

It does not appear that ordinary natural barriers such as high hills, densely wooded areas, or bodies of water, constitute any appreciable barrier to the flight of the moths.

Although there is a tendency for the moths to disperse along valleys and areas of low ground, they have also been observed in active flight on the tops of high hills. Cornfields situated on the tops of hills west and north of Boston, Mass., at an elevation of from 200 to 400 feet, have in some instances been found to be infested to at least an equal extent with the cornfields on lower ground in the immediate vicinity. It is problematical whether the moths would be able to make flights over high mountain ranges.

Relative to the efficiency of densely wooded areas as barriers to flight, in some instances fields of corn which were totally or partially surrounded by wooded areas were infested to a lesser degree than fields in the vicinity which were not so situated. This apparent protection, however, was by no means universal, as certain other fields situated amid similar surroundings were found to have an average infestation for the vicinity. In one case moths were observed in flight during the late afternoon among the trees between the open spaces of a wooded area, approximately 300 yards wide, which separated two large cornfields. It was not possible actually to trace individual moths through these woods from one field to the other, but evidently this strip of woodland was not acting as a barrier to flight.

Judging from experimental observations, ordinary bodies of water do not act as barriers to the flight of the moths. During the progress of preliminary observations to determine this point, moths of both sexes were liberated from a boat during the daytime at a point in the center of a lake at Arlington, Mass. These moths, without exception, flew rapidly with the prevailing wind toward the nearest shore, approximately 800 yards distant, and were soon lost to view. When moths were experimentally placed upon the surface of the water they rode the waves for a few minutes, but after a few struggling movements of the legs and wings they took flight in a normal manner. Moths which were experimentally plunged beneath the surface of the water immediately came to the surface and eventually took flight. When moths were liberated at the edge of the water during a strong offshore wind, about 15 to 20 miles per hour, they attempted to fly inland against the wind, but in almost every instance

they were borne aloft during their struggles and eventually carried over the water. In this experiment the moths were liberated upon a strip of ocean beach affording no protection from the wind, whereas in a similar experiment where a beach protected by a steep cliff approximately 50 feet high was selected, some of the moths succeeded in fighting their way back to land and disappeared over the edge of the cliff.

As a continuation of the investigations to determine the effectiveness of large bodies of water as barriers to the flight of the moths, as well as to determine their flight capabilities, a total of 60,988 stained moths were liberated at Manomet Point, Plymouth, Mass., during the period from June 5 to July 23, 1922. These liberations were made only while the wind was blowing offshore (southwest to southwest by west) toward the tip of Cape Cod (Provincetown). Before liberation the moths were stained with an aqueous solution of carbol fuchsin (acid) applied as a fine spray. The majority of the moths had recently emerged from a large collection of cornstalks and weeds kept in a barn near by, which had been altered to serve the purpose of an insectary. The sexes were about equally represented. At the Provincetown end three crews, comprising a total of 12 men, systematically swept all corn and other vegetation likely to be used as a shelter by the moths during the day, throughout that portion of Cape Cod extending from the tip of the cape to the village of Orleans. Especial attention was given to the cultivated fields and waste areas in the vicinity of Provincetown and Highland Light. During the progress of this sweeping a total of 474 adults were found, but only one, a male, showed unmistakable evidence of the stain. This male was collected in corn on Bradford Street, Provincetown, on July 18, at an air-line distance of approximately 20 miles (fig. 47) across Cape Cod Bay from the point of liberation. From observations made at the time of liberation it was noticed that during the prevalence of strong offshore winds, reaching at times a velocity of 30 miles per hour, the moths attained a height of 50 feet or more, immediately after liberation, before being carried beyond the range of vision by the wind. Owing to the height attained and the influence of the wind, it seems possible that many of them were unable to alight when reaching Cape Cod, and were carried out to sea.

From what has been shown, it is evident that the moths are able to make flights to a considerable distance over bodies of water and that when necessary they are able to alight upon the surface of the water and again take flight. This facility may be an important factor in the dispersion of the insect along the Atlantic coast and in the Lake Erie region.

FEEDING HABITS OF ADULTS

In captivity the moths have been observed sipping the pure water, and also the sweetened water, which was sprayed on the plants and soil in their cages. Whether they feed under natural conditions has never been observed, but they have lived as long and deposited as many eggs in the cages where pure water was supplied as in the cages where sweetened water was substituted. The moths in captivity fed to a slight extent on honey and also upon the

juices of various fresh and decaying fruits, but when these substances were used under natural conditions in an effort to attract the moths, only negative results were obtained. In Hungary Jablonowski¹¹ observed large numbers of *P. nubilalis* moths swarming, in

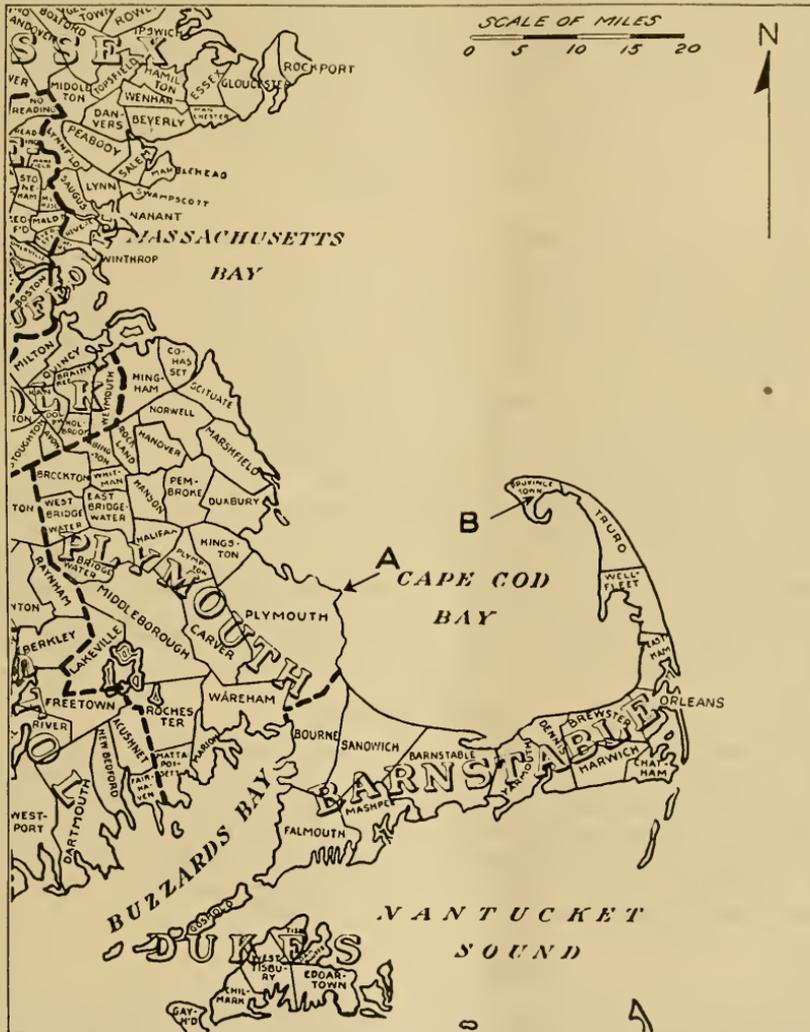


FIG. 47.—Map showing scene of flight experiment across Cape Cod Bay in 1922. A, liberation point. B, recovery point

the dusk of the evening, over blossoming fields of clover, alfalfa, and potatoes. His explanation of this occurrence was that the moths were drinking the dew found on the leaves and flowers by night. It is also possible that the moths were sipping nectar from the flowers of these plants.

¹¹ See footnote 1.

PHOTOTROPISM

Repeated observations in New England with various types and colors of lights have failed to show that *Pyrausta nubilalis* moths were attracted to artificial lights to any extent, even though these observations were carried on in fields where the moths were very numerous and during their seasonal period of greatest activity. Gasoline and kerosene lanterns, acetylene lights, and electric lights of white, yellow, blue, green, red, and violet were used in these experiments. During June, 1920, a gasoline trap lantern was suspended 8 feet above the ground and run for 20 consecutive nights in a cornfield at Watertown, Mass., where hundreds of these moths were in flight. During this period 87 moths were captured, consisting of 57 males and 30 females. This result was typical of similar experiments in which were used kerosene trap lanterns with yellow, white, blue, green, and red colored globes at distances of from 2 to 8 feet above the ground. Practically the same results were obtained with uncolored acetylene lights and with electric lights of white, yellow, blue, green, red, and violet. Three 100-candlepower nitrogen bulbs were used in each of the electric trap lights. Judging from the comparative number of moths captured at the different colored lights a slight preference was shown for white and yellow lights. The proportion of males captured usually was greater than that of the females. Most of the latter were gravid.

Little difference was noted between the comparative attractiveness of moving and stationary white lights.

Jablonowski¹² records an observation by L. Baross, of Bankut, Hungary, in which 80 per cent of the total Lepidoptera captured at acetylene trap lights during the period from June 24 to July 7, 1904, were *P. nubilalis* moths. The exact number of moths captured and the proportion of sexes were not recorded.

CHEMOTROPISM

The moths were not attracted to various sirups, fresh or decaying fruit, honey, stale near beer, or to various aromatic oils. These baits were placed in wire-screen cylinders and inclosed in Shaw moth traps, the sides of which were coated with sticky tree-banding material in such a manner that any moths attracted to the bait would be captured. The traps were suspended in cornfields where the moths were numerous, but with negative results.

SEXUAL ATTRACTION

Although it is apparent that the attraction between the sexes of *Pyrausta nubilalis* must be highly developed, the phenomenon of assembly does not appear to be as pronounced as that exhibited by many other Lepidoptera. Only occasional males were attracted, at any hour during the day or night, to large screened inclosures in the laboratory yard at Arlington, Mass., where several hundred females were emerging daily, although large numbers of males were present in the immediate vicinity. In field tests seven wire-screen assembly cages containing newly emerged virgin females were erected in fields where the moths were numerous. Fresh virgin females were placed in the cages at intervals of two or three days and the

¹² See footnote 1.

older ones removed. These cages were in operation for an average period of 18 days, and during that period an average of only five males per cage were caught in the coating of sticky tree-banding material with which the surfaces of the cage and its support were covered, although large numbers of males were observed in the immediate vicinity. Most of the captured males were attracted to these cages within 24 hours after fresh females were added. During the progress of the flight experiments discussed in preceding paragraphs an attempt was made to recover the stained males by employing a similar cage but with negative results.

DISPERSION

The principal factor contributing to the long-distance dispersion of *Pyrausta nubilalis* is the transportation of infested plant products or plant remnants. After the insect becomes established in an area local dispersion also occurs by means of flight or carriage of the moths, and in some instances through the drift of infested plant material in water.

ARTIFICIAL DISPERSION

Mention has previously been made of the probability that the European corn borer originally gained entrance to North America in shipments of raw broomcorn (fig. 2) from Italy and Hungary: a probability that was apparently confirmed when commercial shipments of this material, received at the port of New York during February and March, 1920, in April, 1922, and again in March, 1923, were found by inspectors of the Federal Horticultural Board to be infested by *P. nubilalis* larvae. This occurrence illustrates the ease with which the insect may be transported for great distances, especially during its larval period; and from what has already been stated concerning the ability of the larvae successfully to complete their development under adverse circumstances, it is apparent that at least a small percentage of the individuals contained in such material may transform to adults and start new infestations, provided they are able to gain access to any of their many host plants.

The great variety of plants infested by the insect, and its habits with relation to these plants, also contribute to the danger of dispersion by common carrier. This danger is especially pronounced in the instance of the shipment of infested ears of sweet corn in the roasting-ear stage, corn on the cob, cornstalks used as packing material or otherwise, broomcorn (including all parts of the stalk), the stalks of all sorghums, and Sudan grass. In New England the plant products likely to be infested during certain periods of the year and which commonly enter commerce include, in addition to the above, celery, green beans in the pod, beets with tops, spinach, rhubarb, oat and rye straw as such or when used as packing material; also cut flowers or entire plants of chrysanthemum, aster, cosmos, zinnia, hollyhock, gladiolus, and dahlia. In some instances larvae or pupae have been found in the cracks and crevices of boxes or other containers which had been used in shipping infested vegetables. These containers are permanent equipment of farmers and produce dealers, and are used in turn for shipping a great variety of vegetable products. Unless carefully inspected, they may serve as a means of dispersing the insect.

Quarantine restrictions are now in force prohibiting the transportation of the above products, or their containers, outside the limits of areas known to be infested, except when duly inspected and found to be free of infestation by the European corn borer. The activities in connection with the quarantine will be discussed in a separate publication.

TRANSPORTATION OF ADULTS

No direct evidence has been obtained relative to the transportation of the moths on trains, autos, and other vehicles, but it is believed that this factor may contribute to the dispersion of the insect. In the New England area the waste places adjacent to railroad yards are commonly overgrown with favorite weed hosts of the insect, and in some instances such weed areas are very heavily infested. It is possible that the moths which habitually seek protection from the direct sunlight might alight upon cars standing upon these tracks and later be carried to distant points. There is the same danger, though perhaps to a lesser degree, when autos and other vehicles halt along the roads adjacent to infested cornfields and weed areas. In experimental tests wherein moths were liberated inside an auto during the early evening, two moths which alighted upon the outside of the machine remained in this position until the auto had traveled distances of 3 and 5 miles, respectively, from the starting point. Under similar conditions two moths which alighted upon the inside of the auto remained in this position until 12 and 19 miles, respectively, had been covered.

GARBAGE

During the summer and early fall the kitchen garbage from hotels, restaurants, private homes, and the like may contain living larvæ or pupæ in ears or cobs of sweet corn, or portions thereof, which have been discarded after purchase on account of the presence of the insect. Larvæ are also frequently present in the husks, silk, undeveloped tips and ear stems. These portions are commonly removed from sweet-corn ears before cooking and thrown into the swill container. Other plant material which frequently harbors the insect and which is commonly discarded during preparation for the table include the outer stalks of celery, and injured portions of beet tops, rhubarb, Swiss chard, spinach, and string beans. Garbage of this character may act as a vehicle for the insect, as it is frequently transported considerable distances for use as food for pigs or disposal otherwise. Under these conditions the larvæ may escape en route, or before the garbage is disposed of. Corncobs which have been thrown into pigpens, and subsequently removed when cleaning out the pens, have been found to contain living larvæ. Garbage is sometimes thrown into streams or bodies of water which may carry such material long distances through the influences of currents, wind, or tide.

Collections of garbage made during the summer, fall, and spring very frequently contain quantities of infested material consisting of cornstalks, and the remnants of other crops, flowering plants, weeds, and similar plant material which have been collected during the process of cleaning up kitchen gardens. This material is usually hauled to a public dump, and unless promptly burned or otherwise destroyed becomes a source of infestation to the surrounding terri-

tory. Sometimes this material is dumped along the edges of flood levels of streams or bodies of water, with the consequent danger of its dispersion. Infested cornstalks and other plant material containing living larvae have been found distributed along the beaches of New England and also upon the shores of an island several miles from the mainland. Infested material of this kind has also been found distributed along the shore of Lake Erie on the Canadian side.

WASTE PRODUCTS

The refuse from canning factories using sweet corn from infested fields commonly contains large numbers of living larvae or pupæ. This refuse usually consists of the cobs, husks, silk, ear stems, and ears on which the kernels are not properly developed, or which are affected by insects or plant diseases. Most of this infested material is hauled away by farmers, often to points outside the infested



FIG. 48.—Waste from canning factory dumped at edge of field. Many of these sweet-corn cobs were infested. They should be collected when dry and burned. Silver Creek, N. Y., September, 1920

area, and fed to livestock or used as fertilizer. Under these conditions an opportunity is afforded for any borers contained within the materials to escape en route, and others may escape after reaching the farm (fig. 48), thus starting new infestations.

Reference has previously been made to the danger of dispersing the insect in refuse from broom factories. During the process of manufacturing brooms, sections several inches long are usually removed from the butts and discarded. The European corn borer has been found commonly in that portion of the plant comprising the butt in broomcorn grown in Massachusetts and also in the butts of raw broomcorn imported from Italy and Hungary. This refuse may become a source of danger, especially when dumped along the banks of water courses. The original infestation along the Mohawk River in eastern New York is supposed to be directly traceable to infested refuse from a broom factory at Amsterdam.

NATURAL DISPERSION

FLIGHT OF ADULTS

From what has been stated concerning the flight and oviposition habits of the moths, together with their long period of life, it is evident that dispersion by flight is an important factor. It has been shown that the moths of both sexes are possessed of strong powers of flight and that they have been observed making single flights of nearly 300 yards. The duration of adult life as shown in Table 24 averages approximately between 14 and 20 days for both sexes, thus giving the moths ample opportunity for wide dispersion in a series of flights, even if each flight was of short duration. In experimental tests individual moths of both sexes were recovered at a maximum distance of 5 miles on land and 20 miles by water from the point of

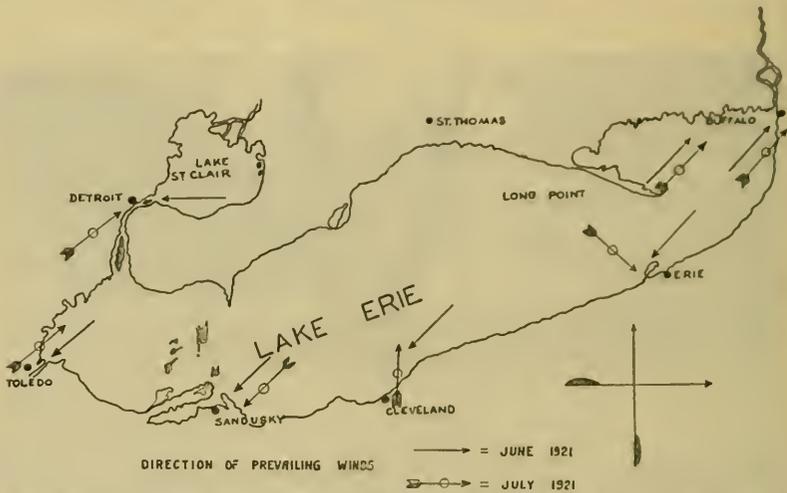


FIG. 49.—Map of Lake Erie, showing direction of prevailing winds at principal lake ports, from Weather Bureau records, during June and July, 1921. Arrows fly with the wind

liberation in the direction of the prevailing wind, indicating that they are able to disperse to at least this distance and probably for greater distances under favorable conditions. The duration of the oviposition period of the females in New England as shown in Table 24 averages approximately between 10 and 14 days, and by reference to Table 38 and the discussion concerning the daily rate of oviposition it is seen that the egg clusters are well distributed throughout the oviposition period. This affords an opportunity for the females to deposit eggs at practically any point to which they may disperse.

In New England, and to a more limited extent in the eastern and western New York areas of infestation, the dispersion has been greatest in a general northerly direction. It appears that this direction of dispersion may have been influenced by the fact that during the flight period of the moths the prevailing winds are from the southwest. The transportation of infested plant products or plant remnants and the drift of infested material by water must also be considered as probably affecting the direction of dispersion.

The flight of moths from the older and much more heavily infested area in Ontario is believed to be the most plausible explanation of the origin of the infestation along the shore of Lake Erie in Michigan, Ohio, and Pennsylvania, and on the islands in the western end of the lake, although no conclusive evidence of this method of introduction has been established. The possibility that this infestation originated from the drift of infested plant material in the waters of the lake or from the shipment of infested plant products must also be considered. A study of the available wind records of the Lake Erie weather stations for the period 1916 to 1921 showed that during the flight period of *Pyrausta nubilalis* the prevailing winds were from the southwest, which fact would apparently prevent the possibility of the moths flying toward the southern or western shore of Lake Erie, but on certain days of that period, particularly during 1921, when infestation was first found in the American areas in question, the directions of the winds and of occasional summer gales were from points north (fig. 49), which would aid the moths in any flight toward the American side. According to Crawford and Spencer (72) the flight period of the moths in Ontario extended from approximately June 16 to July 25 in 1921. During this period the prevailing winds, particularly during June, blew directly from southern Ontario toward the southern and western shores of the lake. (See map, fig. 1.) Although the direction of the prevailing winds during July, 1921, was from the southwest at most of the lake stations where wind records were available, at Erie, Pa., the prevailing winds were from the northwest, or from the direction of the infested areas of Ontario. Moreover, there were gales from the northwest at some of the other southern and western lake stations during this month, as shown in Table 40.

It is apparent from the information shown in Table 40 that there was an unusual amount of wind movement from the north and east during June and July, 1921, as compared with previous years. The fact that the original infestation in Ohio and Michigan was confined to the islands and the townships bordering the lake, and that this infestation followed an unusual amount of wind movement from the direction of the infested areas in Ontario, would appear to indicate the probability of wind spread from Ontario as the causative agent.

TABLE 40.—Direction and velocity of wind movement in Lake Erie region during June and July, 1916 to 1921, inclusive

Locality	Year	June				July			
		Prevailing wind direction	Gales (maximum velocity)			Prevailing wind direction	Gales (maximum velocity)		
			Velocity	Direction	Date		Velocity	Direction	Date
			<i>Miles per hour</i>			<i>Miles per hour</i>			
Long Point, Ont.-----	1916	SW.	37	SW.	2	SW	31	W.	31
			36	E.	6				
			32	E.	7				
	1917	SW.	37	SW.	3	SW	35	SW.	1
			34	SW.	29		33	SW.	29
	1918	NW.	41	SW.	11	SW.	37	NW.	1
			32	NW.	12				
			37	S.	21				
			32	N.	23				
	1919	NE.	33	NE.	28	SW.	33	SW.	10
							32	NW.	23
	1920	SW.	30	N.	5	SW.	30	SW.	23
			31	NE.	17				
			37	SW.	21				
Buffalo, N. Y.-----	1921	SW.	31	NE.	1	SW.	None.		
	1916	SW.	58	SW.	9	SW.	42	SW.	2
	1917	SW.	68	SW.	13	SW.	72	NW.	9
	1918	SW.	60	NW.	11	SW.	60	SW.	1
	1919	SW.	37	W.	5	SW.	47	SW.	10
	1920	SW.	56	W.	29	SW.	56	W.	23
	1921	SW.	46	SW.	11	SW.	44	SW.	28
Erie, Pa. (169 feet) ¹ -----	1916	SE.	52	SW.	24	S.	43	W.	8
	1917	SW.	46	SW.	3	SW.	44	SW.	13
	1918	S.	42	SW.	11	S.	42	W.	1
	1919	NE.	34	NE.	28	NE.	46	W.	10
	1920	W.	41	W.	21	NW.	43	W.	18
	1921	NE.	37	W.	13	NW.	36	W.	27
Cleveland, Ohio.-----	1916	S.	39	W.	16	NE.	44	NW.	2
	1917	SW.	58	NW.	23	S.	36	N.	27
	1918	NE.	43	W.	12	NE.	48	NW.	12
	1919	NE.	39	NE.	28	NE.	36	N.	15
	1920	SW.	23	W.	16	SW.	44	N.	18
	1921	NE.	35	NE.	4	S.	46	NW.	14
Sandusky, Ohio.-----	1916	SW.	38	W.	2	E.	39	NW.	20
	1917	SW.	38	NW.	19	SW.	34	E.	21
	1918	SW.	40	W.	30	NE.	46	NW.	29
	1919	W.	26	NE.	21	NE.	42	NW.	9
	1920	SW.	38	NE.	17	SW.	33	NE.	25
	1921	NE.	35	NE.	3	SW.	42	W.	30
Toledo, Ohio (243 feet) ¹ -----	1916	SW.	45	SW.	2	NE.	48	NW.	20
	1917	SW.	48	SW.	7	SW.	41	SW.	1
	1918	SW.	44	SW.	1	W.	40	W.	1
	1919	SW.	45	SW.	19	SW.	47	NW.	9
	1920	SW.	38	W.	21	SW.	44	SW.	8
	1921	NE.	39	W.	27	SW.	56	NW.	29
Detroit, Mich. (256 feet) ¹ -----	1916	S.	37	W.	2	(?)			
	1917	SW.	46	W.	2	(?)			
	1918	E.	44	W.	1	(?)			
	1919	E.	38	N.	20	(?)			
	1920	W.	35	SW.	28	(?)			
	1921	E.	40	NW.	27	SW.	56	SW.	27

¹ Elevation of anemometer.² No data.THE WATER-DRIFT THEORY OF DISPERSION ¹³

The water-drift theory in the dispersion of the European corn-borer has resulted from attempts to explain the spread of this insect in the Lake region of the United States during the years 1919, 1920, and 1921 and about the shores of Lake Ontario during subsequent years. This theory, although difficult to prove, must be considered together with the flight-of-moths theory of dispersion about these

¹³ Prepared by Geo. W. Barber, assistant entomologist.

Lakes, because either one or both of these methods of dispersion may have been in a large measure responsible for this spread, and each may have a very important bearing on the future dispersion of this insect in the United States.

The spread of this insect in the Lake region of the United States, which is believed to have had as a center the large infestation in south-central Ontario, Canada, was found by scouting records to have been as follows: The earliest discovered infestation in this area was a section southwest of Buffalo, N. Y., embracing 13 townships, and the township of Girard, Pa., found to be infested in 1919. In 1920 13 additional townships in the vicinity of the larger infestation near Buffalo were added, and during the same season a large infestation was found in south-central Ontario, bordering Lake Erie, together with a small strip bordering the lake just west of Buffalo (fig. 50). In 1921 a most important infestation was found comprising a narrow strip of territory almost completely surrounding the southern shore of Lake Erie and including the islands situated near Sandusky, Ohio. The spread of the insect in this area since 1921 has been largely an advance inland from the southern shore of Lake Erie, a great spread northward in eastern Michigan, and a spread to the shores of the western half of Lake Ontario (fig. 1).

If there is any possibility in the water-drift theory, it is important that it should be discussed at the present time (1924) when the spread of the insect in Ohio has in some localities already crossed the crest of the watershed toward the south. In this direction lie great chains of rivers, large and small, emptying into the Ohio River, and it, joining the Mississippi, opens up the great valleys of these waterways, containing some of the richest, most valuable, and important agricultural lands in this country, to possible infestation by this dangerous insect. It is not difficult to picture infested cornstalks being carried, first into the smaller streams by means of the spring thaws, thence into larger streams, eventually into the Ohio or the Mississippi, and finally being cast on the bank of one of these rivers, possibly hundreds of miles from the place of origin, there to dry in the spring sunshine, the insect developing, finding food plentiful, multiplying, and perhaps eventually causing a large and important infestation before being discovered, too late to undertake measures for complete eradication.

At present there seem to be five important points where water drift in relation to dispersion in the near future may prove of great importance: (1) Through the tributaries and head waters of the Ohio to the great river valleys already mentioned; (2) through the Michigan streams flowing into Lake Michigan, thence to the shores of Wisconsin and Illinois; (3) from Lake Erie or Lake Ontario into the St. Lawrence; (4) from the isolated infestation about Albany, N. Y., down the Hudson, and not only menacing the banks of the Hudson, but also threatening the shore of New Jersey, should infested material be finally thrown into the ocean; and (5) in New England, where the infestation in Massachusetts and New Hampshire is spreading toward the Connecticut Valley, cornstalks may be carried down the Connecticut River, endangering the lower Connecticut Valley, in Massachusetts and Connecticut, an important farming section.

A further reason for apprehension concerning the possibilities of this means of spread lies in the increase in the intensity of the infesta-

tion at the probable centers from which such spread may proceed. If there is only a light infestation at these points—for example, if cornstalks average only one individual per stalk—the element of chance may result in drifting stalks being cast on shore singly. The ability of the individual from such a cornstalk to produce progeny will naturally depend upon whether an individual of the opposite sex is to be found. When the infestation at the center of the spread is of more than a single larva per stalk, a new infestation may result from a single cornstalk thrown on shore, since the larvae it contains may result in several adults of each sex. While in the first instance the carrying of cornstalks by water drift may rarely result in new infestations or in infestations only in localities where several stalks have been thrown on shore together, in the second case infestations are much more likely to result. Furthermore, in the case of cornstalks being carried long distances by water, many of the larvae contained in such stalks may perish before the stalks are cast on shore, but in this case the chance of larval survival and resulting infestation is increased in proportion to the rate of the infestation of such cornstalks.

Another reason for apprehension as the infestations increase in intensity lies in the breakage of cornstalks because of the feeding of larvae of this insect. Heavily infested stalks break over much more easily than stalks containing only a few larvae, and for this reason they would be much more likely to be swept away by rains or floods in the spring.

A case illustrative of this condition may be mentioned in regard to the isolated infestation of the insect in eastern New York around Albany. The question has been asked, if water drift is an important means of dispersion, why has no infestation appeared along the lower Hudson to indicate a distribution of this sort from the Albany area? There are two facts that may be offered in reply: (1) The infestation in the Albany area has never been heavy as compared with New England infestations, so that the conditions favorable to the establishment of a new colony, as described in the two preceding paragraphs, may not have obtained; (2) the discovery of a new infestation, when individuals are few and scattered, is by no means a simple matter, and although repeated and careful scouting has failed to bring to light any infestations indicative of water spread along the Hudson, this is not necessarily proof that such infestations may not eventually be found.

Because it is necessary to face this danger if it exists, the arguments that seem to support the water-drift theory in the dispersion of the insect about Lake Erie are presented, together with remarks on the infestation in New England. What factors caused the distribution of the insect about Lake Erie are now of minor importance, since the infestation is already general, but it is important that the evidence be examined to the end that if it is possible a repetition of this occurrence may be prevented.

The discovery during 1921 that a narrow band of infested territory (fig. 50) practically surrounded Lake Erie on the American side was rather remarkable. Although the discovery of the infestation during that year was not proof that such infestation had originated during that or the preceding year, the evidence indicated that the infestation was not of long standing and had probably originated during 1921.

It is very difficult to obtain exact information on the flight habits of the adults of this insect, especially because natural flight occurs at night, and what is now known concerning the detailed habits of flight has been obtained during the hours of daylight when flight of the insects is possibly somewhat abnormal. One theory concerning air currents that pass over a body of water is that they tend to drop objects that they are carrying on reaching land. This theory would help to explain the regularity in which early infestations on the southern shore of Lake Erie followed the shore line, had air currents or winds played an important part in this distribution of the insect. But even if this were true, the possibility that water drift was of equal importance in dispersion about the lake still exists.

Certain of the factors that support the water-drift theory of distribution of this insect about Lake Erie may now be considered.

THE NEW ENGLAND INFESTATION

The New England infestation is fairly illustrative of the possible spread of the insect by water drift, particularly as applied to Cape Cod. The early infestation on Cape Cod was principally on the northern shore, or that joining Massachusetts Bay, facing the original New England infestation of this insect, as it has been conceived, and where the most severe infestation is found to-day. Had water drift played no part in this infestation, it seems remarkable that the infestation should develop in this way. The northern shore is a much poorer agricultural section than is the southern part of Cape Cod, yet in the southern part the infestation has been slow in developing and is of much less intensity. The infestation here, then, has developed in the way that would be expected, had water drift played an important part in dispersion. Had flight of moths played an important part in this spread, it seems improbable that so large a proportion of them would have been able to descend so soon after reaching land, but that many would have been carried either farther inland on the cape, or completely over it, and thence out to sea. In this connection it may be remarked that the distance that the moths would have been carried by such winds would have been somewhat less than half the distance from the probable original seat of infestation across Lake Erie. The shipment of infested vegetables to summer resorts as a means of dispersion of the insect is often mentioned in this case, but although this factor has undoubtedly been of importance, it must be said that the large summer resorts on Cape Cod are on the south shore, whereas the important infestation of the insect has been found on the north shore. That infested cornstalks do float out into Massachusetts Bay has been proved by several examinations of the islands in Boston Harbor. In 1920 a thorough examination of one of the larger of these islands (Inner Brewster Island) showed that the only infestation on the island at that time was in a single plant of cocklebur which contained several larvae. This plant was growing on an arm of the island extending toward the mainland, and on which considerable quantities of refuse had been thrown by the sea. The following year a second examination of the island showed that the only larvae then present were contained in a piece of drifted cornstalk that, together with a considerable quantity of refuse, had been cast on the island, curiously

enough, in nearly the exact spot on which the infested cocklebur had been found the preceding year. This island is situated about a mile from the nearest mainland, so that this cornstalk may have been carried by the water for this short distance or for a much greater distance, it being impossible to determine the exact spot of its origin. This case, however, is very suggestive when the infestation in New England is studied and it is seen how closely the oldest and most important infestation of this insect follows the shore line.

THE FLIGHT HABITS OF MOTHS

The adults of this insect are strong flyers, active at night and resting during the day on the underside of leaves of plants or in other sheltered places. They are not easily dislodged by winds, being able to cling tightly to the leaves that offer them protection. Experiments at the seashore have shown that they are unable to make headway against a wind of from 20 to 30 miles an hour, although contesting the force of the wind as best they can.

So little is known concerning the cause of natural migration of night-flying insects that it is impossible to say whether this phenomenon has entered into the problem under discussion. However, a natural migration of adults might be more probable in areas of dense population of the insect than in areas only moderately infested.

HABITS OF LARVAE IN REGARD TO WATER

In order to prove that distribution of the larvæ of this insect is possible by means of water drift, it is necessary to know that larvæ are able to survive after cornstalks have floated in water for a considerable period. In winter and early spring, when the larvæ are in a dormant condition, it is known that they survive after stalks have floated for a few weeks or have even been submerged. In fact larvæ in experiments have been known to pupate in floating cornstalks. Table 41 gives some results of the survival of larvæ in infested cornstalks that remained in water for protracted periods during the winter of 1921-22. In this case the stalks floated until the surface of the water was frozen, holding them in ice for some time, and in the spring they were submerged after the ice melted.

TABLE 41.—*Survival of larvæ of Pyrausta nubilalis in cornstalks placed in water*

Date placed in water	Kind of water	Date of recovery	Total number of larvæ	Number that survived
Dec. 3, 1921.....	Salt.....	Apr. 10, 1922	150	1
Dec. 3, 1921.....	do.....	Mar. 4, 1922	146	17
Dec. 2, 1921.....	Fresh.....	Mar. 21, 1922	141	0
Dec. 2, 1921.....	do.....	Apr. 10, 1922	122	10
Nov. 22, 1921.....	do.....	Feb. 14, 1922	90	1

Other experiments of this sort have been conducted with varying results, the following being one of the most interesting.

On February 7, 1921, a number of cornstalks and stubble containing overwintering larvæ of this insect were placed in a burlap bag, weighted down with stones, and thrown into a small brook in Arling-

ton, Mass. This bag was recovered on March 7, and of a total of 166 larvae that these stalks contained 81 were found to be alive, 73 dead, and 12 were injured in examination of the stalks. The live larvae were kept in a cage for observation of future development and 67 pupated, from which 33 moths emerged, 13 being females, all of which deposited eggs. There seems no question, therefore, but that larvae contained in cornstalks carried into a body of water and thrown on land again within a reasonable period of time may survive in numbers sufficient to cause an infestation of the insect in the new locality.

THE WATER CURRENTS OF LAKE ERIE

In Figure 50 the direction of the water currents of Lake Erie are shown, together with the Canadian infestation found in 1920, the infestation in New York and Pennsylvania found in 1919, and the infestation on the United States side of this lake in 1921. It may be seen that drift carried into the lake on the Canadian side may first be carried somewhat toward the west until it meets counter-currents, when it may travel around and between the group of islands located off Sandusky, Ohio, and finally, meeting the main current of the lake, may be deposited at almost any point on the southern shore of the lake. The infestation found in 1921 very closely coincides with this movement of the water of the lake. There is the further possibility that infested stalks were carried into Lake Huron from the western watershed in Ontario and thence to the Michigan shore, or eventually to Lake Erie and thence cast on shore.

If the large infestation discovered in south-central Ontario in 1920 is accepted as the source of all the spread of this insect in the lake region of America, and if water drift of infested cornstalks from this Canadian area played an important part in this dispersion of the insect, the heaviest infestation resulting from such dispersion might be expected at the points where the greatest number of stalks would be likely to be thrown on shore. The water currents of Lake Erie show that such a point would be the shore line of the lake between Buffalo and Dunkirk, N. Y. (fig. 50), and it is an exceedingly interesting, not to say curious, coincidence that this is in fact the point on the southern shore of the lake that was originally found to be most severely infested.

Although considerable scouting has been done along the southern shore of Lake Erie, no cornstalks have been found that might have been thrown on shore by the waters of the lake except those traceable to American origin. Although the inability to find such material in the localities and on the dates when such work was done may be advanced as proof of the flight theory of dispersion, a careful examination of the entire southern shore line of hundreds of miles is a difficult project in which bits of cornstalks may be easily overlooked. Furthermore, great numbers of cornstalks may be cast on the southern shore of Lake Erie only during certain years when particularly favorable conditions occur, in which case extensive unsuccessful scouting along the shore during certain years when such favorable conditions for much water drift did not obtain, would not prove that during a previous year, more favorable to this phenomenon, such conditions did not exist. In other words, extensive

water dispersion may not be an annual occurrence, but may vary considerably from year to year, depending on a number of natural factors.

THE WATER CURRENTS OF LAKE ONTARIO

The water currents of Lake Ontario (fig. 51) are suggestive of the possible means of spread of the insect to the territory about this lake now known to be infested. Here the infestation on both the northern and southern shores has been found to be spreading more rapidly along the shores of the lake. The water currents indicate that if water drift of infested cornstalks does play an important part in the dispersion of the insect, their direction is such as to carry infested cornstalks to all the shores of the lake, as well as to carry them into the St. Lawrence River, thus opening up a large area to possible infestation by this insect.

DISPERSION IN RELATION TO THE SEASON

The period of maximum flight of adults in the area about Lake Erie extends over a period of two or three weeks in July and early August, so that dispersion by flight must take place within this short period. Larvae becoming full grown by late August or September remain in the host plant until the following June, and during most of this time they are inactive. Over all this period, therefore, dispersion by the movement of infested stalks may take place, and from November to April the disposition of the stalks would be attended by little movement of larvae since they are in a dormant condition.

THE NATURAL PHENOMENA OF SPRING

The melting of snow in the spring and the breaking up of ice usually result in a swelling of streams and rivers, an increase in the rapidity of flow in many of them, and the distribution of debris that has been brought to them by the melting snow and ice. There are, then, two ways in which infested cornstalks may be distributed by water: (1) By floating free cornstalks, which may take place at any time during the fall, winter, or spring, and (2) by the distribution of cornstalks frozen in blocks of ice, which takes place mainly during the general thaws in the spring. In connection with this point, a note by Crawford (1) may be highly suggestive. He states that on April 4, 1923, "Considerable quantities of cornstalks were found to have been carried into Lake Erie by water from the spring floods. Material was also found frozen in the dislodged ice. This ice was later blown out into the the lake by the winds from the north, suggesting a probable means of infesting the southern shore of Lake Erie." The same authority has reported the finding of a submerged infested cornstalk at a point in Lake Erie 17 miles from Port Stanley, Ontario. In this case, although there was considerable scouting on the southern shore of Lake Erie in the spring of 1923, no cornstalks were found to have been cast on shore, so that it appeared that this material had not reached the southern shore of the lake that year.

In many cases it is probable that the insects may be more successfully transported by cornstalks frozen in ice than in free stalks,

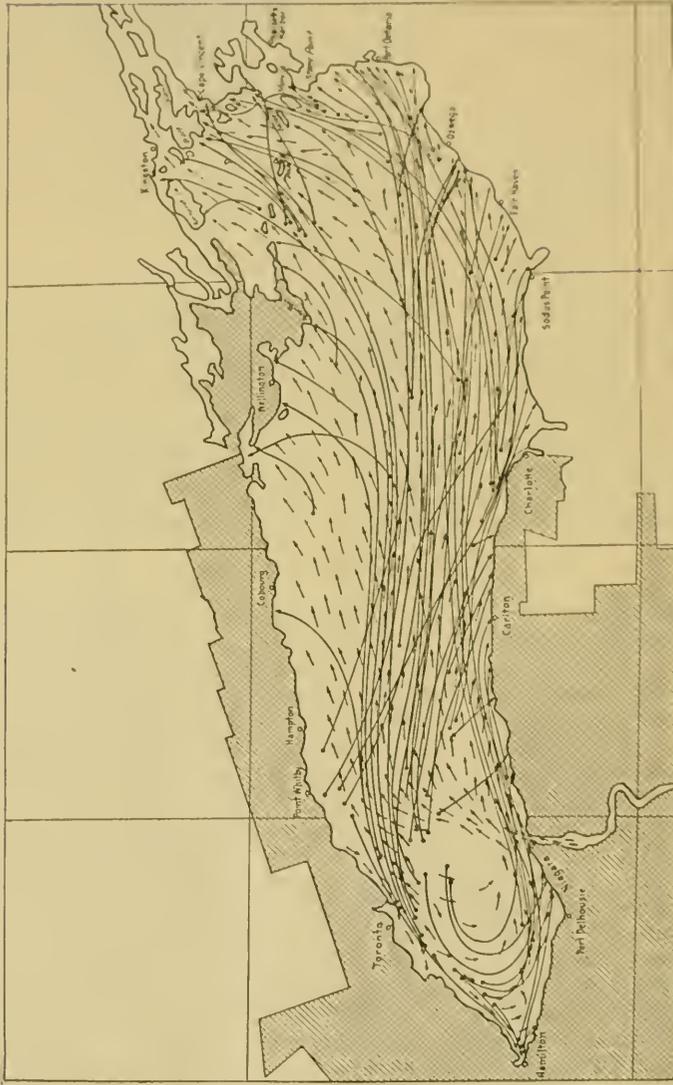


FIG. 51.—Lake Ontario and adjacent territory; showing water currents of the lake currents and battle paper courses of 1862, 1892, and 1894 (lines) redrawn from map by Weather Bureau. The shaded area shows the known infestation of the European corn borer up to December, 1924

for if the ice melts slowly and the current bearing it is swift enough, it may be carried considerable distances before being thrown on shore or melted. Free cornstalks tend to become saturated with water and sink after a varying length of time in water, so that although great numbers of stalks may be carried into a body of water like Lake Erie, many may sink before reaching another shore, and although some of these may eventually reach shore, for example by the movement of water during storms, the possibility is that as a usual thing most of the larvae contained in such stalks perish.

Cornstalks would be more likely to be swept along in the rivers where quicker currents are found, particularly in the spring when many rivers are swollen and more active, than in large bodies of water such as lakes, where cornstalks might sink before being carried to another shore.

SURVIVAL OF LARVAE AND PUPAE IN WATER

In order to determine the survival of larvae or pupae when contained in floating or submerged plant material, a series of experiments were carried on in New England in both fresh and salt (sea) water. The reaction to water of free larvae and pupae was also investigated. The results of these experiments are shown in Table 42.

TABLE 42.—Survival of *Pyrausta nubilalis* larvae and pupae in water

Materials	Date placed in water (1920)	Date removed (1920)	Du-ration pe-riod	Num-ber of speci-mens	Per cent alive	Remarks
Cornstalks submerged in fresh water. Overwintering larvæ.	Feb. 7	Mar. 7	Days 28	173	79.8	67 larvæ pupated; 33 produced moths.
Do.....	Mar. 9	Apr. 21	43	89	1.1	Larva died 16 days later.
Do.....	do.....	May 10	62	98	None.	
Cornstalks floating in fresh water. Overwintering larvæ.	Mar. 16	Apr. 21	36	55	3.6	1 surviving larva pupated and produced a moth.
Cornstalks floating in sea water. Overwintering larvæ.	Mar. 15	Apr. 21	37	212	1.4	3 surviving larvæ died 15, 37, and 41 days later.
Do.....	do.....	May 16	62	42	None.	Majority of surviving larvæ pupated and produced moths.
Free larvæ submerged in fresh water in wire-screen cages. Overwintering larvæ.	{ May 4	May 6	2	26	88.5	
	{ do.....	May 9	5	23	95.9	
	{ do.....	May 13	9	22	22.7	
{ do.....	May 18	14	5	40		
Cornstalks submerged in fresh water in wire-screen cages. First-generation larvæ.	{ July 29	July 31	42	10	20	1 larva pupated and produced a moth.
	{ do.....	Aug. 2	96	10	None.	
	{ do.....	Aug. 3	120	10	None.	
Cornstalks submerged in sea water in wire-screen cage. First-generation larvæ.	{ Aug. 5	Aug. 6	18	8	(A) None.	In (B) 2 larvæ pupated in stalks. Did not produce moths. 1 larva pupated afterwards and produced a moth. No pupation in (D).
	{ do.....	Aug. 7	42	6	(B) 16.6	
	{ do.....	Aug. 8	67	6	(C) None.	
	{ do.....	Aug. 14	216	59	(D) None.	
Cornstalks floating in fresh water inclosed by screen cylinder. First-generation larvæ.	Aug. 2	Aug. 9	163	59	11.9	5 larvæ pupated in floating stalks but did not produce moths. Three surviving larvæ pupated afterwards and produced moths.
Same as above in sea water.....	July 31	Aug. 2	48	100	None.	In (A) 5 surviving larvæ pupated and produced moths. Same in (B).
Free larvæ submerged in fresh water in wire-screen cages. First-generation larvæ.	{ July 28	July 29	24	10	(A) 60	
	{ do.....	July 30	48	10	(B) 10	
	{ do.....	July 31	65	10	None.	
{ do.....	Aug. 1	89	10	None.		

TABLE 42.—Survival of *Pyrausta nubilalis* larvae and pupae in water—Con.

Material	Date placed in water (1929)	Date removed (1929)	Duration of period	Number of specimens	Per cent alive	Remarks	
<i>1929</i>							
Cornstalks submerged in fresh water. Weighted down in large wire-screen cage. Second-generation larvae.	Aug. 27	Aug. 28	24	4	100	Larvae left stalks within 1 hour and came to top of submerged cage. Surviving larvae normal, not observed for pupation.	
	do	Aug. 29	38	2	50		
	do	Aug. 30	72	1	None		
Cornstalks submerged in sea water in glass cylinder. Held in place with weighted gauze. Second generation larvae.	Sept. 11	Sept. 17	48	5	(A) 100	Larvae (A) to (D) left stalks within 1 hour. Surviving larvae died 2 days later. (E) larvae emerged in burrows. Surviving larvae alive Oct. 7.	
	do	Sept. 18	72	5	(B) 20		
	Sept. 17	Sept. 21	56	5	(C) None		
	do	Sept. 22	120	5	(D) None		
	Sept. 29	Oct. 2	72	20	(E) 25		
Cornstalks floating in sea water in glass cylinder. Tanglefoot at edge of water. Second-generation larvae.	Sept. 15	Sept. 16	24	5	(A) 100	Larvae in (A) alive Nov. 30. (B) and (C) dead 7 days later. (D) to (F) alive Nov. 30.	
	do	Sept. 17	48	5	(B) 40		
	do	Sept. 18	72	5	(C) 10		
	do	Sept. 19	96	5	None		
	do	Sept. 20	120	5	None		
	Sept. 24	Sept. 27	72	5	(D) 80		
	Oct. 4	Oct. 7	72	11	(E) 54.5		
Oct. 3	Oct. 8	120	14	(F) 7.1			
Free larvae submerged in fresh water in wire-screen cages. Second-generation larvae.	Sept. 27	Sept. 30	72	25	40	Surviving larvae strong and vigorous. Not observed for pupation.	
Cornstalks submerged in sea water in wire-screen cage. First-generation pupae.	Aug. 6	Aug. 7	20	10	90	6 males and 3 females emerged.	
	do	Aug. 8	46	10	60		4 males and 2 females emerged.
	do	Aug. 9	68	10	60		2 males and 4 females emerged.
Cornstalks floating in sea water 1 week. First-generation pupae.	Aug. 3	Aug. 10	96	10	None.	1 female emerged.	
Cornstalks floating in fresh water. First-generation pupae.	July 26	Aug. 9	336	10	None.	3 males and 5 females emerged.	
	Aug. 5	Aug. 6	17	10	80		
	Aug. 5	Aug. 6	17	10	80		
Free pupae submerged in sea water in wire-screen cages. First-generation pupae.	do	Aug. 7	41	10	60	3 males and 3 females emerged.	
	do	Aug. 8	67	10	10		
	do	Aug. 9	89	10	None.		
Free pupae submerged in fresh water in wire-screen cages. Second-generation pupae.	June 1	June 2	24	5	None.	None of these pupated, although they lived for a maximum of 41 days after being taken	
	do	June 3	48	5	None.		
	do	June 4	72	5	None.		
	do	June 5	96	5	None.		
	do	June 5	96	5	None.		
Free pupae floating in sea water 2 weeks. First-generation pupae.	Aug. 7	Aug. 21	336	50	24	12 males emerged. All emergence in first 7 days.	

According to the data in Table 42 the larvae of the second or overwintering generation proved to be much more resistant to drowning during their period of inactivity in the late fall, winter, and early spring than the first-generation larvae during summer or the second-generation larvae during early fall. Some of the larvae which survived prolonged exposure to water in either floating or submerged plant material eventually pupated and emerged as adults. Very little difference was noted between the comparative effects of fresh or sea water upon the larvae and pupae.

When infested cornstalks were submerged in water for 28 days during the winter, nearly 80 per cent of the overwintering larvae contained therein survived and many of such larvae eventually pupated and emerged as moths. Less than 2 per cent of the larvae survived for 43 days, however, when they were submerged under similar conditions a little later in the season. None of these pupated, although they lived for a maximum of 41 days after being taken

from the water. A small percentage of overwintering larvae contained in floating cornstalks survived, and one produced a moth, after being in the water for 36 days during the spring. Of the free larvae submerged in the water for 14 days during the month of May, 40 per cent survived and eventually developed into moths. In this and in similar experiments many larvae, which appeared to be dead when taken from the water, revived after a period of several days. It was, therefore, necessary to keep all larvae used in the experiments under observation until they revived or until decomposition began. Naturally these larvae which were retained for observation could not be returned to their natural position in the stalks of plants, but were kept in screen wire cages containing sections of cornstalks. The cages were placed in an outdoor insectary. It is believed that the chances of dispersion of infested material by water is greater during the spring than at any other period. Hence the resistance of larvae to drowning in submerged or floating material at this time is especially important. In these experiments old cornstalks remained afloat in fresh water for a maximum period of 62 days in the spring, or until taken from the water. Partly matured cornstalks placed singly in fresh water during the last week in August floated for an average period of 40 days and a maximum period of 68 days before sinking. These cornstalks were partly green, as is usual with cornstalks taken from the field at this time of year. The upper portions of the stalks were dry and the lower portions were green and succulent. Bundles of cornstalks similar to those just described, placed in fresh water on September 18, floated until they were frozen in the ice just prior to December 1, a period of 73 days. Small stalks and pieces of stalks sank sooner than entire stalks bearing ears. It appears, therefore, that in the spring or fall cornstalks may float for a sufficient period to become widely dispersed.

A small percentage of first-generation or summer larvae survived and eventually developed into moths from cornstalks completely submerged in water for 42 hours. Larvae of this generation also survived and produced moths from stalks floating in water for 163 hours, or nearly 7 days. Free larvae survived and produced moths after submergence in water for 48 hours.

When cornstalks containing second-generation larvae were submerged in water during late August, certain of the larvae survived an exposure of 48 hours, whereas two weeks later they survived a similar treatment of 72 hours in submerged and also in floating cornstalks. During the first week in October certain of the larvae survived from cornstalks floating in water for 120 hours, indicating that their resistance to drowning increased with the approach of the inactive period. Free larvae of this generation survived when submerged in water for 72 hours during the last week in September.

First-generation pupae in cornstalks which had been submerged in water for 68 hours, and in cornstalks which had floated in water for one week, produced adults. Free pupae of the first generation submerged in water for 67 hours produced a single adult, and free pupae of the second generation receiving a similar treatment for 24 hours produced no adults. Free pupae of the first generation floating in sea water for two weeks produced adults during the first 7 days. Pupae in fresh water produced adults for 6 days.

NATURAL ENEMIES

Although a variety of natural enemies of the European corn borer have been recorded in this country, usually they do not attack the insect in any appreciable numbers and can not from present indications be relied upon to hold it in check.

The fact that the larvae normally feed within their hosts greatly reduces the opportunity for attack by parasitic and predacious enemies. The small larvae, however, are exposed to attack for a short time before entering the plant. This is true also for certain individuals of the larger larvae when feeding on or near the exterior of the plant, or when migrating to other parts of the same or adjacent plants, and when seeking shelter in unprotected locations.

PARASITES

NATIVE PARASITES

In New England the small chalcid *Trichogramma minutum* Riley periodically parasitizes considerable numbers of *Pyrausta nubilalis* eggs, particularly those of the second generation in the latter part of the season. Toward the end of the summer of 1919 an average of 43.5 per cent and a maximum of 75 per cent of the second-generation eggs were parasitized in 23 towns in representative parts of the area where egg collections were made. In 1921 this species destroyed an average of 30.7 per cent, and a maximum of 74 per cent of the second-generation eggs in 24 representative towns. This chalcid is apparently very variable, however, in occurrence from year to year, as in 1920 only 6.6 per cent of the second-generation eggs were parasitized in this same area. Although the parasitism of the second-generation eggs was comparatively high during these two years, less than 1 per cent of the first-generation eggs were parasitized in this same area. In the New York areas of infestation no parasites have been found in any of the eggs collected. Table 43 summarizes the results of egg collections in New England for parasitism by *T. minutum* from 1919 to 1921, inclusive.

TABLE 43.—Parasitism of *Pyrausta nubilalis* eggs by *Trichogramma minutum* in New England, from 1919 to 1921, inclusive

Year	First generation			Second generation		
	Number of eggs collected	Number of eggs parasitized	Per cent of parasitism	Number of eggs collected	Number of eggs parasitized	Per cent of parasitism
1919.....	11,384	15	0.13	28,418	12,948	45.5
1920.....	28,046	29	.10	53,198	3,501	6.6
1921.....	36,835	266	.72	79,892	23,997	30.1
Total.....	76,265	310		161,418	40,446	
Average.....			.406			25.05

The fact that most of the parasitism by *T. minutum* is confined to the second-generation eggs, and particularly the eggs deposited during the late season, rather reduces the effectiveness of the species as a factor in preventing injury by its host.

During 1921 a special effort was made to determine the seasonal variation in the parasitism by *T. minutum* and also to obtain a more correct average of the parasitism for the entire season than had previously been obtained in 1919 and 1920 when collections were made without proper regard to seasonal variation. The plan used in 1921 called for six uniform collections of eggs of *Pyrausta nubilalis*, three of each generation, in each of the 24 towns selected. In this manner an early, medium, and late collection of eggs was made from each town during the seasonal progress of each generation, thus effectively covering all the seasonal variations that might occur in parasitism. As a result of this system the percentage of parasitism for 1921, as given in Table 44, is probably more nearly correct than the figures given for 1919 and 1920. These collections also showed very plainly the seasonal variation in parasitism. Table 44 gives results of the six collections in four typical towns in Massachusetts during 1921.

TABLE 44.—Seasonal variation in parasitism by *Trichogramma minutum* in New England in 1921

Town (Massachusetts)	First generation, per cent of parasitism			Second generation, per cent of parasitism		
	Early	Medium	Late	Early	Medium	Late
Wakefield.....	0	0	0	0.5	4.3	78.5
Scituate.....	0	0	0	3.4	15.5	90.5
Peabody.....	0	0	0	5.5	11.9	62.7
Danvers.....	1.1	0	0	2.1	7.2	13.6

A small percentage of corn-borer larvae and pupae have been destroyed in New England each year by several different species of dipterous and hymenopterous parasites. The species which have been reared from *Pyrausta nubilalis* larvae and pupae are listed below:

DIPTEROUS PARASITES

- | | |
|-------------------------------|------------------------------------|
| <i>Phorocera erecta</i> Coq. | <i>Exorista nigripalpis</i> Towns. |
| <i>Exorista pyste</i> Walk. | <i>Carcelia ochracea</i> V. D. W. |
| <i>Masicera myoides</i> Desv. | <i>Comptosia concinnata</i> Meig. |

HYMENOPTEROUS PARASITES

- | | |
|-------------------------------------|--------------------------------------|
| <i>Hoplactis conquisitor</i> Say. | <i>Habrobracon gelechiae</i> Ashm. |
| <i>Sagaritis dubitatus</i> Cress. | <i>Epiurus pterophori</i> Ashm. |
| <i>Agrypon</i> sp. | <i>Epiurus tecumseh</i> Vier. |
| <i>Amblyteles brevicinctor</i> Say. | <i>Epiurus indagator</i> Cress. |
| <i>Amblyteles rubicundus</i> Cress. | <i>Bassus agilis</i> Cress. |
| <i>Cryptus incertus</i> Cress. | <i>Labrolychus prismaticus</i> Nort. |
| <i>Ephialtes aequalis</i> Prov. | <i>Microgaster zonaria</i> Say. |
| <i>Campoplex</i> sp. | <i>Meteorus toxostegi</i> Vier. |
| <i>Micobracon caulicola</i> Gahan. | |

The combined parasitism by the species listed above has totaled less than 1 per cent of the larvae and pupae collected each year. The parasitism of the first generation has been slightly greater than that of the second. A few individuals of the tachinid *Exorista nigripalpis* Towns. have been reared from *P. nubilalis* larvae collected in New

York State, but less than 1 per cent of the hosts collected were parasitized by this species, and no other parasites have been recorded in this area to date. Table 45 summarizes the results of the collections of *P. nubilalis* larvae and pupae in New England to determine parasitism during the period from 1919 to 1921, inclusive.

TABLE 45.—Parasitism of *Pyrausta nubilalis* larvae and pupae by various Diptera and Hymenoptera in New England

Year	LARVAL COLLECTIONS					
	First generation			Second generation		
	Number collected	Number parasitized	Per cent of parasitism	Number collected	Number parasitized	Per cent of parasitism
1919.....	5,525	80	1.45	6,231	2	0.03
1920.....	4,741	68	1.43	17,951	49	.27
1921.....	7,577	133	1.75	4,241	22	.52
Total.....	17,843	281	28,423	73
Average.....	1.5729

Year	PUPAL COLLECTIONS					
	First generation			Second generation		
	Number collected	Number parasitized	Per cent of parasitism	Number collected	Number parasitized	Per cent of parasitism
1920.....	536	27	5.04	4,497	6	0.13
1921.....	2,965	65	2.21	2,801	4	.14
Total.....	3,441	92	7,298	10
Average.....	2.67137

These figures on parasite rearings do not, of course, show the actual percentages of the host killed under field conditions by the action of parasite adults and from which no parasites are reared, but it is evident from the data in Table 45 that but little help can be expected of the native parasites of the larva and pupa in suppressing *P. nubilalis*.

FOREIGN PARASITES

Foreign literature contains very few records of parasites bred from *P. nubilalis* in any of its stages, and most of the literature dealing with the species emphasizes the absence of any parasites. Schmidt (54) in Austria, and Köllar (34, p. 108) in Germany, reared hymenopterous parasites from *P. nubilalis* larvae, but the species concerned and their status were not mentioned. Jablonowski (29) in Hungary reared a single individual of *Masicera senilis* Rond. from the larva, and two or three individuals of undetermined parasitic wasps from larvae and pupae. The same author found *P. nubilalis* eggs parasitized by a very small unknown hymenopteron, but it was not possible to estimate the economic importance of this parasite. The author also mentions in this connection that *Oophthora semblidis* Aur. is known as an egg parasite of many insects in Europe, and intimates that this may be the species concerned. Kostinsky recorded the rearing of parasites from *P. nubilalis* in Russia (Kiev) and Dobrodeiv (14) in the Don Province of Russia, but their names or their importance are not mentioned.

During 1919 the Bureau of Entomology established a laboratory in southern France for the purpose of investigating the parasitic

enemies of *Pyrausta nubilalis* in Europe, with a view of introducing the most promising species into this country. W. R. Thompson, in charge of this work, is now engaged with two assistants in conducting a study of the biology and economic importance of several species of parasites which he has found attacking *P. nubilalis* in France, Italy, and Belgium. Eight species of the more promising parasites of the corn-borer larva and pupa have already been sent to this country by Doctor Thompson and liberated in the severely infested portion of the New England area. These consisted of the hymenopterons *Habrobracon brevicornis* Wesm., *Eulimneria crassifemur* Thom., *Exeristes roborator* Fabr., *Angitia (Dioctes) punctoria* Roman, *Microgaster tibialis* Nees, *Phaeogenes planifrons* Wesm., and two tachinids, *Masicera senilis* Rond and *Zenillia roseanae* B. B. Prior to the introduction of these species Doctor Thompson conducted a thorough study of their habits, with special reference to the possibility of detrimental conflict between them.

In addition to the foregoing, Doctor Thompson reports that he has reared from *P. nubilalis* larvae the tachinid *Nemorilla maculosa* Meig. *Trichogramma* sp., probably closely allied to the American species, was also found as an egg parasite, but not very abundant. According to Doctor Thompson a few specimens of the tachinid *Dexodes nigripes* Fall. and of the hymenopteron *Eulophus* sp. have been reared from *P. nubilalis* larvae by Professor Silvestri at Naples, Italy.

The history, habits, and present status of the imported species of parasites have been reported (31) by D. W. Jones, of the Arlington, Mass., corn-borer laboratory, substantially as follows:

Zenillia roseanae B. B. is a tachinid of much promise which parasitizes small host larvae and emerges just before the pupation of the host. The two generations of this parasite synchronize perfectly with the seasonal history of its host in southern France. Hibernation occurs as a second-instar larva within the host. Ninety adults were liberated during 1920 and 784 adults were liberated in 1921. It is planned eventually to carry on an extensive rearing project with this species to furnish a large number for liberation.

Masicera senilis Rond. is a tachinid which is believed to be very closely related to the native species *M. myoideia* Desv. A total of 70 adults of this species were liberated in 1920 and 300 adults were liberated in 1921.

Eulimneria crassifemur Thom. is a large hymenopterous parasite having two generations a year in southern France. This species usually parasitizes small host larvae while they are in their feeding webs, and hibernates as a full-fed larva within a very compact cocoon. Thirty-one adults were liberated in 1920, 4,968 adults in 1921, 733 adults in 1923, and 128 adults in 1924.

Angitia (Dioctes) punctoria Roman is a very effective summer parasite in Italy. This species is very similar to *E. crassifemur* in appearance and habits, except that it parasitizes free-crawling larvae as well as those in feeding webs. Only 10 adults were liberated in 1921, 168 adults in 1922, and 555 adults in 1924.

Exeristes roborator Fabr., one of the old *Pimpla* group, is a large hymenopteron equipped with a long, powerful ovipositor. This species is able to locate and parasitize full-grown larvae through cornstalks and other large woody stalks in which host larvae may

be present. It has several generations each year, and hibernates as a full-fed larva in a very thin, tough cocoon. In October, 1922, a total of 1,061 cocoons were received from France. This shipment produced 500 adults, of which 56 were liberated in the field during 1921 and the remainder were used in breeding experiments. With this breeding stock as a basis, a total of 28,935 adults were bred and liberated during 1923. In 1924, 11,341 were liberated in New England, 7,920 sent to Sandusky, Ohio, and 2,880 to Silver Creek, N. Y., for liberation. Females predominated, and through the use of a special emergence cage they were well mated before liberation.

Habrobracon brevicornis Wesm. is a small hymenopteron which paralyzes full-grown host larvae and deposits external eggs. The resulting larvae feed externally and produce an average of 18 cocoons per host. From 8 to 10 generations per year would be possible with this parasite, as the life cycle is very short, varying greatly with the temperature. Hibernation occurs in the adult stage. In September, 1921, a total of 1,210 cocoons were received from France. This shipment produced 715 males and 213 females. With this breeding stock as a basis, 400 adults were bred and liberated in 1921 and 1,054,000 in 1922. Late in 1924 approximately 25,000 were liberated in Sandusky, Ohio, and in Silver Creek, N. Y. In the 1921 liberations the females averaged only 14 per cent of the total whereas improved breeding methods during 1922 increased the proportion of females to 40 and later to 60 per cent.

Microgaster tibialis Nees is a small hymenopteron which has been particularly effective as a parasite of *P. nubilalis* larvae inhabiting weeds in northern France and Belgium, and is also found in corn in Italy. This species parasitizes second-instar host larvae, feeding internally and emerging from the host in the late fourth or early fifth instar. Hibernation occurs as a full-fed larva within a very tough white cocoon. A total of 100 cocoons were received from France in 1923, and although no liberations were made during 1923 an attempt was made to develop a satisfactory technic for rearing the species. There were 449 adults and 2,815 parasitized larvae liberated in 1924 in the Massachusetts area.

Phaenogenes planifrons Wesm. is a large hymenopterous parasite which emerges from the pupa. It is particularly valuable as a summer-generation parasite in Italy, according to Doctor Thompson's records. There were 1,460 adults liberated in New England in 1924.

RECOVERIES OF FOREIGN PARASITES

With the exception of *Habrobracon brevicornis*, no systematic collections for the recovery of liberated parasites have been attempted. The results in attempting to recover *H. brevicornis* were negative to January 1, 1925. Encouraging results, however, were secured with *Exeristes roborator* and *Microgaster tibialis*. Incidental collections during the summer of 1923 showed that a maximum of 8 per cent of the corn-borer larvae were parasitized by *E. roborator* in the vicinity of the colony sites in Massachusetts, and from 1 to 4 per cent of the larvae were parasitized in a cornfield 3 miles from one of the liberation points. One incidental recovery was made at a distance of 5 miles from the nearest point of liberation. Several recoveries were made of individuals of this species which had suc-

cessfully passed the winter of 1923-24. A few cocoons of *M. tibialis* were also recovered during 1924 under circumstances which indicated that this species had passed at least one generation in the field since liberation in its new environment.

It is proposed to continue the large-scale rearing in the laboratory and liberation in the field with each of the parasitic species, for which a satisfactory rearing technic can be developed, supplemented by extensive collections abroad of the species which can not be successfully or economically reared in the laboratory. It is problematical, of course, whether any of these species will become permanently established in this country, and several years may elapse before the results will be definitely known.

PREDATORS

BIRDS

In the late winter and spring of 1922 as high as 95 per cent of the larvae were removed from standing cornstalks in some of the small home gardens in the environs of Boston, presumably by woodpeckers. Their beneficial activities were also noted in many widely separated localities in the New England area, and to a lesser extent in New York State. From 10 cornstalks used in one particular hibernation experiment at Arlington, Mass., 160 larvae out of a total of 200 (80 per cent) were removed from their burrows by birds during this period. A downy woodpecker (*Dryobates pubescens* Linn.) was observed drilling into these cornstalks and removing the larvae. Judging from the character of the holes made in the cornstalks by this individual in its search for the larvae (fig. 52), it seems probable that this and allied species may be credited with much of the work mentioned previously. Prior to 1922 only occasional instances of similar work in infested cornstalks had been observed. According to Barber (6), from a series of 20 special observation stations which were maintained at widely distributed points in New England during the winter of 1922-23, birds were found to have taken 61 per cent of the larvae in five of these stations, and the remaining 13 stations which were recovered in good condition exhibited little or no feeding by birds.



FIG. 52.—Cornstalks from which European corn borer larvae have been removed by birds, probably the downy woodpecker. Medford, Mass., April 13, 1922

The number of larvae taken by birds in the 18 stations recovered was 17 per cent of the total larvae involved. Judging from direct observation and from the character of the work, it is believed that the downy woodpecker was responsible for most of this beneficial activity. Each of the stations mentioned above consisted of 60 cornstalks tied to wooden stakes, simulating natural conditions, and containing an average of 27.5 larvae per stalk. In a similar experiment during the winter of 1923-24 an average of 19 per cent of the larvae involved were taken by birds. This series was conducted in 47 widely separated localities in the New England area.

With the exception of the somewhat local activity by woodpeckers, birds are not known to have exerted an important influence in reducing the numbers of the corn borer throughout the infested areas as a whole, although the comparative ease with which insectivorous birds may secure larvae from collapsed and broken-over cornstalks and other plant material, especially during the late fall and spring, would appear to render this source of food supply very attractive to them.

In one instance a robin (*Planesticus migratorius* Linn.) was observed, late in the spring, removing and devouring loose larvae from a heap of cornstalks. Robins, grackles, blackbirds, and starlings commonly frequent the vicinity of infested cornstalks and other plant material during the spring and have been observed feeding upon the larvae contained therein. Late in the spring many of the overwintering larvae are migrating in search of suitable quarters for pupation, and some of them are easily accessible to insectivorous birds. In several instances where infested ears of corn in the field were fed upon by crows, blackbirds, and pheasants, many of the *P. nubilalis* larvae known to have been feeding on the grain disappeared along with the corn, but no direct evidence of ingestion by birds could be obtained. Most of this type of bird activity was observed in sweet corn during the marketing season and in field corn before the grain had begun to harden. During the spring and fall of 1920, C. C. Sperry, of the Bureau of Biological Survey, investigated the relation of birds to the European corn borer in New England and found the remains of one larva in the stomach of a pheasant (*Phasianus torquatus* Gmelin) and the remains of six larvae in the stomach of a single starling (*Sturnus vulgaris* Linn.). No other species of birds were found feeding on the insect at this time.

OTHER PREDATORS

Larvae of the coccinellid *Megilla maculata* De G. have been frequently found devouring *P. nubilalis* eggs and larvae, and nymphs of the pentatomid *Podisus placidus* Uhl. and the reduviid *Sinea didema* Fab. have been occasionally observed attacking the larvae. Many of the dead larvae found in partly or wholly decayed heaps of cornstalks in the spring, and in cornstalks or other plant material which has been buried in the soil, are frequented by mites, but it has not been determined whether these mites were the primary cause of death. Centipedes and the larvae or adults of several of the predacious beetles have also been found frequently in the decayed remains of such material. Whether any of these agencies were directly

responsible for the death of the larvae is not known. In breeding cages several species of spiders have interfered with the experiments by attacking and killing migrating larvae, and occasional occurrences of a similar nature have been recorded in the field.

DISEASE

Occasionally, both in the field and in confinement, nearly full-grown larvae have been found during the summer and fall which apparently had succumbed to a disease resembling bacterial wilt. In the breeding cages at Silver Creek, N. Y., the rearing work was seriously hampered because of the mortality due to this disease. Specimens of larvae which had died, apparently from this disease, were submitted to G. F. White and A. T. Speare of the Bureau of Entomology, who reported that they were unable to find any protozoa, fungi, or polyhedral bodies in the samples submitted, but that an undetermined bacterium was present in great numbers. Later an attempt to isolate the causative organism was made by H. W. Allen of the Arlington, Mass., laboratory, in cooperation with R. W. Glaser of Bussey Institution, but the results were negative. Since only a comparatively small number of larvae have been killed by it in the field, this disease is evidently not important enough to be of material benefit.

CONTROL AND QUARANTINE

CONTROL

The details relating to the control, quarantine, and scouting phases of the European corn-borer activities will be given in a separate publication and may be summarized briefly as follows:

From the fact that the insect passes the greater part of its larval stage and its entire pupal stage within the host plant, thus affording but little chance for insecticidal or other remedial measures under large-scale field conditions, it is evident that the major control efforts should be directed toward cultural practices leading to the utilization or the destruction of infested plants, particularly by feeding to livestock, burning, or plowing under; supplemented by preventive agronomic adaptations in the culture of corn, particularly the selection of varieties least susceptible to severe injury, combined with the regulation of the time of planting these varieties to escape serious infestation and yet produce satisfactory yields. None of the insecticides tested can be recommended for general use, although nicotine dusts containing 2 or more per cent of free nicotine directed against the newly hatched larvae have given encouraging results in limiting injury to valuable crops of corn. The possibility of developing more effective treatments is still under investigation.

When considering general control measures for the corn borer it is necessary to make proper allowance for the fact that two generations occur annually in the New England area and that in this area the insect infests commonly a great variety of plants, including corn, vegetables, flowers, field crops, and large-stemmed grasses and weeds; whereas in the western areas, including New York, Pennsylvania, Ohio, and Michigan, the corn borer is single brooded and is confined principally to corn. In New England, therefore, it is necessary to utilize or destroy all plants or crop residues which are listed as hosts of the corn borer, and in the middle western area

the control efforts are directed principally against the corn plant and its residues, under present conditions.

The value of corn and other plants for fodder is not materially lessened when infested by the corn borer, except under conditions of extreme infestation. The proper ensiling or shredding of such infested plants leads to the destruction of the borers contained therein. Feeding infested fodder direct to livestock is an effective method, providing all uneaten portions are collected and destroyed. The burning of infested material is, of course, a method of wide application, and although not a desirable agronomic practice in many respects, it is very effective when conducted in a thorough manner. In all methods of cutting cornstalks preparatory to their utilization or destruction, the stalks should be cut at or near the surface of the soil and as early in the season as possible, since there is a decided movement of the borers to the lower part of the stalk during the later part of the season. Based upon the results of plowing experiments to date, it appears that clean plowing is to be recommended for the destruction of cornstalks, corn stubble, and other infested material remaining in the field, which it is impracticable to eliminate by burning or feeding. Late fall plowing in the two-generation area of New England has proved more effective than spring plowing, but in the middle West it appears from results of experiments to date that *clean* plowing at any season is effective.

Relative to the selection of varieties as a cultural practice, none tested have shown any indication of possessing practical immunity to attack, but those varieties characterized by large stalks and ears have shown a greater resistance to severe injury by the corn borer than the varieties which have smaller stalks and ears.

Experimental data and field observations have shown in general that in the single-generation areas field and sweet corn planted during April or early May have sustained the maximum infestation and plantings made before the last week in May sustained greater injury than fields planted later, whereas plantings made after the first week of June suffered little or no injury. In the two-generation area of New England the early and the late plantings sustained the heaviest infestations, irrespective of type or variety, whereas plantings made during the period from approximately May 20 to May 30 have, in general, escaped serious injury. Phenological observations are now in progress having for their object the application of plant-development phenomena as an indication of the most favorable planting period, irrespective of calendar dates, in order that the vagaries of the seasons may be discounted.

Although the earliest planted fields of sweet corn have almost invariably sustained the maximum infestations in both the one and the two generation areas, thus indicating the possibility of using early planted sweet corn as a trap crop, actual attempts to apply this method of field control have thus far failed to show appreciable benefits, except under restricted conditions.

QUARANTINE

Quarantines have been established by the Federal authorities and by the various States concerned, which prohibit the movement out of infested areas of all plants and plant products which are likely

to harbor the European corn borer. In the two-generation area this quarantine applies to corn and broomcorn, including all parts of the stalk, all sorghum, Sudan grass, celery, green beans in the pod, beets with top, rhubarb, chrysanthemum, aster, cosmos, zinnia, hollyhock, gladiolus, dahlia, and oat and rye straw as such or when used as packing material. In the single-generation areas the quarantine applies to corn, broomcorn, and all sorghum and Sudan grass, except the grain or seeds thereof when properly cleaned.

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SUPPLEMENT

In addition to the material presented in this bulletin, it seems desirable to summarize a few of the more important recent developments which have occurred since the manuscript was prepared. The following matter therefore has been included as a supplement.

DISTRIBUTION

At the close of 1926 the European corn borer had extended its range in the middle western portion of the United States to in-

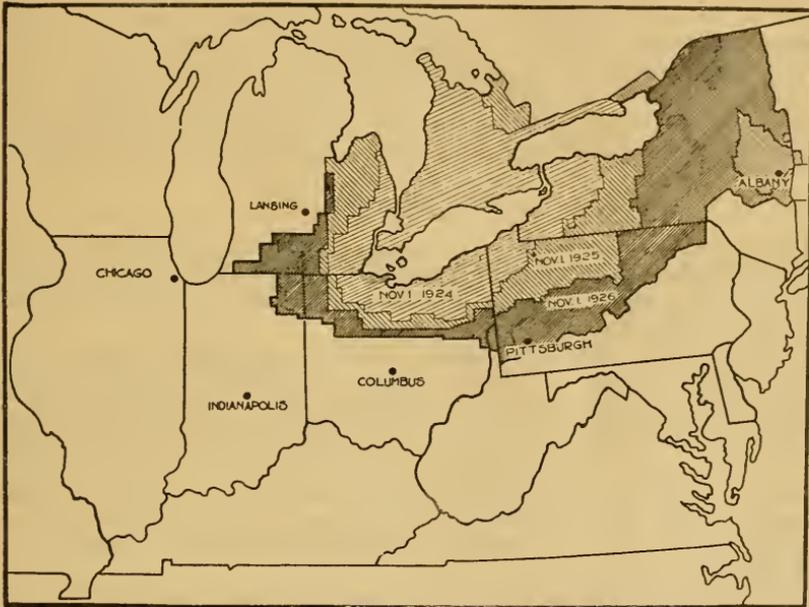


FIG. A.—Map showing the distribution of the European corn borer as known November 1, 1926. The outside (darkly shaded area) indicates the spread of the pest which is believed to have occurred during the summer of 1926. (Infested area in New England not shown.)

clude the area shown on the accompanying map (fig. A). The entrance of the insect into the extensive corn-producing regions of Michigan, Ohio, and Indiana is fraught with possibilities of great economic losses. Dispersion of the corn borer in New England recently has been very limited and the area now infested is practically the same as indicated in the map included in the body of this bulletin. Slight extensions have occurred along the Connecticut shore line, on Long Island, and on Staten Island. Two small, independent infestations have been found in the Bayonne and Jersey City sections of New Jersey. Since the summer of 1923 the corn-borer situation in southern Ontario, Canada, has rapidly grown worse. At the close of 1924 the Dominion entomologists reported that commercial losses occurred in 21 townships located in Oxford, Elgin, Middlesex, Kent, and Essex Counties, where the stalk infestation varied from 50 to 100 per cent. "In one canning district 25 per cent of the contracted acreage was refused at the factory on account of

the severe corn-borer infestation." By the close of 1925 the course of the infestation had progressed so that in Kent and Essex Counties the crop throughout at least 400 square miles was completely ruined. Control measures were adopted very slowly by growers, as there existed no legislation requiring their adoption. This situation culminated during 1926, when it was found that throughout an area of 1,200 square miles the corn acreage had been reduced to 10 per cent of the land devoted to that purpose in 1922. In this area of intense infestation many fields showed a loss of the entire crop and losses of 75 per cent were common. Legislation requiring corn growers to clean up their fields became effective October 1 of that year. In the meantime the infestation in Canada had progressed eastwardly, completely surrounding Lake Ontario and joining with the infested area in New York, which had made progress along the southern shore of the lake. Distribution surveys in southern and central Europe have demonstrated the presence of the borer in practically all areas where corn and other susceptible crops are grown.

HOST PLANTS

No change has occurred in the status of corn as the preferred host of the European corn borer in America, since in all areas it continues to be more generally infested and sustains more serious injury than any other plant attacked.

In the middle western areas a light infestation has developed in several of the more susceptible weeds and field crops when such plants were associated with badly infested corn. No severe economic injury, however, to crops other than corn has occurred in these areas to date. The corn borer has been found infesting a total of 46 species of plants (principally large succulent weeds) in western New York, 18 species in Ohio, and 8 species in Michigan. The plants of most of those species function primarily as shelter plants rather than as true food plants.

In New England a total of 224 species have been recorded as hosts of the corn borer. In those species are also included all of the western host species. Of the total number of species not more than 38 are known to constitute true food plants. The severity of the infestation in vegetables, field crops, flowers, and weeds has decreased in New England during 1925 and 1926 as a phase of the general reduction in the importance of the insect as a pest in that region.

EXTENT OF INJURY AND ECONOMIC LOSS

In Michigan, Indiana, Pennsylvania, and Ohio, with the exception of a few fields in northwestern Ohio, there has been very little economic loss caused by the corn borer to the close of 1926. In western New York, however, the estimated commercial loss exceeded 25 per cent in certain dent cornfields grown for grain in the older portion of the infested area, while the loss in sweet corn ears for canning in 1926 reached approximately the same figure (24.8 per cent).

The widespread dispersal of the pest in this entire Lake Erie-Lake Ontario region during 1925 and 1926 was accompanied by an increase in intensity of infestation which amounted in 1926 to approximately

500 per cent for the area, when compared with conditions existing in 1925 (based upon larval population). Should the rate of annual increase which prevailed during the years 1923 to 1926 be continued, it appears reasonable to expect that losses will become general throughout this area in the near future, unless recommended control practices are strictly and generally followed.

An analysis of the data from 46 townships in New England showed a decrease of 38 per cent in intensity of infestation for 1926 as compared with 1925 (based upon larval population). Great decreases were especially apparent in commercial sweet corn plantings where an average of 20 per cent ear infestation existing in 1922 had been reduced to approximately 5 per cent in 1925 and to slightly less than 5 per cent in 1926. Similar reductions of infestation and damage were observed in susceptible vegetables and flowers, particularly in beets, beans, celery, rhubarb, potatoes, gladioli, dahlias, asters, and greenhouse chrysanthemums.

Detailed studies pertaining to the effect of borer injury to the cornstalks on the number, weight, and quality of ears, and on the grain produced, have demonstrated that this indirect injury usually is far more important than the direct injury to the ears caused by the larvae feeding thereon.

A remarkable decrease has been observed in the larval populations in areas of weeds and large-stemmed grasses formerly existing in the New England area. This former source of infestation, from which large numbers of moths issued to deposit their eggs upon cultivated crops, has been removed as a result of the enforcement of the Massachusetts law requiring clean-up action, plus the experience of local vegetable growers who have learned the necessity of clean culture.

SEASONAL HISTORY

Only one generation annually of the corn borer has developed in New York (not including the New York Bay area), Pennsylvania, Ohio, Michigan, and Indiana, although occasional instances of summer pupation, denoting a two-generation tendency, have been observed each year.

Two generations have developed both in New England and in the scattered infestations in the New York Bay area each year, although the percentage of individuals developing a second generation has varied from 40 to 100 per cent in different years. No indication of a third generation was observed in 1925 or 1926.

An analysis of meteorological data for New England with reference to the generation cycle has shown that a preponderance of precipitation, coupled with normal temperatures in March, April, and May, and followed by a dry June, induced an early start of the corn borer in New England. Under these conditions a complete second generation has developed. On the other hand, a deficiency in precipitation during March, April, and May, followed by a rainy June, was unfavorable to the insect. Under such conditions there has been a diminution in the number of individuals developing a second generation, with a consequent reduction of injury caused by the insect.

Single-generation material transferred to a two-generation area in 1920 and reared continuously there in large field cages retained its

single-generation seasonal cycle at the close of 1926. Two-generation material treated in a similar manner retained the seasonal cycle of its original habitat in the same series of experiments. Since these experiments were conducted in the United States, where the corn borer may not yet have become thoroughly adapted to its environment, the results thus far obtained must be accepted with caution. All experimental cross breeding of two-generation and one-generation individuals has resulted in the production of two-generation progeny.

It has been demonstrated that the seasonal history, and especially the number of generations annually, is greatly influenced by the seasonal distribution of temperature and precipitation.

LARVAL HABITS

Studies to determine the percentage of larval establishment on corn have shown that an average of from 10 to 15 per cent of all larvae emerging from the eggs succeed in establishing themselves in or on the plant and reach maturity. This percentage of larval establishment may vary greatly in individual instances according to climatic conditions, type, variety, and strain of corn, and the condition of the individual host plant.

Definite records were obtained, as a result of extensive studies, that less than 1 per cent of full-grown larvae were able to migrate for a distance of 30 feet. About 2 per cent of the borers involved migrated a distance of 25 feet. The typical farm fence row, or field border, provides an ideal shelter for larvae migrating from plowed fields or elsewhere, particularly when such refuges contain large growths of weeds.

The average winter mortality above ground remains at about 10 per cent, as previously reported, and there does not appear to be any climatic limitation to the distribution or multiplication of the borer which depends upon winter mortality. Moisture secured by contact immediately prior to pupation seems essential for overwintering larvae.

Although many of the larvae contained in cornstalks that were stored indoors died as a result of the deprivation of contact moisture (so essential for the completion of histolysis) and the subsequent development of the survivors was delayed, a very large percentage of such larvae completed their development under storage conditions similar to those found on the average farm. Moreover, adults emerging from such storage conditions late in the season deposited eggs which developed into mature larvae before the end of the season.

ADULT HABITS

Detailed biological studies have demonstrated that the fecundity of the moths is greatly influenced by the character of the weather which occurs during their period of oviposition. Warm nights with abundant moisture, and the absence of heavy dashing rains, are conducive to maximum oviposition.

A study of wind movement during the flight period of European corn borer adults, in the Lake Erie region, has indicated strongly that dispersion to neighboring States probably occurred from the severely infested areas of Ontario. This method of natural dispersion was

especially important during 1926, when the nocturnal temperatures and the direction of the prevailing wind during critical periods were both very favorable for the flight of large numbers of the moths.

PARASITES

NATIVE

Native parasites have not exhibited any tendency to increase their effectiveness as natural enemies of the corn borer. The egg-parasite *Trichogramma minutum* Riley continues periodically to parasitize considerable numbers of the eggs, but its effectiveness is confined usually to the second-generation eggs in New England every second or third year. A few additional species parasitic on the larvae and pupae of the corn borer have been recorded, but their combined parasitism usually has affected less than 1 per cent of the total number of hosts collected or observed each year.

FOREIGN

Including the month of October, 1926, a total of about 225,000 foreign parasites have been liberated in nine different locations of the corn-borer infested areas of Michigan, Indiana, Ohio, Pennsylvania, and New York. Seven distinct species were involved in these liberations, viz: *Exeristes roborator* Fab., *Microgaster tibialis* Nees, *Habrobracon brevicornis* Wesm., *Eulimneria crassifemur* Thom., *Apanteles* sp., *Angitia punctoria* Roman, and *Phaeogenes planifrons* Wesm. Recoveries of *E. roborator* were made in New York during 1924, 1925, and 1926. This species was recovered in Ohio during 1925 and 1926. A very recent recovery of what may prove to be *M. tibialis* was made in Ohio. Special precautions, of course, were taken to prevent the escape of foreign hyperparasites.

Similar introduction work in New England has resulted in the liberation of about 1,187,000 foreign parasites in infested cornfields of that section. Ten different parasitic species were involved, consisting of the seven species listed in the preceding paragraph and in addition *Macrocentrus* sp., *Zenillia roseanae* B. B. and *Masicera senilis* Rond. Five species of these foreign parasites have been recovered in New England under circumstances indicating their permanent establishment, viz: *E. roborator*, *M. tibialis*, *E. crassifemur*, *A. punctoria*, and *P. planifrons*. In certain fields the collections have demonstrated that the prevailing total parasitism by the foreign species exceeds that of the native species. The rate of importation of foreign parasites from Europe has been increased and preliminary shipments have been received from India. It is expected that this work will be greatly stressed in the near future.

CONTROL

None of the types, varieties, or strains of corn thus far tested has shown any practical immunity to corn-borer attack except when involved with time of planting such varieties.

Those varieties of corn characterized by large stalks and ears have continued to exhibit a greater resistance to severe injury by the corn borer than the varieties which possess smaller stalks and ears.

PLOWING AS A MEANS OF CONTROL

Recent field experiments conducted by the bureau in the Lake Erie region have demonstrated the value and necessity of plowing under cornstalks and stubble as a means of corn-borer control. The effectiveness of plowing depends upon turning under the corn refuse and other plant débris so completely that none of it remains upon the soil surface. It requires also that the material shall not be dragged to the surface by later cultivation.

Clean plowing is the best practical method of control for application to fields containing high stubble or stalks in case it is impracticable to cut the stalks close to the ground and dispose of them by feeding or burning. Existing methods of cutting stalks or breaking them off at the soil surface, raking them into windrows, and burning them are less effective than clean plowing alone, except where such raking and burning are followed by plowing under the remaining débris.

In the Bono-Reno area of northwestern Ohio during May and June, 1926, the number of borers per acre remaining in cornfields which had been poled, raked, and burned, or disked for small grain, was nearly twice as great as the number remaining in fields where cornstalks or stubble had been plowed under.

In disked corn-stubble fields where small grains were seeded the previous fall or in the spring, 89 per cent of the original borers remained alive in the corn remnants and other plant débris on the soil surface.

Studies made in five plowed fields of Lucas County, Ohio, revealed that on an average 75 per cent of the borers were killed by the operation, although no special effort was made to plow under cleanly. Two of these fields contained standing stalks and three were in high stubble.

Similar field work at Silver Creek, N. Y., showed an average of 97 per cent of the borers killed in three fields where standing stalks were poled down and then plowed under. In three fields where high stubble was plowed under, an average of 78 per cent of the borers were killed.

Less than 10 per cent on an average were killed by winter conditions, predators, parasites, and disease.

In the region previously mentioned an average of 59 per cent of the borers were killed by poling, raking, and burning the standing stalks in four fields. Many living borers were found in pieces of stalks not burned properly, as well as in stalks not broken off during the poling process, and in stalks missed by the rake. Fourteen per cent of the borer population were left in small pieces of corn husk, leaves, etc., which it was not possible to gather with the type of rake ordinarily used for such purposes.

DISKED CORNFIELDS SHOW VERY POOR RESULTS

In four fields of high stubble where oats were seeded after disking, without previous cultivation, only 11 per cent of the borers were killed. Therefore, the seeding of small grain on disked corn stubble or stalks is a dangerous practice under corn-borer conditions, since it leaves so many of the borers alive. The growing grain also provides shade and ideal protection from the wind for the borers left in such fields during the late spring.

Regardless of any necessary change in farm practice, the disking for small grain on infested corn lands will have to be discontinued if the corn borer is to be held in check. Where unavoidable, this practice should be limited to fields in which the operations of cutting or breaking off the stalks at the soil surface and completely disposing of them together with all trash, by burning or otherwise, have been carefully conducted.

In a field where standing stalks were poled down, raked in windrows, and burned, and the remaining débris plowed under, practically all of the borers were killed. Although there were about 5,100 borers per acre in the standing stalks before operations began, no living borers could be found in such small portions of trash as remained. This method, if widely adopted, would act as a very severe check on corn-borer infestation, and therefore it is strongly recommended.

Although the plowing under of infested cornstalks and corn stubble has given encouraging results where carried on in a careful manner it should be emphasized that careless plowing leaves many pieces of stalks, stubble, weeds, etc., upon the soil surface and is not effective. This débris shelters many borers which crawl to the surface after being plowed under. They bore into, or encase themselves, in such débris, and here many of them transform into moths. Where such shelter is lacking the vast majority of the borers finally perish, either being eaten by birds, beetles, or ants, or killed by various native parasites or by exposure to the weather. The use of plows with wide bottoms and a chain or wire to aid in burying all débris is an important help in doing a clean job.

The importance of clean plowing was strikingly shown by a series of experimental tests at Bono, Ohio.

Infested cornstalks were plowed under at intervals from late September to mid-December, 1925, and were surrounded by "recovery traps." At least 38 per cent of the borers in these plowed-under stalks crawled to the soil surface during the fall and the following spring. The remaining 62 per cent died in the soil or were destroyed by their natural enemies and weather conditions after reaching the surface.

In tests where the soil surface was practically free of all plant débris an average of only 2 per cent of the plowed-down borers were able to find adequate shelter. In similar tests where the quantity of stalks on the soil surface was the same as on average fields in the vicinity, 13 per cent of the total borers plowed down found adequate shelter in débris on the surface. In two other tests where "recovery traps," which provided shelter, were placed 25 feet distant from the plowed area, and stalks were left on the soil surface in average quantity, 22 per cent of the total number of plowed-under borers succeeded in entering the surface débris. An additional 5 per cent crawled at least 25 feet to the "recovery traps."

Thus it is shown that under circumstances closely imitating field conditions following clean plowing only 2 per cent of the borers escaped destruction. On the other hand, where average quantities of corn remnants were left on the soil surface, from 13 to 22 per cent of the borers survived.

In certain small tests where minute examination was possible, evidence was obtained that 28 per cent of the borers had died in the soil.

CORNSTALKS IN BARNYARD, FEED LOT, AND MANURE MUST BE DESTROYED

The warning should be repeated against throwing large quantities of cornstalks and other corn remnants into the manure unless buried deeply within it. It is also dangerous to permit large quantities of cornstalks to accumulate in barnyards and feed lots. An examination of the cornstalks in barnyards and on the surface of manure piles of five typical farms in Lucas County, Ohio, showed borers present in such cornstalks at the rate of 51 borers per 1,000 linear feet of stalks. No living borers were found in stalks buried deeply in the manure or in shredded corn plants which had been used for feed or bedding.

Judging from the history of the corn borer in Europe and in America, the pest may be expected to cause more damage in areas where the farming practices allow large quantities of stalks to remain undestroyed on farms than in areas where less corn is grown and stalks and other corn remnants are promptly consumed or destroyed.

HUSKERS AND SHREDDERS VERY EFFECTIVE IN KILLING BORERS

The existing types of husking machines equipped with shredder heads or cutter heads, or combination shredder and cutter heads, kill most of the borers in infested cornstalks. The efficiency of the machines is increased where special care is taken to apply sufficient pressure on the snapping rolls to produce a crushing effect. In six tests wherein cornstalks infested by the corn borer were run through six different types of husking machines an average of 98 per cent of the borers were killed by the machine. The greater part of the remaining 2 per cent undoubtedly perished during the process of storing the shredded material, feeding it to livestock, and using the residue as bedding, ultimately to be trampled into the manure, as results from the general practice.

This method of disposing of fodder is strongly recommended, and its use in corn-borer territory should be greatly extended.

The cutting box as ordinarily used has not proved effective in killing borers contained in cornstalks. If used at all, it should be adjusted so as to cut the stalks in pieces not to exceed one-half inch in length.

ORGANIZATION OF THE UNITED STATES DEPARTMENT OF AGRICULTURE

January 27, 1927

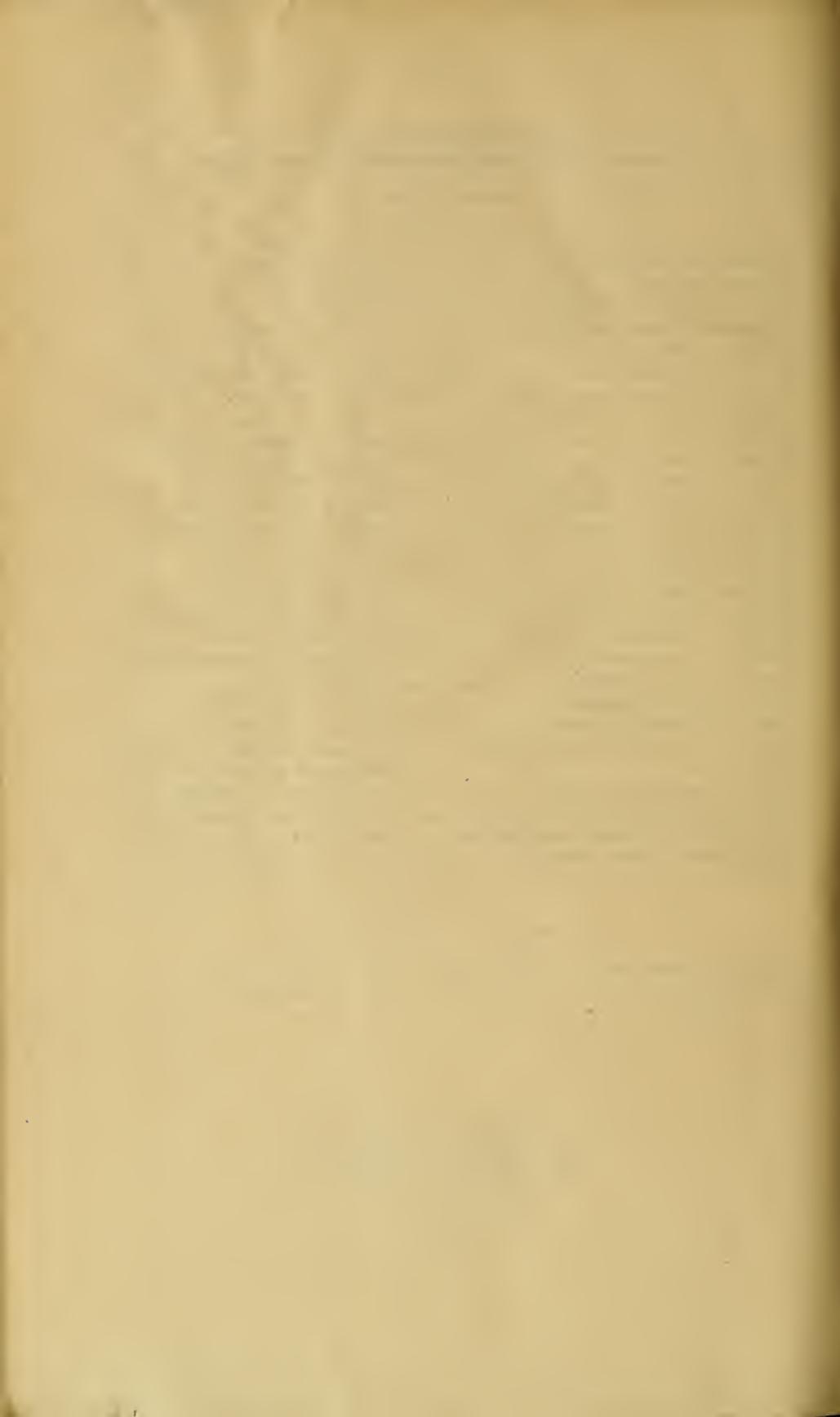
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DEPARTMENT BULLETIN No. 1482



Washington, D. C.

April, 1927

EXPERIMENTS ON THE CONTROL OF THE PLUM CURCULIO, BROWN ROT, AND SCAB, ATTACKING THE PEACH IN GEORGIA

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INTRODUCTION

Perhaps the most severe infestation on record of the plum curculio (*Conotrachelus nenuphar* Hbst.) on the peach was experienced in Georgia in the season of 1920. Owing to the abundance and destructiveness of the insect that year, only a small proportion of the Georgia Belle and Elberta peaches could be marketed, the larvæ having rendered the greater part of them unmerchantable. Much of the fruit that was shipped in 1920 arrived at its destination greatly damaged by curculio larvæ, as in many cases wormy peaches were packed because the presence of the tiny larvæ just hatched could not be detected. It has been conservatively estimated that the curculio alone damaged the Georgia peach crop of 1920 to the extent of \$2,000,000. The very heavy infestation of that year also provided innumerable punctures in the skins of the fruit, through which the brown-rot fungus, *Sclerotinia fructicola* (Wint.) Rehm,² gained easy access and frequently finished the work of destruction begun by the curculio. Since the peach crop of 1919 had also been a partial

¹ The authors are indebted for assistance to John B. Gill (1921) and W. D. Whitcomb (1921), of the Bureau of Entomology; Lee M. Hutchins (1921), of the Bureau of Plant Industry; and William F. Turner (1921-22) and Luther Brown (1923), of the Georgia State Board of Entomology, who have respectively helped to conduct the work during the seasons indicated.

² Other names which have been applied to this fungus are *Sclerotinia fructigena*, *S. cinerea*, *S. cinerea* forma *americana*, and *S. americana*.

failure owing to curculio and brown rot, a serious financial condition loomed up in the Georgia peach belt at the close of the 1920 season, which caused the growers to become greatly alarmed over the situation. For many years growers had kept their fruit practically free from these pests by spraying according to methods and schedules worked out and successfully put into practice by Quaintance (3),³ Scott and Ayres (5), Scott and Quaintance (6), and Chase (1, 2). The losses of 1919 and 1920, however, showed that additional means of control were necessary, at least for the time being or until losses not more than normal again became the rule.

At the urgent request of the growers for assistance in solving the problem then threatening the Georgia peach industry, the Bureau of Entomology of the United States Department of Agriculture established, in the fall of 1920, a field station at Fort Valley, Ga., to undertake a study of the life history and control of the curculio. In the spring of 1921, when extensive experiments on spraying and dusting peaches were begun, the Georgia State Board of Entomology and the Federal Bureau of Plant Industry became cooperating agencies. The experiments were continued through four consecutive seasons at Fort Valley by the three cooperating organizations. The present publication is a report of the results obtained in each season, together with recommendations relating to spraying and dusting for the control of the curculio, brown rot, and scab,⁴ in sections of the South where these pests, especially the two first named, are particularly destructive.

THE GEORGIA PEACH BELT

Central Georgia is one of the largest peach-growing regions in the United States. Within a radius of 40 miles of Fort Valley, said to be the largest peach-shipping station in the world, there are some 12,000,000 bearing and nonbearing peach trees.

The topography of the Georgia peach belt varies from generally level in the vicinity of Fort Valley to rolling in the more northern districts. The elevation varies from 350 to 800 feet above sea level. The altitude of Fort Valley is 526 feet.

The climate of this section is characterized by long, hot summers, during which the changes in temperature from day to day are very small, and by mild, brief winters. The normal annual temperature for the region is about 66° F. High temperatures continue during June, July, and August, and September is occasionally the hottest month in the year. The average annual rainfall in central Georgia is 48 inches (9, p. 2).

RELATIVE ABUNDANCE OF THE CURCULIO IN GEORGIA FROM 1920 TO 1924

Life-history studies of the curculio, which were conducted by the senior writer during each of the four years that the experiments on spraying and dusting were under way, show that two generations of the insect may occur annually in the latitude of central Georgia. Quaintance and Jenne (4, p. 126) also report the rearing of a second generation of the curculio at Barnesville, Ga., in the summer of 1910.

³ Reference is made by number (italic) to "Literature cited," p. 32.

⁴ Caused by *Cladosporium carpophilum* Thüm.

The life-history studies of the senior writer in 1921 and 1922 showed that in those seasons two full generations of the curculio occurred in Georgia, and a large percentage of the "worms" in the fruit harvested late in the season in those years were larvæ of the second brood. In 1923 there was only one generation of the insect in central Georgia, whereas in 1924 there was a partial second generation. Marked variation in the yearly life cycle of the curculio in Georgia is therefore evident, and may be ascribed to seasonal climatic conditions.

Prior to 1921 the importance of the possible presence of a second generation of the curculio was not fully realized, and the schedules for spraying and dusting were formulated with control measures directed against only one brood of the insect. It had been an accepted fact that for practical purposes the curculio produced only one well-defined generation annually (6, p. 20). Another reason for not recommending additional applications of spray lay in the desire to minimize the risk of injury from them. In view of the fact that recent studies have emphasized the possibility and importance of the occurrence in Georgia of two generations of the curculio in some years, and since the severe infestation of the curculio in 1920 did not manifest itself to any great extent until the late varieties of peaches were ready to be harvested, one would suspect the presence of two generations in the season of 1920. The schedules for spraying and dusting in 1920 were based on a single brood of curculio per season, and a second brood would have no control measures directed against it. It is very probable that two broods of curculio larvæ occurred in each of several seasons prior to 1920; that in each case the second brood was allowed to work unchecked, and that as a result its progeny appeared in uncontrollable numbers in 1920, when weather conditions were especially favorable for the development of the insect. It is also quite probable that after years of success in the control of the curculio and brown rot, growers had become rather careless in the conduct of spraying operations.

In each of the four years the experiments in spraying and dusting were conducted on the Hiley and the Elberta, two of the varieties most commonly grown in Georgia. The relative abundance of the curculio in the Hiley orchards in these four seasons is very indicative of the gradual reduction of the general infestation in Georgia as a result of the vigorous campaign waged during the period for the suppression of the curculio. The Hiley variety is seldom attacked by the second-brood larvæ of the curculio in years when there are two generations of the insect. As a consequence, the difference in the number of broods annually does not cause any considerable fluctuation in the yearly infestation of the Hileys. It is only in years when there is a heavy second generation of the curculio in a season characterized by late blossoming that second-brood larvæ are found in the Hileys.

Because of the tremendous curculio population left in the orchards in 1920, when Georgia experienced the heaviest infestation of the curculio in the history of the peach industry, the infestation was heavier in the season of 1921 than in the three seasons which followed. Assuming the infestation of 1921 to be 100 per cent, the relative abundance of the curculio in the Hiley experimental orchards for

each of the years 1921 to 1924, inclusive, expressed as a percentage, was, respectively, 100, 61, 39, and 30.

The yearly infestation of the curculio in Elberta orchards will fluctuate with the variation year by year, influenced largely by climatic conditions, in the number of generations of the insect in the South. An explanation is found in the fact that when there are two broods of larvae in a year the second brood will make its appearance in numbers at the time of the harvest of Elbertas. Thus, in 1921, 1922, and 1924, years in which there were two generations of the curculio in Georgia, the infestation was much heavier in the Elberta orchards than it was in 1923, when there was only one generation. A partial third generation of the insect was reared in the insectary in 1922. Again, assuming the severest infestation in any of the four years as 100 per cent, the relative abundance of the curculio in the Elberta experimental orchards for each of those years, taken in order and expressed as a percentage, was, respectively, 100, 99, 35, and 95.

CLIMATIC CONDITIONS AND CURCULIO BEHAVIOR

Climatic conditions have considerable influence on the development of the curculio and the severity of its infestations. It therefore may be of interest to tabulate the weather conditions that prevailed during the four seasons at the locality where the experiments were conducted, and to consider them in connection with the recorded activities of the curculio for the same seasons. Table 1 presents the mean temperature and the precipitation at Fort Valley for each of the nine months of February to October, inclusive, and the mean temperature and total precipitation for the duration of the nine months, in each of the four years of the experiments here reported. The "season" consisting of these nine months covers the entire range of the activity of the curculio in central Georgia. Of the four seasonal mean temperatures, that for 1921 was highest, and that for 1922 almost as high; these were the years in which two full generations of the curculio appeared.

TABLE 1.—*Precipitation and monthly mean temperatures, Fort Valley, Ga., February to October, 1921, 1922, 1923, and 1924 (8)*

Month	1921		1922		1923		1924	
	Mean temperature	Precipitation						
	° F.	Inches						
February.....	51.4	2.77	56.9	4.67	49.4	3.87	47.3	5.15
March.....	64.9	1.10	58.0	9.73	57.8	7.51	52.6	3.37
April.....	64.4	3.10	68.0	2.63	64.4	3.27	63.5	4.79
May.....	71.0	3.80	72.5	5.90	69.5	9.71	69.8	3.94
June.....	81.2	2.91	80.0	3.74	76.3	5.99	80.4	4.93
July.....	80.0	8.24	80.6	5.95	79.7	2.64	80.0	6.18
August.....	79.8	4.31	78.8	4.28	80.8	5.00	82.6	1.39
September.....	82.4	1.80	77.2	2.63	77.0	2.83	71.7	11.25
October.....	64.8	2.21	66.5	2.91	65.3	.46	63.4	.81
Mean temperature for season.....	71.1	70.9	68.9	67.9
Total precipitation for season.....	30.24	42.44	41.28	41.81

For 29 years, 1892 to 1920, the United States Weather Bureau has maintained climatological observations and records at Marshallville, Ga., 7 miles from Fort Valley, and, like the latter, in the heart of the Georgia peach belt. Data from the Marshallville records are therefore equally available for the purposes of these experiments, with the added advantage that the mean temperatures and precipitations for each month of the year, and for the year as a whole, derived from the records for the 29 years, afford satisfactory climatic data for use as normal or standard. In Table 2, therefore, are shown the mean temperature and the precipitation for each month of the year in each of the years 1921, 1922, 1923, and 1924, together with the means for each month, and for the year as a whole, derived from the observations for 29 years recorded at Marshallville.

The Marshallville data for the several months have been translated into graphical terms in Figures 1, 2, 3, and 4, there being one diagram for each of the four seasons covered by the study. The mean temperature and the total precipitation for each month is denoted by the location of a dot, as referred to the scale of temperature, at the left, and that of precipitation at the bottom of each graph. The dots denoting the 29-year means for the consecutive months are connected by a solid line, representing the normal values for the 12 months of the year, and this curve is shown without change in each figure. The dots for the consecutive months in each of the four years are connected by a broken line, each in its respective figure. With these curves the eye can readily compare each season with the others and with the normal.

TABLE 2.—*Precipitation and monthly mean temperatures, Marshallville, Ga.; means for 29 years, 1892 to 1920, and by months, for 1921, 1922, 1923, and 1924 (S)*

Month	1892 to 1920		1921		1922		1923		1924	
	Mean temperature	Mean precipitation								
	° F.	Inches								
January.....	47.8	4.42	51.3	2.04	48.0	4.96	53.0	7.41	44.4	6.11
February.....	49.0	5.91	52.6	3.67	57.5	5.73	51.3	5.25	48.4	6.19
March.....	58.1	5.47	66.3	1.18	58.2	12.31	59.6	8.87	53.4	3.98
April.....	64.4	4.30	65.0	4.82	68.4	1.63	65.4	3.71	64.6	4.98
May.....	73.4	3.21	71.3	4.49	73.2	8.24	71.0	12.85	70.4	3.76
June.....	79.3	4.14	81.8	2.15	80.2	6.87	77.0	5.54	81.4	7.28
July.....	80.9	6.04	80.8	10.46	81.4	3.36	80.4	4.44	81.0	8.09
August.....	80.5	5.04	80.8	2.63	79.0	5.83	81.6	4.43	83.0	3.30
September.....	76.2	3.07	83.5	2.45	77.6	2.53	78.5	1.14	73.0	9.83
October.....	66.0	2.92	65.5	2.14	67.5	2.84	67.5	T.	63.6	.97
November.....	55.6	3.07	60.2	4.13	59.4	.82	54.1	2.78	57.2	1.23
December.....	48.1	4.44	53.8	1.76	56.0	7.11	56.8	3.69	52.0	7.71
Mean temperature for year.....	-----	-----	67.7	-----	67.2	-----	66.4	-----	64.4	-----
Total precipitation.....	-----	-----	-----	41.92	-----	62.23	-----	60.11	-----	63.43

It may be seen from Table 2 and Figure 1 that the spring of 1921 was warmer than the normal spring, with less than normal precipitation. In the Georgia peach belt these conditions, especially during the month of March, promote the early emergence of the adult curculios from hibernation. When the curculio gets an early start

in the spring, and when weather conditions are favorable for pupation during May, June, and July, two generations of the insect will usually occur. The pupation of the insect is greatly facilitated by damp soil and high temperatures; the precipitation in May and July, 1921, was greater than normal, and the temperature for June was higher than normal. Two generations of the insect occurred in 1921, as a result of these conditions. The abnormal precipitation for July, 1921, more than 10 inches, is reflected in the very heavy infection of brown rot in the experimental orchard of Elberta peaches.

In 1922 there were again two generations of the curculio in central Georgia, and it may be seen from Table 2 and Figure 2 that the temperature in February of that year was considerably above normal. In this region a warm February has a tendency to bring the curculio out of hibernation earlier than usual, even though the temperature is normal during March, the month when a majority of the beetles appear. In May and June the precipitation was much greater than

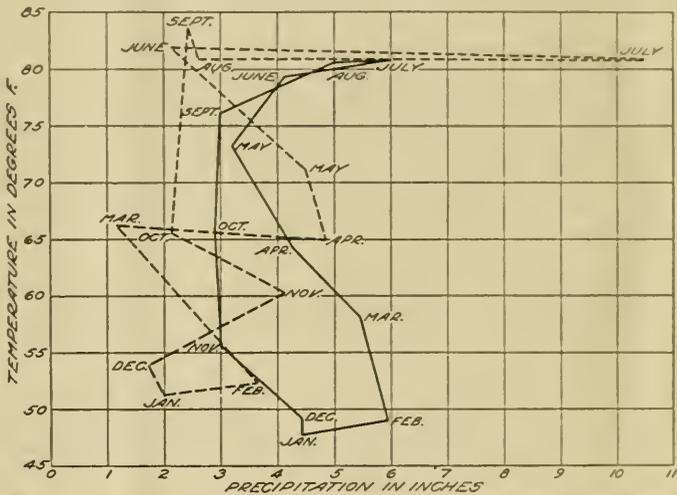


FIG. 1.—Comparison of normal monthly precipitation and temperature at Marshallville, Ga., for 29 years, with precipitation and mean temperature by months for the year 1921. Points indicating normal data are connected by a solid line; those indicating data for 1921 by a broken line

normal, tending to hasten the development of first-generation adults in time to produce a second generation. The heavy precipitation for May and June is reflected in the scab infection of 1922. There was also a moderate infection of brown rot in the same year.

In 1923 there was but one generation of the curculio. A cool, wet spring so prolongs the hibernation of adult curculios that they do not have sufficient time to produce a second generation before the peach crop is harvested. Figure 3 and Table 2 show a precipitation much above the normal for the first half of that year. Temperatures were about normal. The heavy precipitation in May is reflected in the heavy scab infections in 1923 in the experimental orchards of Hiley and Elberta peaches.

A small second generation of the curculio occurred in 1924. Weather conditions during the period when the insects usually leave hibernation were not very favorable for their early appearance in

orchards. Temperatures were unusually low; the precipitation for March, however, was below normal. (Fig. 4.) Although the insect did not leave hibernation especially early in 1924, weather conditions

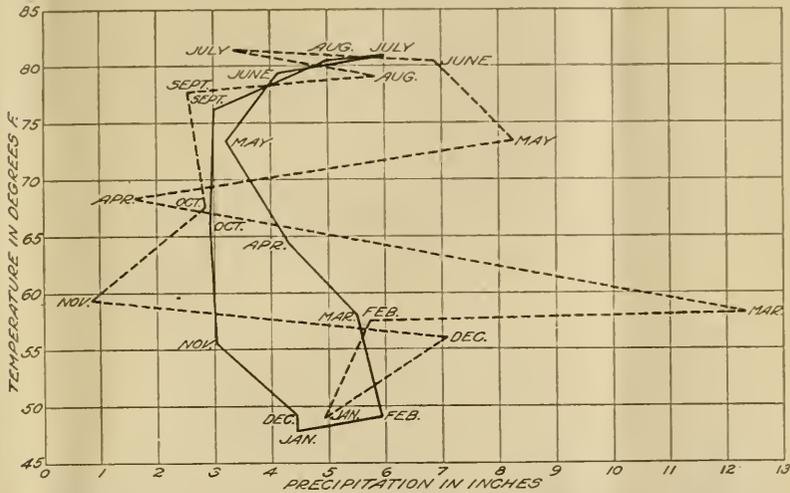


FIG. 2.—Comparison of normal monthly precipitation and temperature at Marshallville, Ga., for 29 years with precipitation and mean temperature by months for the year 1922. Points indicating normal data are connected by a solid line; those indicating data for 1922 by a broken line

during May, June, and July were so favorable for the pupation of the insect that the development of first-generation adults was hastened, and a small second generation was produced; the precipitation for

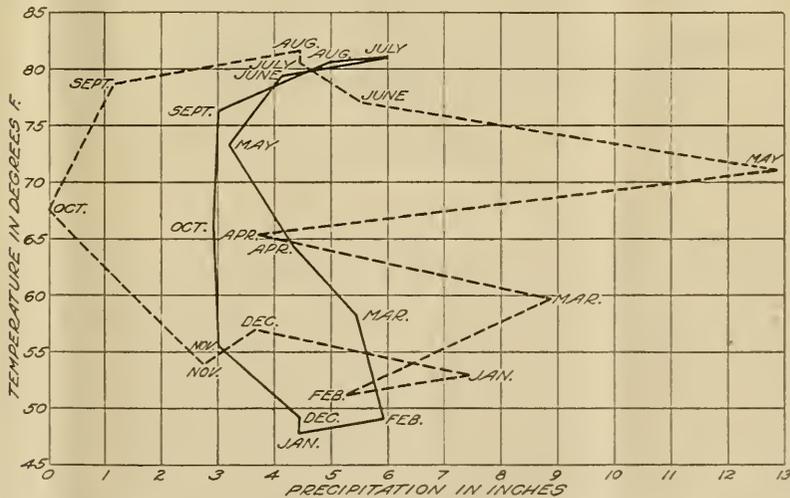


FIG. 3.—Comparison of normal monthly precipitation and temperature at Marshallville, Ga., for 29 years, with precipitation and mean temperature by months for the year 1923. Points indicating normal data are connected by a solid line; those indicating data for 1923 by a broken line

these months was higher than normal, and the temperatures higher than usual in June and July. The abnormally high precipitation in the early summer of 1924 is reflected in the heavy scab infection in the

experimental orchards of the Hiley and Elberta peaches and the moderately heavy brown rot infection in the Elberta orchard.

In each of the four years that this experimental work was under way there was a precipitation above the normal for the period from April to July, which undoubtedly facilitated the development in those years of brown rot and scab in the peach orchards of Georgia. In most cases the check plats in the experimental orchards showed heavy infections of these diseases.

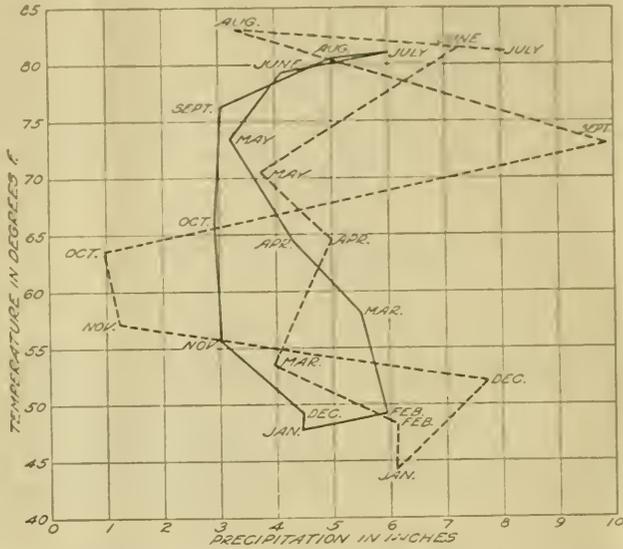


FIG. 4.—Comparison of normal monthly precipitation and temperature at Marshallville, Ga., for 29 years, with precipitation and mean temperature by months for the year 1924. Points indicating normal data are connected by a solid line; those indicating data for 1924 by a broken line

EXPERIMENTS ON SPRAYING AND DUSTING IN THE GEORGIA PEACH BELT

In the seasons of 1921, 1922, 1923, and 1924 the extensive spraying and dusting experiments in the Georgia peach belt were performed in duplicate in orchards of Hiley and Elberta peaches, two of the varieties most commonly grown in the State. An effort was made to select for this purpose orchards which had suffered severely from attacks of curculio and brown rot in the previous season. In each year one orchard of each variety was chosen, the two orchards being at some distance from each other, so that a test of the various treatments would be afforded in two different localities. Each orchard was divided into sections, each including a convenient number of trees. In the central part of each section a certain number of trees (10, except in the case of a few small sections) were reserved as "record" trees, the fruit from which was harvested separately, including the fruit picked and that dropped from the tree during and just before the harvest season. Each record tree was designated by a white cloth band or tape encircling the tree and resting on the outer limbs. Each peach was cut open, examined, and recorded, so that the exact percentages of sound fruit from these trees and of fruit

injured by the curculio, brown rot, and scab could be ascertained. Throughout the season all dropped fruit under the record trees was collected and examined to determine the extent of curculio infestation. In the season of 1922, 110,648 peaches were cut open in one orchard alone and in the four seasons a total of 551,361. Besides the detailed data concerning the fruit from the record trees, data were also obtained on the commercial production of merchantable and cull fruit from all the trees in each plat.

In drawing up the outlines for the experiments a special effort was made to include schedules which would result in ascertaining the best time for making applications of lead arsenate for controlling the second brood of the curculio. A number of arsenate-of-lead treatments were therefore included for tests one month before the ripening of the peaches and again 7 to 10 days before ripening, as suitable times for making this application.



FIG. 5.—Peach blossoms, showing curculio feeding marks on the calyces

Observations by the senior author in Mississippi in 1920, substantiated by similar observations in Georgia in 1921, revealed the fact that when the adult curculios first appear from hibernation in the spring they feed to a considerable extent on the green calyces of the peach flower. (Fig. 5.) A number of plats were therefore provided to ascertain the results of poisoning the calyces with arsenate of lead before the beetles visited them for their first meal. Plats were also provided for testing self-boiled lime-sulphur and sulphur dust, respectively, one week before the ripening, to determine their effectiveness in the prevention of brown rot; and several plats were included to compare the efficiency of the spray with that of the dust.

EXPERIMENTS IN 1921

An account of the 1921 experiments, including results obtained and a detailed discussion of the data, has already been published by the Department of Agriculture as Department Circular 216 (7). A dis-

ussion of the data for 1921 will not be repeated in this publication but the results will be referred to in deriving conclusions.

EXPERIMENTS IN 1922

In planning the experiments in spraying and dusting for the season of 1922, special attention was given to plats which should receive an application of arsenate of lead when 75 per cent of the petals had fallen and another application four weeks before the fruit ripened, besides other more usual applications. The two applications were intended for continuing the tests of the early treatment with arsenate of lead as a preventive of curculio infestations in the young fruits, and tests of the late arsenical treatment as a protection of the ripening peaches from the second brood of larvæ. Schedules were also included for testing the comparative effectiveness of the sprays and dusts. A combination of sulphur, lime, and calcium caseinate, the ingredients of which are mixed together dry before adding water, was tested on one plat for effectiveness against brown rot and scab. To test the possible usefulness of a "sticker," or "spreader," a plat was provided which received the same treatment as the standard plat, except that in each application calcium caseinate was added to the spray. Table 3 gives an outline of the experiments planned for the season of 1922.

TABLE 3.—Outline of experiments in spraying and dusting peach trees, for the season of 1922, Fort Valley, Ga.

Plat	Time of application				
	As petals fall	When calyces are shedding	Two weeks after shedding of calyces	Four weeks before harvest	Just before picking
I.....	A. L. L.....	A. L.-L.....	A. L.-S. B.....	A. L.-S. B.....	
II.....	A. L. L. C.....	A. L.-L.-C.....	A. L.-S. B.-C.....	A. L.-S. B.-C.....	
III.....	A. L.-L.....	A. L.-L.....	A. L.-S. B.....	S. B.....	
IV.....	A. L. L.....	A. L.-L.....	A. L.-S. B.....	A. L.-S. B.....	80-20 dust
V.....	A. L. L.....	A. L.-L.....	A. L.-S.....	A. L.-S.....	
VI.....	80-5-15.....	80-5-15.....	80-5-15.....	80-5-15.....	
VII ¹					

¹ Check plat; not treated.

A. L. = Arsenate of lead powder, 1 pound to 50 gallons of spray.

L. = Milk of lime, made from 3 pounds of stone lime per 50 gallons of spray.

C. = Calcium caseinate, 6 ounces to 50 gallons of spray.

S. B. = Self-boiled lime-sulphur mixture, 8-8-50.

S. = Sulphur 6 pounds, hydrated lime 4 pounds, and calcium caseinate 8 ounces, per 50 gallons spray.

(Sulphur, lime, and calcium caseinate were mixed dry and then the water was added.)

80-5-15 = Dust; sulphur, 80 per cent; arsenate of lead, 5 per cent; lime, 15 per cent.

As in 1921, the experiments were performed on trees of the varieties Hiley and Elberta. Both orchards were practically level and had a sandy loam soil. The crop that matured in the Elberta experimental orchard, however, was so light that the results from it are not reliable, and only the results of the experiments with the Hiley peaches will be given. From 500 to 1,000 fruits should be harvested from each record tree for reliable results from spraying or dusting. An average of only 54.7 fruits per tree were harvested from the Elberta record trees in 1922.

The orchard was divided, as in 1921, into plats of as nearly equal size as practicable. Each plat consisted of about 150 trees, except the check plat, which was in two parts, in opposite corners of the

orchard, and contained in all 70 trees. An effort was made to place all plats at equal distance from the hibernating quarters of the curculio. (Fig. 6.)

The applications of dust were made with large power dusting machines and the liquid was applied with power sprayers, developing from 250 to 275 pounds pressure. The spraying and dusting were done only when favorable weather conditions prevailed. These and all other operations in the present research were performed by the parties named as writers of this bulletin.

In Tables 4, 5, and 6 the results of the experiments in spraying and dusting conducted on the Hiley peach trees in the season of 1922 are

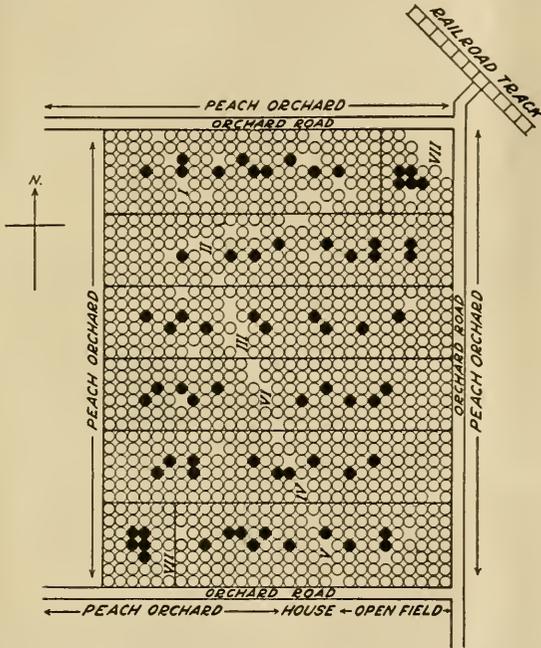


FIG. 6.—Diagram of orchard of Hiley peaches used for experiments in the season of 1922. Each tree is represented by a circle, the solid black circles representing record trees

given in terms of percentages. Table 4 presents the results obtained from the examination of the fruit from the record trees of each plat at harvest time, besides which the last two columns give the percentages of merchantable and cull fruit harvested from those trees, as determined by grading the fruit before it was cut open for examination. In Table 5 are the numbers of fruit that dropped to the ground from the record trees in the different plats from shortly after the pollination season until the fruit was ready to be harvested, and the percentage of curculio-wormy fruit in each. Table 6 gives the commercial results of fruit from all trees in each plat.

TABLE 4.—Summary of results of experiments in peach dusting and spraying at Fort Valley, Ga., in 1922; fruit harvested from record trees of the Hiley variety

Plat	Total number of fruit	Percentage of total fruit having—										Percentage of total fruit found to be sound ¹	Percentage of total fruit as graded before being opened for examination							
		Curculio larvae		Brown rot		Scab		Curculio larvae only		Brown rot only			Scab only		Curculio larvae and—	Brown rot and scab	Brown-rot infection at curculio puncture	Scab and brown-rot infection at curculio puncture	Merchantable fruit	Cull fruit
		Curculio larvae	Brown rot	Scab	Curculio larvae only	Brown rot only	Scab only	Brown rot and scab	Brown rot	Scab	Brown rot and scab									
I.....	8,107	1.8	1.1	0.8	1.6	0.9	0.8	0.2	96.5	79.9	20.1
II.....	9,727	3.4	.6	.8	3.2	.5	.7	0.11	95.4	82.6	17.4
III.....	9,433	17.0	4.9	.5	15.3	3.3	.4	0.1	1.5	70.3	76.4	23.6
IV.....	11,620	3.4	.9	.8	3.1	.7	.72	95.0	85.1	14.9
V.....	8,685	4.2	1.1	.3	3.9	.8	.33	94.5	74.7	25.3
VI.....	9,782	11.3	5.2	.9	9.4	3.3	.9	1.9	84.5	81.7	18.3
VII ²	8,180	22.9	32.0	64.9	3.6	11.3	42.7	0.23	7.8	9.2	6.0	5.0	13.9	50.0	50.0

¹ Some fruits on these plats were small, hence the high percentage of culls.

² Check plat; not sprayed or dusted.

TABLE 5.—Number of peaches dropping from Hiley peach trees, and percentage of them infested by curculio, in experimental orchards at Fort Valley, Ga., season of 1922

Plat	Total number of drops	Total percentage of drops infested by curculio
I.....	5,160	11.8
II.....	5,207	15.2
III.....	7,264	25.7
IV.....	7,669	12.4
V.....	3,840	17.0
VI.....	7,869	28.4
VII.....	8,105	43.1

TABLE 6.—Commercial results of fruit from all trees in each plat of the Hiley variety, used in the peach spraying and dusting experiments, Fort Valley, Ga., 1922

Plat	Number of trees in plat	Average merchantable fruit per tree (expressed in cups; six cups equal one crate)	Average cull fruit per tree (expressed in cups; six cups equal one crate)
I.....	147	¹ 13.5	3.4
II.....	164	17.1	3.6
III.....	165	15.2	4.7
IV.....	168	21.7	3.8
V.....	151	² 13.0	4.4
VI.....	168	18.7	4.2
VII.....	³ 70	8.1	8.1

¹ Some of this fruit was small. Much sound fruit was graded as culls on account of size.

² Fruit very small on account of serious foliage burn.

³ In two portions, in opposite corners of the orchard.

A study of Table 4 shows that there was a moderate infection of brown rot and, for central Georgia, a heavy infection of scab. There was a moderately heavy infestation of curculio, although this infestation in the untreated or check plat was not so heavy as in that of 1921. Of the fruit from the check plat, 22.9 per cent was infested with the curculio; 32 per cent showed brown-rot infection, and 64.9 per cent infection with scab.

To determine the effect of early spraying on the control of the curculio all of the small peaches that drop to the ground before maturity must be examined, as the early applications of arsenate of lead are directed especially against injury by the curculio to the small peaches. The efficiency of an early application of arsenate of lead as a killer of adult curculios, as they appear from hibernation and before they have had an opportunity to deposit eggs, was again clearly demonstrated in the work of this year. Table 5 shows that of the "drops" from plat III, which did not receive the early arsenate-of-lead treatment, 25.7 per cent were infested with curculio, whereas the percentages of infestation in the four plats (I, II, IV, and V) which received the early treatment averaged but 14. According to these results the application of arsenate of lead when 75 per cent of the petals had fallen reduced the number of curculio-infested fruits nearly 50 per cent. A reduction of the amount of curculio infestation in the "drops" correspondingly reduced the size of the second brood of larvæ which may attack the peaches later in the season.

The value of an application of arsenate of lead four weeks before the fruit is due to ripen, for the control of overwintered females which may deposit eggs throughout the fruit growing season, or for the control of a second brood of curculio, is shown in Table 4, which contains the data on the harvested fruit alone. Of the fruit harvested from the record trees on Plat III, which did not receive the late arsenate-of-lead treatment, 17 per cent was infested with curculio, whereas the percentages of infestation in the fruit harvested from Plats I, II, IV, and V, which received the late sprays for the control of the second brood of "worms," averaged only 3.2.

The close interrelation between curculio injury and brown-rot infection is indicated in Table 4. Plat III was found to have a curculio infestation of 17 per cent and a brown-rot infection of 4.9 per cent. Plats I, II, IV, and V, the several curculio infestations of which average 3.2 per cent, have an average of brown-rot infections of only 0.9 per cent.

As in 1921, the spray was superior to the dust for the control of curculio. Apparently there was also a somewhat better control of brown rot from the use of the spray than from dusting, although the differences between the two methods of brown-rot control are not great and are probably to be attributed to a greater curculio infestation in the dusted plat. In Plat VI, the dusted plat, 11.3 per cent of the fruit was infested with curculio and 5.2 per cent was infected with brown rot, as compared with a curculio infestation of 1.8 per cent and a brown-rot infection of 1.1 per cent in Plat I (Table 4), the plat which received the sprays at the same time that Plat VI received the dust applications.

The addition of calcium caseinate to the sprays (Plat II) to increase their sticking and spreading qualities did not appreciably increase the

efficiency of either the insecticide or the fungicide. The fruit harvested from Plat II (Table 4) was found to have a curculio infestation of 3.4 per cent and a brown-rot infection of 0.6 per cent, as compared with a curculio infestation of 1.8 per cent and a brown-rot infection of 1.1 per cent for Plat I (Table 4). Plats I and II were sprayed at the same times and with the same materials, except that calcium caseinate was added to each application for Plat II.

The sulphur, lime, and calcium caseinate used in Plat V controlled brown rot and scab, but the burning of the foliage from the use of this fungicide in combination with arsenate of lead was so severe that the size and flavor of the fruit were affected. The trees were entirely defoliated by September, more than a month before they would normally have shed their leaves, and this injury seems to have affected the vitality of the fruit buds for the succeeding year, as revealed by the size of the crop on these trees in 1923. Because of risk of severe injury, the mixture of sulphur, lime, and calcium caseinate tested this year could not be recommended for use in Georgia against brown rot and scab, at least when used with arsenate of lead. As shown in Table 4, the percentage of harvested fruit affected with brown rot was much less in all the treated plats than in the check plat; the percentage of rotted fruits averaged somewhat lower in the sprayed plats than in the dusted plat. The late application of dust in Plat IV, which had previously received two applications of self-boiled lime-sulphur at the regular times, made no appreciable difference in the control of brown rot. The dropping of fruit before harvest time is not considered in the brown-rot data, as the counts showed that very little brown rot developed until the fruit was ready for harvest.

Scab was well controlled by all of the fungicides used in the experimental work for 1922. Table 4 shows that the scab infection of the fruit harvested from all sprayed and dusted plats was less than 1 per cent. The infection of scab was 64.9 per cent on the fruit harvested from the record trees in the check, or untreated, plat.

Table 6 shows that when the fruit from Plat VII was graded 50 per cent of it was thrown into the culls. Furthermore, these untreated trees matured an average of only $1\frac{1}{3}$ crates of merchantable fruit per tree, as compared with an average of from $2\frac{1}{2}$ to $3\frac{3}{4}$ crates for the trees in the plats that were sprayed or dusted.

EXPERIMENTS IN 1923

Since the experiments in 1921 and 1922 had shown the treatment with arsenate of lead four weeks before the ripening of the fruit to be of importance in the control of the curculio, it was decided without further experimentation to incorporate it in the regular schedule. The testing of the early treatment for the poisoning of adult curculios directly after their emergence from hibernation was continued. The effectiveness of four applications of a spray containing three-fourths of a pound of arsenate of lead to each 50 gallons of spray was compared with three applications of spray containing 1 pound of arsenate of lead to each 50 gallons. Tests as to the desirability of adding calcium caseinate as a "sticker" or "spreader" were continued, and two different formulas of the spray containing sulphur, lime, and calcium caseinate were tested for control of brown rot and scab. These formulas were thought to be an improvement on the formula

used in 1922, and were supposed to be safer, since they contained a large excess of lime to reduce the danger of injury from the combination of arsenate of lead and sulphur. Three applications of self-boiled lime-sulphur were compared with two applications of these mixtures for brown-rot and scab control. The testing of the comparative effectiveness of dusting and spraying was continued. Two formulas for dusting, with different percentages of sulphur, were tested for effectiveness against brown rot and scab.

Table 7 gives in outline the schedules used in the experiments in 1923.

TABLE 7.—Outline of experiments in spraying and dusting peach trees, for the season of 1923, Fort Valley, Ga.

Plat	Time of application			
	As petals fall	When calyces are shedding	Two weeks after shedding of calyces	Four weeks before harvest
I.....	A. L.-L.....	A. L.-L.....	S. B.....	A. L.-S. B.
II.....	A. L.-L.-C.....	A. L.-L.-C.....	C.-S. B.....	A. L.-C.-S. B.
III.....	A. L. 3-L. 3.....	A. L. 3-S. B.....	A. L. 3-S. B.....	A. L. 3-S. B.
IV.....	A. L.-L.....	S. B.....	A. L.-S. B.
V.....	A. L.-L.....	A. L.-S.....	A. L.-S.
VI.....	0-5-95.....	0-5-95.....	80-5-15.....	80-5-15.
VII.....	0-5-95.....	0-5-95.....	50-5-45.....	50-5-45.
VIII ¹
IX.....	A. L.-L.....	A. L.-S. 1.....	A. L.-S. 1.

¹ Check plat; not treated.

- A. L. = Arsenate of lead powder, 1 pound to 50 gallons of spray.
 A. L. 3 = Arsenate of lead powder, $\frac{3}{4}$ pound to 50 gallons of spray.
 L. = Milk of lime, made from 3 pounds of stone lime per 50 gallons of spray.
 L. 3 = Milk of lime, made from 2 $\frac{1}{4}$ pounds of stone lime per 50 gallons of spray.
 C. = Calcium caseinate, 6 ounces to 50 gallons of spray.
 S. B. = Self-boiled lime-sulphur mixture, 8-8-50.
 S. = Sulphur 6 pounds, hydrated lime 8 pounds, calcium caseinate 12 ounces per 50 gallons of spray.
 (Sulphur, lime, calcium-caseinate mixture.)
 S. 1 = Sulphur 3 pounds, hydrated lime 4 pounds, calcium caseinate 6 ounces per 50 gallons of spray.
 (Sulphur, lime, calcium-caseinate mixture.)
 0-5-95 = Dust; arsenate of lead, 5 per cent; hydrated lime, 95 per cent.
 80-5-15 = Dust; sulphur, 80 per cent; arsenate of lead, 5 per cent; lime, 15 per cent.
 50-5-45 = Dust; sulphur, 50 per cent; arsenate of lead, 5 per cent; lime, 45 per cent.

As in the two years preceding, the experiments for 1923 were duplicated on two varieties of peaches, the Hiley and the Elberta. The orchards used were on sandy loam soil, and the land was generally level. Since the orchards were about one-half mile apart a test of the various treatments was afforded in two different localities. About 2,600 trees, divided for the most part into plats of as nearly 150 trees as practicable, were used in the experiments. (Figs. 7 and 8.) Three plats of each variety, including the check plats, were composed of about 75 trees each. Near the center of each plat 10 trees were selected as record trees, the fruit from which was cut open and examined for injury from the curculio, brown rot, and scab. All "drops" from these record trees were collected at intervals, and examinations made for data on the curculio infestation. In the season of 1923, 68,746 peaches were cut open to obtain data from which to draw conclusions.

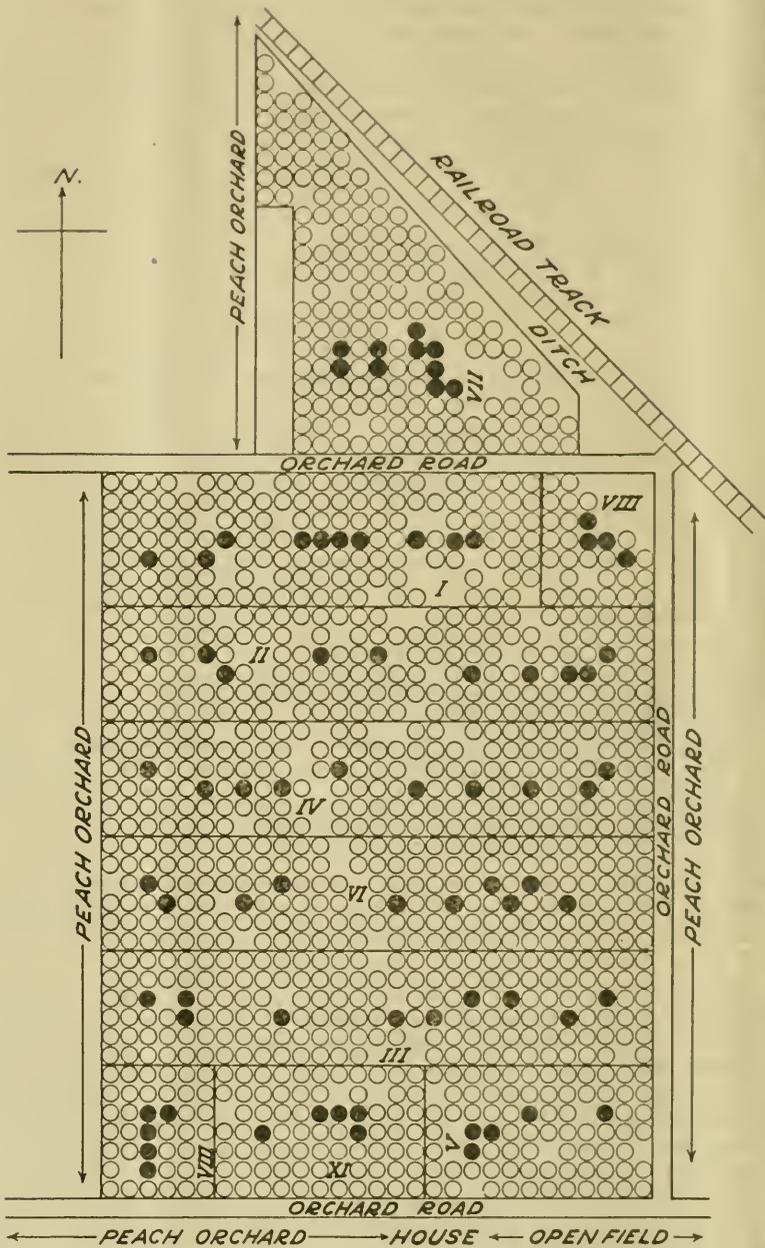


FIG. 7.—Diagram of orchard of Hiley peaches, used for experiments in the season of 1923. Each tree is represented by a circle, the solid black circles representing record trees

No data on curculio control were taken for the fruit from Plat VII, as the arsenate-of-lead treatments on this plat were the same as those on Plat VI. The dust schedule used on Plat VII was used for testing the effectiveness of a low percentage of sulphur for control of brown rot and scab.

All applications of liquid and dust made in the season of 1923 were applied with large power spraying and dusting machines. This, and all other operations in 1923, were performed by the writers.

Tables 8, 9, and 10 present the results, in percentages, of the experiments in spraying and dusting conducted on the Hiley variety during

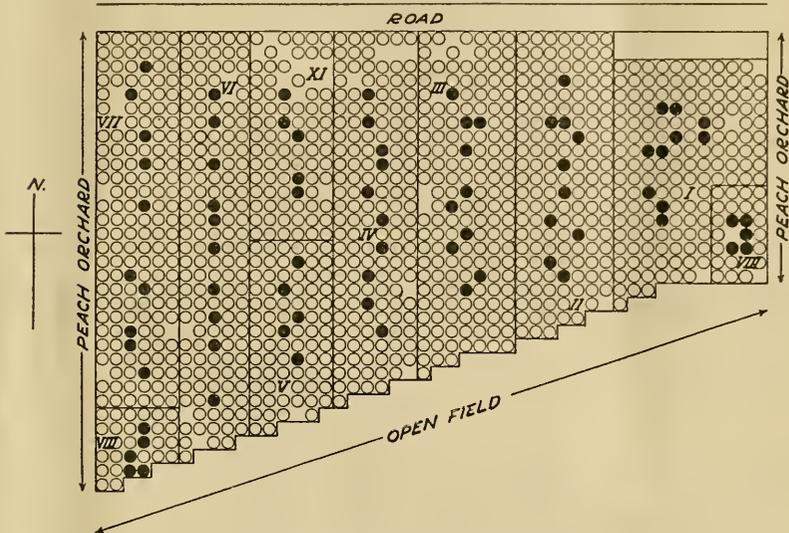


FIG. 8.—Diagram of orchard of Elberta peaches, used for experiments in the season of 1923. Each tree is represented by a circle, the solid black circles representing record trees

the season of 1923. Table 8 presents the data obtained from cutting open the fruit harvested from the record trees of each plat. The apparent discrepancies between "sound fruit" and "merchantable fruit" in this table were due to the fact that many peaches containing only a few scab spots were allowed by the graders to pass as merchantable fruit. Table 9 contains the percentages of curculio-wormy fruit that dropped to the ground from the record trees at various times before harvest, and Table 10 presents the commercial results, in merchantable and cull fruit, from all the trees in each plat.

TABLE 8.—Summary of results of experiments in peach dusting and spraying at Fort Valley, Ga., in 1923; fruit harvested from record trees of the Hiley variety

Plat	Total number of fruit	Percentage of total fruit having—											Percentage of total fruit found to be sound		Percentage of total fruit as graded before being opened for examination		
		Curculio	Brown rot	Scab	Curculio larvae only			Curculio larvae and—			Brown rot and scab	Brown-rot infection at curculio puncture	Scab and brown-rot infection at curculio puncture	Percentage of total fruit found to be sound	Merchantable fruit	Cull fruit	
					Brown rot only	Scab only	Brown rot and scab	Brown rot	Scab								
		Curculio	Brown rot	Scab						Curculio larvae only	Brown rot only	Scab only	Brown rot and scab	Brown rot	Scab		
I.....	2,861	0.9	5.8	18.6	0.6	3.1	16.1
II.....	3,333	1.3	1.8	20.4	.8	1.1	19.4	0.3	.5	.2
III.....	4,585	1.5	2.7	7.7	1.2	2.1	7.02	.5	.1
IV.....	3,936	1.8	3.0	14.0	1.4	2.1	13.21	.6	.2	.1
V.....	1,023	.6	2.2	7.0	.4	1.6	6.41	.5	.1
VI.....	4,813	1.5	10.2	17.8	1.0	7.4	15.02	2.5	.2	.1
VII.....	3,709	6.8	23.0	5.4	21.6	1.4
VIII ¹	4,194	6.4	30.6	92.5	.2	4.4	63.8	0.2	3.0	23.0	.5	2.5
IX.....	880	3.6	2.3	7.5	2.9	1.9	6.9	.14	.1	.2

¹ No records on curculio infestation taken for this plat. ² Check plat; not sprayed or dusted.

TABLE 9.—Number of peaches dropping from Hiley peach trees and percentage of them infested by curculio in experimental orchards at Fort Valley, Ga., 1923

Plat	Total number of drops	Total percentage of drops infested by curculio
I.....	1,304	9.4
II.....	1,467	13.2
III.....	1,922	16.3
IV.....	1,493	13.1
V.....	644	33.1
VI.....	2,933	15.8
VIII.....	2,637	35.9
IX.....	444	8.8

TABLE 10.—Commercial results of fruit from all trees in each plat of the Hiley variety used in the peach-spraying and dusting experiments, Fort Valley, Ga., 1923

Plat	Number of trees in plat	Average merchantable fruit per tree (expressed in cups; six cups equal one crate)	Average cull fruit per tree (expressed in cups; six cups equal one crate)
I.....	141	8.90	0.95
II.....	158	10.85	.85
III.....	165	14.35	.95
IV.....	159	13.25	.90
V ¹	77	7.20	.40
VI.....	166	14.30	1.90
VII ²	157	11.30	.95
VIII ³	68	7.05	5.50
IX ¹	73	5.60	.50

¹ Light crop in 1923 because of severe defoliation in 1922 from the mixture of sulphur, lime, calcium caseinate, and arsenate of lead mentioned on p. 10.

² Fruit damaged by curculio not graded out on this plat.

³ In two portions, in opposite corners of the orchard.

Life-history studies showed that in the season of 1923 there was only one generation of the curculio at Fort Valley, Ga. Similar studies had shown two complete generations in the season of 1921 and again in that of 1922. Since there was only one generation in 1923, the early applications of arsenate of lead did not have a chance to prove their effectiveness against a second brood of larvæ. Therefore, as shown in Table 8, there was little difference between the number of the curculio-infested peaches from the plats that received the early spray and those that were not sprayed until the calyces, or "shucks," were shedding. Since there is no way to predict accurately early in the season whether two generations of the curculio will occur, or only one, peach growers could not afford to omit the early arsenate-of-lead treatment, as this materially reduces the size of the second brood of "worms" in years when two generations occur.

In 1923 the curculio infestation in the experimental orchard of Hiley peaches was light, as only 6.4 per cent of the fruit harvested from the check, or untreated, plat was "wormy." The spray schedule recommended to the growers, which was the one used in treating Plat I, gave the best control of the curculio.

The control of the curculio, as shown by the percentage of infestation in the harvested fruits, was not quite so good in Plat III, which received four applications of arsenate of lead in the proportion of three-fourths of a pound to 50 gallons of spray, as in Plat I, which received three applications in the proportion of 1 pound of arsenate of lead to 50 gallons of spray. (Tables 8 and 9.) Moreover, the four applications of the less poisonous spray were otherwise less desirable than three applications of the stronger, because of the greater injury which the former inflicted on the foliage.

Three applications of self-boiled lime-sulphur gave slightly better control of brown rot (Table 8, Plat III) than two applications. The control of scab was also somewhat better from the three applications. Since in previous years it had been found unnecessary to make an application for the control of scab earlier than about four weeks after the falling of the petals, it is probable that if in the plats receiving two applications of the fungicide the first application had been made slightly earlier, control would have been as good as in the plat receiving three applications. The addition of calcium caseinate did not increase the effectiveness of the arsenate of lead used for controlling the curculio in either the "drops" or the harvested fruit. The plat receiving the regular treatments but with the addition of calcium caseinate to all sprays yielded harvested fruit with a smaller percentage of brown rot (Table 8, Plat II), but the scab on this plat was heavier. The differences, however, were too small to be significant.

The two different mixtures of sulphur, hydrated lime, and calcium caseinate used on Plats V and IX gave very satisfactory control of brown rot and scab, but there was more burning of the foliage in these two plats than in any other plat in the orchard. While this burning was not nearly so severe as that obtained from the mixture used in 1922, it was too serious to warrant an unqualified recommendation of the mixture for use in the South. It should be noted, however, that arsenate of lead was used with it in both applications. The spray continued to give better control of curculio and brown rot

than the dust, as recorded in Table 8 for Plats I and VII. The 50 per cent sulphur dust used on Plat VII gave a somewhat better control of brown rot than the 80 per cent sulphur dust used on Plat VI, but not nearly so good control of scab.

Scab was quite prevalent in this orchard in 1923. The fruit harvested from the check plat was 92.5 per cent scabby, although the individual fruits were not so severely attacked as in northern orchards. Brown rot was moderately severe, as indicated by 30.6 per cent of rotten fruit from the check plat.

Tables 11, 12, and 13 give, in percentages, the results of the experiments in spraying and dusting conducted on the Elberta variety during the season of 1923. Table 11 gives the data obtained from the examination of the fruit harvested from the record trees, Table 12 the percentages of curculio infestation of the "drops" from the record trees in each plat, and Table 13 brings together the commercial results, in merchantable and cull fruit, from all the trees in each plat.

TABLE 11.—Summary of results of experiments in peach dusting and spraying at Fort Valley, Ga., in 1923; fruit harvested from record trees of the Elberta variety

Plat	Total number of fruit	Percentage of total fruit having—										Percentage of total fruit found to be sound		Percentage of total fruit as graded before being opened for examination		
		Curculio	Brown rot	Scab	Curculio larvæ only			Curculio larvæ and—			Brown-rot infection at curculio puncture					Scab and brown-rot infection at curculio puncture
					Brown rot only	Scab only	Brown rot and scab	Brown rot	Scab	Brown rot and scab						
I.....	1,827	6.1	1.0	8.6	5.1	1.0	7.6			1.0				85.3	91.7	8.3
II.....	1,661	4.7	1.5	10.0	4.1	1.2	9.5			.4	0.1	0.2		84.5	91.0	9.0
III.....	1,354	8.1	1.0	6.0	7.0	.9	4.9			1.1	.1			88.1	90.8	9.2
IV.....	1,164	7.0	2.5	13.9	5.7	1.5	12.9			1.0	.7	.3		78.6	89.3	10.7
V.....	630	3.0	3.8	7.0	2.7	2.5	6.0							87.5	90.3	9.7
VI.....	912	16.2	3.4	24.5	11.2	1.9	19.0	0.3	0.2	4.2	.7	.3	0.3	62.2	89.1	10.9
VII.....	1,932	7.3	44.1			4.4	41.2				2.9			51.5	84.0	16.0
VIII ¹	1,407	28.2	11.9	67.0	8.8	3.6	45.8	.6	.9	14.9	3.8	1.1	1.9	18.6	69.1	30.9
IX.....	580	5.1	1.8	3.1	4.6	1.4	2.6			.3	.2	.2		90.7	88.5	11.5

¹ No records of curculio infestation taken on this plat.

² Check plat: Not sprayed or dusted.

TABLE 12.—Number of peaches dropping from Elberta peach trees, and percentage of those infested by curculio, in experimental orchard at Fort Valley, Ga., 1923

Plat	Total number of drops	Total percentage of drops infested by curculio
I.....	2,627	5.2
II.....	2,368	4.3
III.....	2,629	2.1
IV.....	1,269	7.9
V.....	1,257	8.9
VI.....	1,650	12.1
VIII.....	2,367	16.1
IX.....	934	2.6

TABLE 13.—Commercial results of fruit from all trees in each plat of the *Elberta* variety, peach spraying and dusting experiments, Fort Valley, Ga., 1923

Plat	Number of trees in plat	Average merchantable fruit per tree (expressed in cups; six cups equal one crate)	Average cull fruit per tree (expressed in cups; six cups equal one crate)
I.....	148	7.65	0.7
II.....	146	7.15	.7
III.....	158	5.9	.6
IV.....	148	4.95	.6
V.....	77	5.6	.6
VI.....	145	4.05	.5
VII ¹	155	7.9	1.5
VIII ²	54	3.8	1.75
IX.....	79	4.6	.5

¹ Fruit damaged from curculio not graded out on this plat.

² In two portions, at opposite ends of the orchard.

The spraying and dusting treatments for controlling the curculio received a much more severe test in the plats of *Elberta* peaches than in those of the *Hiley* variety during the season of 1923. Of the fruit harvested from the check (or untreated) plat, 28.2 per cent was infested with curculio larvæ. Scab was more prevalent than is usual in central Georgia, the check plat having an infection of 67 per cent. Brown rot was not so serious; 11.9 per cent of the fruit in the check plat was affected with it.

Owing to the fact that there was but one brood of the curculio in 1923, the value of the early application of arsenate of lead was not so distinctly shown in the curculio infestation of the fruit harvested from the various plats. The early spray did, however, reduce the early infestation by the curculio, as evidenced by examination of the "drops." This reduction would have had a corresponding effect on the reduction of the infestation in the harvested fruit had there been two generations of the curculio. The "drops" from plats IV and V, neither of which received the early application of arsenate of lead, were more heavily infested by curculio than the "drops" from Plats I, II, and III, to all of which the early application was made (Table 12).

The fruit harvested from Plat III, which received four applications of spray containing three-fourths of a pound of arsenate of lead to 50 gallons of water, had an infestation of 8.1 per cent; the infestation of Plat I, which received three applications of spray containing 1 pound of arsenate of lead to 50 gallons of water, was 6.1 per cent. Because of the injury inflicted on the foliage sprayed, the schedule for Plat III is not so safe as the schedule by which Plat I was treated.

Three applications of self-boiled lime-sulphur to Plat III gave no better control of brown rot (see Table 11) than did two applications to Plat I, and the control of scab was practically the same in both cases. The addition of calcium caseinate seemed to cause a slight increase in the effectiveness of the arsenate of lead against the curculio in Plat II, but it did not increase the effectiveness of the fungicide against brown rot or scab.

The two sprays of sulphur, hydrated lime, and calcium caseinate in combination with arsenate of lead, when used on Plats V and IX, gave essentially the same results as their application to the Hiley variety. Good control of both brown rot and scab resulted, but the burning of the foliage was too severe to warrant an unqualified recommendation for its use. The sprays controlled curculio, brown rot, and scab in the experimental orchard of Elberta peaches better than did the dust. Plat VI (Table 11) had a curculio infestation of 16.2 per cent, a brown-rot infection of 3.4 per cent, and a scab infection of 24.5 per cent of the dust schedule, as against corresponding percentages of 6.1, 1.0, and 8.6 for Plat I, sprayed with arsenate of lead.

The dust containing 80 per cent of sulphur, used on Plat VI, gave much better results than the dust containing 50 per cent, used on Plat VII. There was a brown-rot infection of 3.4 per cent, and a scab infection of 24.5 per cent in Plat VI; Plat VII had corresponding percentages of 7.3 and 44.1.

Table 13 shows that the schedule used on Plat I, which was the one recommended to the growers for the season of 1923, resulted in the highest yield of merchantable fruit.

EXPERIMENTS IN 1924

Life-history studies of the curculio have shown that when the adults leave their hibernation late in the spring, and that when, also, the pupation season of the first generation is unusually cool and damp, only one generation occurs annually in Georgia. Spray schedules were therefore included in the program of experiments for 1924, arranged to determine the best method of controlling the curculio when the first application of arsenate of lead is omitted. Such a schedule was checked against the regular schedule involving four treatments, carried out on an adjoining plat. Before the experiments were begun, colloidal sulphur, recommended for the control of brown-rot and scab, had made its appearance on the market. Tests were therefore included to determine the effectiveness and safety of this fungicide, with and without lime. Manufacturers had advised growers to use it without lime. The comparative effectiveness of the recommended dusting and spraying schedules was again tested. To determine the results obtained by keeping the fruit continuously covered with dust until the stage when the peach stone hardens, a plat was included which received after each rain an application of dust in the proportion of 0-5-95, from the falling of the petals until two weeks after the shedding of the calyces; an application of the 80-5-15 dust was then given. The treatment for this plat was concluded with an application four weeks before harvest of spray of arsenate of lead and self-boiled lime-sulphur. A plat was also included at the beginning of the season to test the effectiveness of a 2 per cent nicotine dust against the curculio. This test was abandoned after the second application had been made, as the results, correlated with the the results of feeding tests with nicotine dust in the insectary, had shown that the material was not sufficiently economical and effective to warrant further experimentation.

Table 14 gives in outline the schedules tested in the spraying and dusting experiments in 1924.

TABLE 14.—Outline of experiments in spraying and dusting peach trees, for the season of 1924, Fort Valley, Ga.

Plat	Time of application			
	As petals fall	When calyces are shedding	Two weeks after shedding of calyces	Four weeks before harvest
I.....	A. L.-L.....	A. L.-L.....	S. B.....	A. L.-S. B.
II.....	A. L.-L.....	A. L.-L.....	C.....	A. L.-C.-L.
II ¹	A. L.-L.....	A. L.-L.....	C.....	A. L.-C.
III.....	0-5-95.....	0-5-95.....	80-5-15.....	80-5-15.
IV ²	0-5-95.....	0-5-95.....	80-5-15.....	A. L.-S. B.
V ³				

¹ About 20 trees in Plat II were, in the last two applications, treated with colloidal sulphur, without lime.

² The dust in the proportion of 0-5-95 was applied after each rain until two weeks after the calyces were shed, when one application of the 80-5-15 dust was made. After the hardening of the stones the treatment for this plat was concluded with an application of arsenate of lead and self-boiled lime-sulphur.

³ Check plat; not treated.

A. L.=Arsenate of lead powder, 1 pound to 50 gallons of spray.

L.=Milk of lime, made from 3 pounds of stone lime per 50 gallons of spray.

S. B.=Self-boiled lime-sulphur mixture, 8-8-50.

C.=Colloidal sulphur, 5 pounds to 50 gallons of water.

0-5-95=Dust; arsenate of lead, 5 per cent; hydrated lime, 95 per cent.

80-5-15=Dust; sulphur, 80 per cent; arsenate of lead, 5 per cent; hydrated lime, 15 per cent.

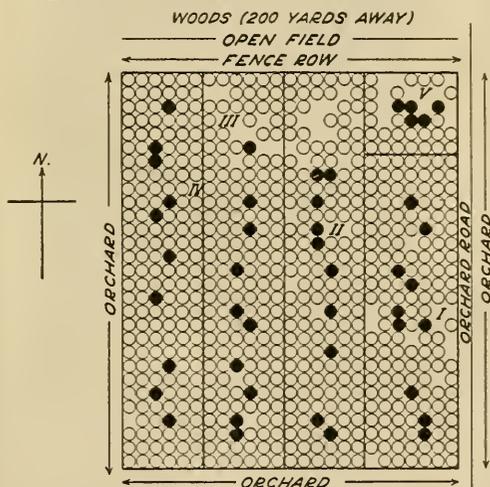


FIG. 9.—Diagram of orchard of Hiley peaches, used for experiments in the season of 1924. Each tree is represented by a circle, the solid black circles representing record trees

As in previous years the experiments in 1924 were duplicated on two of Georgia's most popular varieties—the Hiley and the Elberta. The orchards, which were level and on sandy loam soil, were some 2 or 3 miles from the location of the experiments of the three preceding years, and an opportunity was consequently afforded to test the treatments under conditions of curculio infestation and prevalence of disease in a new location near Fort Valley. The size of the plats treated varied from 150 to 172 trees each. There were 30 check, or untreated, trees in the Hiley orchard, and 35 in the Elberta orchard. (See figs. 9 and 10.) As in the former experiments, 10 trees were selected in the central part of each plat as record trees, the fruit from which was cut open and examined for injury from cur-

culio, brown rot, and scab. All peaches which dropped from these record trees were collected at intervals and examined for data relating to the curculio infestation. In the season of 1924, 135,967 peaches were cut open to obtain data for study. All the spraying and dusting were done with large power machines. The same spray men conducted the work throughout the season.

Tables 15, 16, and 17 present the results, in terms of percentages, of the experiments conducted on the Hiley peaches in 1924. Table 15 presents the data obtained from cutting open the fruit harvested from the record trees of each plat, Table 16 the percentages of curculio-infested fruit that dropped to the ground from the record trees in each plat before harvest, and Table 17 the commercial results in merchantable and cull fruit from all the trees in each plat.

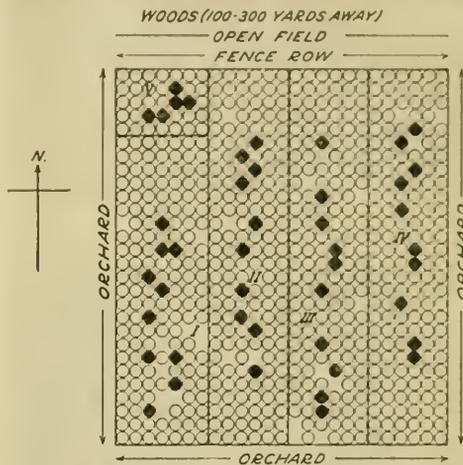


FIG. 10.—Diagram of orchard of Elberta peaches, used for experiments in the season of 1924. Each tree is represented by a circle, the solid black circles representing record trees

TABLE 15.—Summary of results of experiments in peach dusting and spraying at Fort Valley, Ga., in 1924; fruit harvested from record trees of the Hiley variety

Plat	Total number of fruit	Percentage of total fruit having—										Percentage of total fruit found to be sound	Percentage of total fruit as graded before being opened for examination			
		Curculio	Brown rot	Scab	Curculio larvae only	Brown rot only	Scab only	Curculio larvae and—			Brown rot and scab		Brown-rot infection at curculio puncture	Scab and brown-rot infection at curculio puncture	Merchantable fruit	Cull fruit
								Brown rot and scab	Brown rot	Scab						
I.....	8,107	3.9	2.3	8.6	3.3	1.9	8.0	0.1	0.4	0.2	0.1	86.0	95.4	4.6	
II.....	6,485	1.3	.7	1.7	1.2	.2	1.61	96.4	96.2	3.8	
III.....	7,409	4.6	1.6	9.1	3.2	3.9	1.3	8.36	.1	85.6	96.4	3.6	
IV.....	9,012	2.8	1.6	3.7	2.6	1.5	3.611	92.1	95.7	4.3	
V.....	4,233	10.5	16.1	71.5	0	5.1	55.5	0.4	.3	6.0	8.5	.7	1.1	20.4	77.9	22.1

¹ Check plat; not sprayed or dusted.

TABLE 16.—*Number of peaches dropping from Hiley peach trees, and percentage of them infested by the curculio, in experimental orchard at Fort Valley, Ga., 1924*

Plat	Total number of drops	Total percentage of drops infested by curculio
I.....	10,558	1.5
II.....	6,692	2.1
III.....	7,520	1.4
IV.....	8,202	3.2
V.....	6,072	22.5

TABLE 17.—*Commercial results of fruit from all trees in each plat of the Hiley variety, peach spraying and dusting experiments, Fort Valley, Ga., 1924*

Plat	Number of trees in plat	Average merchantable fruit per tree (expressed in cups; six cups equal one crate)	Average cull fruit per tree (expressed in cups; six cups equal one crate)
I.....	150	20.00	0.95
II.....	158	15.40	.60
III.....	162	18.80	.70
IV.....	172	22.10	1.00
V.....	30	16.20	4.60

The winter of 1923-24 was unusually cold. At one time the temperature dropped to a minimum of 7° above zero at Fort Valley. As a result of the abnormal weather many adult curculios were undoubtedly killed in hibernation. It was found that only 11.5 per cent of the beetles that went into leaves for hibernating quarters in the fall of 1923 appeared during the spring of 1924, as compared with an appearance of 63.2 per cent from the same conditions of hibernation in the spring of 1923. The spring of 1924 was unusually cool and late, and the beetles that did survive the winter were rather late in leaving hibernation. As a result, the Hiley peaches suffered only a light infestation of the curculio. The infestation in the fruit harvested from the check, or untreated, plat of this variety was only 10.5 per cent, and the infestation in the "drops" from the same plat was only 22.5 per cent. The schedules had therefore a very mild test against the curculio in the Hiley orchard, and because the beetles were scarce at the beginning of the season of 1924 the early treatments with arsenate of lead had little chance to prove their effectiveness. As the season progressed the weather became very hot, and by midsummer there were some abnormally high temperatures and frequent rains. As a result, the development of the curculio was accelerated; two broods of the insect were produced in the season, although the overwintering adults left hibernation late in the spring. By the time the Elberta peaches were ready to be harvested the curculio population had materially increased in the orchards. All treatments were much more severely tested in the Elberta experimental orchard than in the orchard of the Hiley variety.

In the Hiley orchard infection by scab was heavier than is usual in central Georgia, as indicated by an infection of 71.5 per cent in the check plat. Of the fruit harvested from the check plat in the Hiley orchard 16.1 per cent had brown rot. This moderately light infection was to be expected because of the light infestation of the curculio. Such an infestation is generally reflected in the degree of brown rot, as there is a close interrelation between the injuries caused by the two pests.

Because of the very light infestation of the curculio at the beginning of the season, no data of value were obtained on the control of the insect in the Hiley orchard. According to Table 16 the "drops" from Plat II, which did not receive the early treatment with arsenate of lead, suffered an infestation of 2.1 per cent. A curculio infestation of 1.5 per cent was found in the "drops" from Plat I, which received the first arsenical treatment as the petals fell. There was little difference between the curculio infestations of the "drops" from the plats receiving the spray and those from the plats treated with dust. The "drops" from Plat I, sprayed with liquid, suffered a curculio infestation of 1.5 per cent, whereas those from the two plats receiving dust suffered infestations of 1.4 and 3.2 per cent, respectively.

Colloidal sulphur gave good control of brown rot and scab, as indicated by 0.7 per cent brown rot and 1.7 per cent scab (Table 15, Plat II). This material in combination with arsenate of lead, without lime, produced very severe burning of the foliage, resulting in almost complete defoliation shortly after the harvest. When lime is used with the colloidal sulphur in combination with arsenate of lead, the burning is materially reduced.

Plat III, which received the recommended dust schedule, suffered a curculio infestation of 4.6 per cent, a brown-rot infection of 1.6 per cent, and a scab infection of 9.1 per cent. Plat I, which received the recommended spray schedule, had a curculio infestation of 3.3 per cent, a brown-rot infection of 2.3 per cent, and a scab infection of 8.6 per cent. Judging from the data of other years, this difference would undoubtedly have been much greater had the curculio infestation and brown-rot infection been heavy.

Plat IV, which was given a dusting after every rain until the peach stones began to harden, and which was finally sprayed, manifested about the same control of the curculio as did Plat I, which received the regular spray treatments.

It is seen from Table 17 that Plat IV, which received a treatment of both dust and liquid, and Plat I, which received the recommended treatment with spray, bore more merchantable fruit per tree than the other plats.

Tables 18, 19, and 20 present, in percentages, the results of the experiments in spraying and dusting on the Elberta peaches in 1924. Table 18 presents the data for the fruit harvested from the record trees, Table 19 the percentages of curculio-infested fruit that dropped to the ground from the record trees in the several plats before harvest, and Table 20 the commercial results in merchantable and cull fruit from all the trees in each plat. The apparent discrepancies between "sound fruit" and "merchantable fruit" in Table 18 were due to the fact that some peaches containing a few scab spots were graded as merchantable fruit.

TABLE 18.—*Summary of results of experiments in peach dusting and spraying at Fort Valley, Ga., in 1924; fruit harvested from record trees of the Elberta variety*

Plat	Total number of fruit	Percentage of total fruit having—										Percentage of total fruit as graded before being opened for examination				
		Curculio larvae only					Curculio larvae and—									
		Curculio larvae	Brown rot	Scab	Curculio larvae only	Brown rot only	Scab only	Brown rot and scab	Brown rot	Scab	Brown rot and scab	Brown-rot infection at curculio puncture	Scab and brown-rot infection at curculio puncture	Percentage of total fruit found to be sound	Merchantable fruit	Cull fruit
I.....	6,329	21.9	6.9	23.3	13.4	4.7	14.2	0.1	0.3	7.6	1.3	0.4	0.1	57.9	83.0	17.0
II.....	7,238	28.5	5.1	39.0	13.0	1.7	22.8	.5	.5	13.6	1.5	.3	.6	45.5	81.0	19.0
III.....	5,636	30.7	8.4	44.9	13.7	3.1	26.3	.8	.4	14.3	2.6	.6	.9	37.3	78.8	21.2
IV.....	6,316	24.4	3.5	38.2	12.2	1.2	25.1	.2	.1	11.2	1.3	.4	.3	48.0	86.3	13.7
V ¹	4,163	54.1	30.3	89.7	1.9	3.5	27.9	4.0	.6	37.0	11.6	1.4	9.2	2.9	-----	100.0

¹ Check plat; not sprayed or dusted.TABLE 19.—*Number of peaches dropping from Elberta peach trees and percentage of them infested by curculio in experimental orchard at Fort Valley, Ga., 1924*

Plat	Total number of drops	Total percentage of drops infested by curculio
I.....	6,596	6.2
II.....	6,812	13.0
III.....	6,823	8.5
IV.....	6,872	8.4
V.....	4,862	64.8

TABLE 20.—*Commercial results of fruit from all trees in each plat of the Elberta variety, peach spraying and dusting experiments, Fort Valley, Ga., 1924*

Plat	Number of trees in plat	Average merchantable fruit per tree (expressed in cups; 6 cups equal 1 crate)	Average cull fruit per tree (expressed in cups; 6 cups equal 1 crate)
I.....	151	17.6	3.7
II.....	163	21.3	5.0
III.....	158	16.4	4.4
IV.....	164	18.9	3.0
V.....	35	-----	25.2

As stated in the discussion of the results with Hiley peaches in 1924, unusually high temperatures prevailed in Georgia just before the harvest of Elberta peaches. These, accompanied by almost daily showers, greatly hastened and facilitated the development of the first generation of adult curculios and the production of a second brood. The check, or untreated, plat in the Elberta experimental

orchard suffered the heavy curculio infestation of 54.1 per cent for the harvested fruit and 64.8 per cent for the "drops." This is the heaviest infestation of the curculio in any orchard of those in which were tested the spraying and dusting schedules considered in this publication. The difference between the curculio infestations of the "drops" in the Hiley and Elberta orchards is in all probability due to the fact that because of a late spring the beetles did not begin to appear from hibernation in numbers until after the calyces of the Hiley peaches had begun to dry. This would cause them to seek the Elberta calyces for feeding purposes, as these remain green later than do those of the Hiley variety. The occurrence of first-generation adults in the orchards just before the harvest of Elberta peaches, in addition to the few adults surviving the preceding winter, caused the infestation of the Elberta peaches to be greater at harvest time than that of the other variety. The frequent rains also greatly promoted the development of brown rot and scab in the Elberta orchard, as indicated by a brown-rot infection of 30.3 per cent, and a scab infection of 89.7 per cent, in the check plat. All of the treatments with spraying and dusting were therefore tested much more severely on the Elberta peaches than on the Hileys. The severity of the test to which the treatments were put can be realized by noting the proportion of sound fruit harvested from Plat V, which received no treatment at any time in the season. In Table 18 it may be seen that this, the check plat, produced only 2.9 per cent of sound fruit at harvest, the remaining 97.1 per cent being damaged by the curculio, brown rot, or scab.

In interpreting the results of this work it must be kept clearly in mind that the efficiency of the early application of arsenate of lead must be judged largely from the table giving data on the infestation of the "drops," as the early arsenical treatment is applied especially for the control of the curculio in the "drops" and has a bearing on the control of the insect from the time of application until the fruit is harvested. The efficiency of the late application of arsenate of lead can be measured only from tables giving results in harvested fruit, as practically all "drops" have fallen before this application is given.

The value of the arsenate of lead spray applied just as soon as the petals are down, especially in years when the curculio infestation is heavy, is again clearly demonstrated by the results of the experiments on Elberta peaches. Table 19 shows that of the "drops" from Plat II, which did not receive the early arsenate of lead spray, 13.0 per cent were infested with the curculio, whereas in the case of Plat I, which received the early treatment, only 6.2 per cent of the "drops" were infested. Again, the treatment of Plat I with arsenate of lead when 75 per cent of the petals had fallen reduced the curculio infestation of the "drops" a little over 50 per cent. A reduction of the infestation in the "drops" has a corresponding effect on the infestation in the harvested fruit, as revealed in Table 18. Of the fruit harvested from Plat II, which did not receive the early spray of arsenate of lead, 28.5 per cent was wormy, whereas there was an infestation of 21.9 per cent in the case of Plat I, which was treated with that spray.

The curculio infestation of the "drops" from Plat III, which was dusted on each occasion for treatment, was 8.5 per cent (Table 19),

whereas the "drops" of Plat I, which was sprayed according to schedule, had an infestation of 6.2 per cent (Table 19). The infestation of the "drops" was not lowered by an application of dust after each rain, as Plat IV, treated in that manner, had an infestation of 8.4 per cent, whereas Plat III, which was dusted at the several times specified, suffered an infestation of 8.5 per cent (Table 19).

The spray continued to show its superiority over the dust for curculio, brown-rot, and scab control. Of the fruit harvested from Plat III, which was dusted according to the recommended schedule, 30.7 per cent was "wormy," 8.4 per cent rotten, and 44.9 per cent scabby; whereas of the fruit harvested from Plat I, which was sprayed according to the recommended spray schedule, 21.9 per cent was "wormy," 6.9 per cent rotten, and 23.3 per cent scabby. The control in all of the treated plats of Elberta peaches can not be called excellent, but in interpreting the results one must first consider the very severe test to which all treatments were put. The value of spraying is clearly demonstrated in the work, however, by comparing in Table 18 the data for Plats I and V. Spraying increased the harvested sound fruit 55 per cent on Plat I, as compared with Plat V, which was untreated.

The two applications of self-boiled lime-sulphur to Plat I gave good control of brown rot and scab, considering the weather conditions and the severity of the test. For this plat the infection of brown rot was 6.9 per cent and that of scab 23.3 per cent, whereas for the check plat the infection of brown rot was 30.3 and that of scab 89.7 per cent (Table 18). Colloidal sulphur, applied to Plat II, again gave good control of brown rot, and fair control of scab (Table 18), but in the treatment of the Hiley peaches such serious defoliation had resulted from the use of this material in combination with arsenate of lead without lime that lime was added to each application in which the combination was used on the Elberta peach trees. The addition of lime reduced the severity of the injury, but did not completely eliminate it.

Plat IV, which received an application of dust after each rain until two weeks after the shedding of the calyces, did not control the curculio quite so well as the spray applied to Plat I at the specific times recommended, but gave better control than the four applications of dust to Plat III. The infestation of Plat IV was 24.4 per cent (Table 18), and the infestations of Plats I and III 21.9 and 30.7 per cent, respectively.

From Table 20 it may be seen that no merchantable fruit was harvested from Plat V, untreated. Plat IV, treated with both dust and spray, and Plat I, sprayed according to the recommended schedule, bore the minimum of cull fruit.

CONCLUSIONS

The following conclusions are drawn from the results of the experiments in spraying and dusting peaches, conducted for four years and reported upon in this bulletin. A numerical summary of these results is presented in Table 21.

An application of arsenate of lead, when 75 per cent of the petals have fallen, materially reduces the curculio infestation in the small peaches that drop to the ground before maturing. In seasons in

which there are two generations of the curculio this treatment has a substantial effect in reducing the infestation in the peaches harvested. The importance of this application is apt to be overlooked by the grower who is not inclined to insure his crops early in the season against attacks of pests.

An application of arsenate of lead, made four weeks before mid-season or late varieties of peaches are due to ripen, is indispensable if the curculio is to be satisfactorily dealt with in the South, where two generations of the insect frequently occur.

Arsenate of lead, used at the rate of three-quarters of a pound to each 50 gallons of water, is not so effective against the curculio as when used at the rate of 1 pound to each 50 gallons of water.

The insecticidal action of triplumbic arsenate of lead is too slow for best results in controlling the curculio. The diplumbic arsenate should always be used (experiments in 1921).

The addition of calcium caseinate did not increase the effectiveness of arsenate of lead or that of self-boiled lime-sulphur in controlling the pests that attack the peach fruit.

The mixture of sulphur, hydrated lime, and calcium caseinate, tested in combination with arsenate of lead, gave good results in controlling brown rot and scab, but under the conditions prevailing in central Georgia the mixtures tested resulted in injury to the foliage sprayed. This is especially true of the mixture used in 1922, which at an abnormally early date caused complete defoliation.

TABLE 21.—Summary of results, in 1921 to 1924, of using the standard schedules for spraying and dusting recommended to peach growers

FROM HILEY PEACHES

Year	Treated with standard spray				Treated with standard dust				Untreated			
	Plat No.	Per cent of total fruit—			Plat No.	Per cent of total fruit—			Plat No.	Per cent of total fruit—		
		Infested with curculio larvae	Infested with brown rot	Infested with scab		Sound	Infested with curculio larvae	Infested with brown rot		Infested with scab	Sound	Infested with curculio larvae
1921	II..	6.9	3.2	90.5	X..	18.1	2.9	79.8	XII..	40.8	4.9	57.2
1922	I...	1.8	1.1	96.5	VI..	11.3	0.9	84.5	VII..	22.9	32.0	13.9
1923	I...	.9	5.8	77.5	VI..	1.5	10.2	73.6	VIII..	6.4	30.6	92.5
1924	I...	3.9	2.3	86.0	III..	4.6	1.6	85.6	V....	10.5	16.1	20.4

FROM ELBERTA PEACHES

1921	II..	28.3	35.9	3.4	44.1	X..	54.9	55.8	2.2	16.2	XII..	45.4	77.8	45.6	4.0
1922	I...	6.1	1.0	8.6	85.3	VI..	16.2	3.4	24.5	62.2	VIII..	2.2	11.9	65.0	18.6
1923	I...	21.9	6.9	23.3	57.9	III..	30.7	8.4	44.9	37.3	V....	54.1	30.3	89.7	2.9

¹ The total number of Elberta peaches harvested in 1922 on the count trees was 3,802, or an average of 54.3 peaches for each of the 70 count trees. The total number of Hiley peaches harvested in the same year on the 70 count trees was 65,534, or an average of 936.2 per tree, this average being 17 times as great as that for the Elberta peaches.

Colloidal sulphur also gave good results in controlling brown rot and scab, but when this material is used with arsenate of lead lime must be added or severe burning will result. In these experiments

even when lime was added the combination has a tendency to burn more than properly prepared self-boiled lime-sulphur.

The results gained from three applications of self-boiled lime-sulphur were not enough better than those from the usual two applications to warrant the extra application.

In each of the four years of the experiments the spray was more effective than the dust against the curculio, brown rot, and scab.

Although the schedule which combined dust and spray, and provided for an application of dust after each rain until the hardening of the peach stones, was more effective against the curculio than the schedule providing for applications of dust at specified times, it was not so effective as the schedule for applications of spray at specified times.

Dust containing 10 per cent of arsenate of lead gave no better control of the curculio than did the dust containing only 5 per cent, and resulted in more burning of the foliage.

Dust containing only 50 per cent of sulphur did not control brown rot and scab so well as one containing 80 per cent.

A dust composed of 80 per cent of sulphur and 20 per cent of lime, when applied 7 to 10 days before harvest as an auxiliary to the usual spray, did not diminish infections of brown rot and scab, but nevertheless might be desirable in very moist seasons.

RECOMMENDATIONS FOR SPRAYING AND DUSTING

The following schedules for spraying and dusting are formulated from the results reported in this bulletin, and are recommended for future use in the South, where two broods of the curculio frequently occur.

SPRAYING SCHEDULE

FIRST APPLICATION

When 75 per cent of the petals (pink part of flower) have fallen: One pound powdered arsenate of lead, plus enough milk of lime (made from three pounds of stone lime to each 50 gallons of water) to make 50 gallons of spray mixture.

SECOND APPLICATION

When calyces or "shucks" are falling or when small peaches are exposed (this usually occurs about 10 days after the falling of the petals): Spray mixture made as for the first application.

THIRD APPLICATION

Two weeks after the second application, or about four weeks after the petals have been shed: Self-boiled lime-sulphur, 8-8-50, alone. (No arsenate of lead in this application.)

FOURTH APPLICATION

Four weeks before the peaches are due to ripen: One pound powdered arsenate of lead to each 50 gallons of 8-8-50 self-boiled lime-sulphur.

Should a grower fail to make the first application recommended, he should use arsenate of lead in the third application with the self-boiled lime-sulphur; but this should never be done unless, for an unavoidable reason, the first spray could not be applied. Because of the risk of injury, arsenate of lead should not be used in all four applications of the above schedule.

EARLY PEACHES

Early peaches should be sprayed three times. Use the materials recommended for the first, second, and fourth applications, applying them at the times already prescribed. For added protection against brown rot in early varieties, self-boiled lime-sulphur should also be used in the second application.

DUSTING SCHEDULE

FIRST APPLICATION

When 75 per cent of the petals (pink part of flower) have fallen: Arsenate of lead 5 per cent, lime 95 per cent.³

SECOND APPLICATION

When calyces or "shucks" are falling, or when small peaches are exposed (this usually occurs about 10 days after the falling of the petals): Arsenate of lead 5 per cent, lime 95 per cent.⁵

THIRD APPLICATION

Two weeks after the second application, or about four weeks after the petals have been shed: Sulphur 80 per cent, arsenate of lead 5 per cent, lime 15 per cent.

FOURTH APPLICATION

Four weeks before the peaches are due to ripen: Sulphur 80 per cent, arsenate of lead 5 per cent, lime 15 per cent.

An additional application of a dust composed of sulphur only or preferably sulphur 80 per cent and lime 20 per cent seven to ten days before the fruit ripens may furnish additional protection against brown rot.

EARLY PEACHES

Early varieties need dusting only three times, using the mixture containing arsenate of lead and lime at the time indicated for the first dusting, and the mixture containing sulphur at the time indicated for the second and fourth dustings.

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³ It is not necessary to use sulphur in the first and second applications, although the regular 50-5-15 dust may be used if desired.

UNITED STATES DEPARTMENT OF AGRICULTURE



DEPARTMENT BULLETIN No. 1487



Washington, D. C.

April, 1927

A STUDY IN HYPERPARASITISM, WITH PARTICULAR REFERENCE TO THE PARASITES OF APANTELES MELANOSCELUS (RATZEBURG)

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INTRODUCTION

Insect hyperparasites, or parasites that attack other parasites, have often seriously interfered with the progress of studies in the biological control of injurious insect species and with the institution of this method of control on a practical basis. A primary parasite, imported for the purpose of combating an introduced injurious insect, may be overwhelmed by hyperparasites before it can succeed in firmly establishing itself in the region to which it has been transported. In any case the hyperparasites will certainly delay very considerably the time when such primary parasite becomes sufficiently abundant appreciably to check the pest for the control of which it was introduced. Hyperparasitism is of such general occurrence that it will be encountered in one form or another in practi-

¹ The writers wish to record their indebtedness to A. B. Gahan and R. A. Cushman, of the Bureau of Entomology, for the determination of most of the species of hyperparasites discussed in this bulletin; to P. B. Dowden for valuable assistance rendered in the course of the work; to A. F. Burgess for his criticism of the manuscript; and to W. N. Dovener for the drawings reproduced in this bulletin.

cally any life-history study, or in the course of the mere rearing of insects for host-and-parasite records. It has been the source of much annoyance in rearing work because the exact nature of parasitism is sometimes difficult to ascertain, and not infrequently hyperparasites have been mistaken for primaries, with consequent confusion in the records.

An exhaustive study covering the entire field of insect hyperparasitism would be a tremendous undertaking. For acquaintance with this subject we shall probably need to rely upon gradual additions to our knowledge supplied by observations made in the course of biological studies in connection with a variety of insect problems. In this way we shall gradually improve our understanding of a most interesting field of insect behavior that has been only superficially investigated, but which is intimately related to problems in economic entomology. This bulletin is an attempt to review briefly the more general features of hyperparasitism, and to present certain data upon the habits, biology, and interrelationships of the hyperparasites affecting *Apanteles melanoscelus* (Ratzeburg), a valuable primary parasite of the gipsy moth.

EXTENT OF HYPERPARASITISM

Practically no parasitic species of primary rank escape the attacks of hyperparasites. The extent to which particular primary parasites are themselves parasitized is in large measure dependent upon the habits of those species, particularly upon the degree of their exposure or concealment while in the cocoon or puparium and upon the length of the period spent in this stage. Some species of primary parasites, of which *A. melanoscelus* is an especially good illustration, remain in their exposed cocoons throughout a large part of the period during which hyperparasites are active, and are extremely heavily parasitized. Certain other primaries spend a long hibernation period as immature larvae within the body of the host and, upon completing their development in the spring, form their cocoons or puparia in situations quite inaccessible to hyperparasites. *A. lacteicolor* Viereck, an important parasite of the brown-tail moth larvae, is one of this type (26)², and only a relatively small proportion of its cocoons are attacked. Nevertheless a certain degree of hyperparasitism occurs in such cases, and even with species whose cocoons or puparia are completely protected from attack. Under some conditions, as will be mentioned later, it may even become severe.

Certainly hyperparasites play an important part in the maintenance of the balance between insect species in nature, for biological relationships between hosts, primary parasites, and hyperparasites are very intimate. This is sometimes not so readily appreciated as affecting primaries and hyperparasites, because of the complexity of their relationships, and because most of the observations regarding hyperparasitism have been merely incidental to other studies.

With some species of primary parasites the prevention of excessive increase is not so obviously the work of hyperparasites. In the case of *Apanteles lacteicolor*, previously mentioned, the failure to find a sufficient number of suitable summer hosts to carry the

² Reference is made by number (italic) to "Literature cited," p. 34.

species over the period before small brown-tail moth larvae are again available is apparently the chief bar to unlimited multiplication. There are always many disturbing factors that modify results for a particular period or in certain localities, making it necessary to view these relationships in a broad way, as they occur in the long run, in order to acquire a clear understanding of them.

Just as there are many conditions and agencies that operate to check the undue increase of primary parasites, so, too, there are numerous factors preventing the excessive increase of hyperparasites. Some of the more important of these are: The lack of sufficient hosts in available situations, because of previous excessive parasitism or destruction by other means; the habit of the adults of most species of feeding at the puncture holes made by the ovipositor, and so rendering many parasitic hosts unfit for sustaining hyperparasitic larvae; competition among hyperparasites for the same host; tertiary parasitism; enemies such as rodents, birds, and predacious insects that destroy both the primary parasite and the hyperparasite feeding upon it; climatic factors, etc. All these and many other factors combine to maintain, in the long run, the proper relation between hyperparasites and primary parasites.

SYSTEMATIC POSITION OF HYPERPARASITES

By far the greater number of the insect hyperparasites are Hymenoptera belonging to the so-called parasitoid groups, and particularly to the Ichneumonoidea and the Chalcidoidea. In the Ichneumonoidea they are found chiefly in the subfamily Cryptinae, and in the tribe Mesochorini of the subfamily Ophioninae, both of which contain many species of very considerable importance as hyperparasites. Very few, if any, members of the true Braconidae are hyperparasitic, although some species of the Alysiidae, which may properly be considered as constituting a subfamily of the Braconidae, have this habit. It is among the Chalcidoidea that hyperparasites are most abundant. Numerous species in the Callimomidae, Chalcididae, Eurytomidae, Microgasteridae, Eupelmidae, Encyrtidae, Pteromalidae, Elasmidae, and Eulophidae have been observed to be hyperparasitic; and some such species may also be found in the Cleonymidae when the habits of this group are better understood. The Cynipoidea and the Serphoidea also contain forms of known hyperparasitic habits; and with further studies upon the biology of members of these superfamilies, more instances of such parasitism will probably come to notice.

There are apparently few true hyperparasites among the Diptera, despite the abundant occurrence of the parasitic habit in this order. But certain Bombyliidae, like (*Hemipenthes*) *Villa morio* L. and *Anthrax velutina* Meig., according to Baer (1), occasionally prove very destructive in Europe as parasites of Tachinidae that are important primary parasites of injurious forest insects. Davis (7) has also recorded the bombyliids *Exoprosopa pueblensis* Jaenn., *E. fasciipennis* Say, and *Anthrax parvicornis* Coq. as hyperparasites. They were reared from cocoons of certain species of *Tiphia* that are parasitic on white grubs, *Phyllophaga* spp. A very few species of Coleoptera have been found to be hyperparasitic, at least under some conditions. The more interesting of such records are those by

Davis (7), who discusses the rhipiphorid *Macrosiagon pectinatus* Fab. as a parasite of *Tiphia*; and Fiske (10), who records the eucenjid *Catogenus rufus* Fab. as a parasite of a braconid primary parasite.

Of course it must be understood that it is impossible to designate absolutely a certain group of species as hyperparasites as distinguished from primary parasites. As will be pointed out in greater detail farther on, there are many species that sometimes act as primary parasites whereas under other conditions they are hyperparasitic.

SPECIFIC HOST RELATIONS

In general hyperparasites are undoubtedly less discriminatory than primary parasites as regards the selection of hosts. Certain forms, such as species of the ichneumonid genera *Hemiteles* and (*Pezomachus*) *Gelis* and the chalcid *Dibrachys boucheanus* (Ratzelburg), attack practically anything resembling the cocoons of hymenopterous primary parasites; and some species parasitize dipterous and hymenopterous parasites alike. Species of the chalcid genus *Melittobia* apparently attack a great variety of Hymenoptera, both parasitic and free-living (13, 14), and are also sometimes serious enemies of Tachinidae (19). The European eupelmid *Eupelmus saltator* Lind., which is now established in the United States, develops upon such dissimilar hosts as the Hessian fly and species of *Apanteles*. And Smith (34) records species among the Tachinidae, Ichneumonidae, Braconidae, and Chalcidoidea as hosts of *Perilampus hyalinus* Say. Many other illustrations of such indiscriminate parasitism could be given. Though a distinct preference is usually exhibited for one general type of host, this ordinarily includes a very wide range of species. Only rarely does a hyperparasite confine itself rather closely to certain few host species, as in the case of (*Chalcis*) *Brachymeria compsiluræ* Crawford and *Monodontomerus aereus* Walk., which are essentially parasites of a few particular Tachinidae having similar habits. As a rule hyperparasites are better able than primary parasites to adapt themselves to a great variety of hosts when the preferred species are not available in sufficient numbers. This doubtless accounts for the continued abundance of certain hyperparasites in a given locality irrespective of the presence of the primaries that are their preferred hosts. It will also account, as Howard (18) has indicated, for the heavy parasitism upon primary parasites introduced from another country, even though these are imported unaccompanied by any of the hyperparasites that attack them in their native habitat.

The term "secondary parasites" is sometimes applied to hyperparasites as a whole, and after making certain allowances may be considered strictly correct. As suggested by Fiske (11), true tertiary or quaternary parasitism, or parasitism of even higher degree, is of rare occurrence. It is doubtful if any species are obligatory tertiary parasites. Some, like the two species of the euphid genus *Pleurotropis*, which are discussed subsequently in this bulletin, are evidently preferably tertiary; but they can, and sometimes do, act as true secondary parasites. More commonly species that are normally primary develop as secondaries; and conversely some of those that are usually secondary become primary under the proper conditions. As an illustration of this latter adaptability the behavior of *Eupteromalus nidulans* (Foerst.) is interesting. This

species, which has been referred to in literature (19) under the name of *Pteromalus egregius* Foerst., usually parasitizes cocoons of *Apanteles* and *Meteorus*, but is sometimes found living as a primary parasite of the brown-tail moth larvae, and recently it has been observed attacking hibernating larvae of the satin moth (*Stilpnotia salicis* L.). And species of *Hemiteles* and *Gelis*, ichneumonids that are notorious enemies of hymenopterous primary parasites, are themselves sometimes primary, attacking spider egg masses and such lepidopterous hosts as *Coleophora* and *Bucculatrix*, the cases or cocoons of which closely resemble the cocoons of hymenopterous parasites. Cases where primary parasites acted as secondaries have been observed even more frequently. Often they are accidentally secondary as a consequence of attacking hosts within which other parasites are already present. This occurs commonly in the case of the boll-weevil parasites *Cerambycobius cyaniceps* Ashm., *Eurytoma tylodermatidis* Ashm., and *Microdontomerus anthonomi* Crawf., according to Pierce (30). It has been noted with parasites of scale insects, such as *Coccophagus* and *Tomocera* (35); with *Galesus silvestri* Kief., a serphoid parasite of the Mediterranean fruit fly (28); with *Theronia fulvescens* Cress., an ichneumonid that attacks various lepidopterous larvae (11), and with numerous other species. It appears to be generally true that hyperparasitism of this accidental type becomes increasingly abundant with the increase in actual numbers of the various primary parasites of certain hosts. It should not be confused with true competitive parasitism, where different species of primary parasites compete for the limited food supplied by a single host, one causing the death of the other only indirectly, by first appropriating the available food. Manifestly competitive parasitism also becomes of more frequent occurrence as the numbers of the various primary parasites of a given host increase, and because of the difficulty of observation it is often confused with accidental secondary parasitism. Sometimes primary parasites become direct secondary parasites and are not merely accidentally so because of the earlier presence of another parasitic species. Thus certain species of the eupelmid genus *Anastatus*, which are regarded as strictly primary parasites of the eggs of Lepidoptera, Orthoptera, etc., and are usually much restricted as to hosts, successfully attack the cocoons of other primary parasites, particularly Braconidae. A similar habit has been observed in the case of various other chalcids, and also with some ichneumonids. At least four such species were encountered among the parasites of *Apanteles melanoscelus*, and will be briefly treated later.

Following the general rule stated by Howard (14) for primary parasites—namely, that they are external feeders when parasitic upon protected hosts, and internal when attacking exposed hosts—most hyperparasites that attack primary larvae which are protected by their cocoons are external feeders, whereas those that parasitize primaries like the eulophids *Comedo*, *Euplectrus*, and *Elachertus*, which form naked exposed pupae, are usually internal. Since relatively very few primary parasites are not protected either within cocoons or puparia, the number of internal feeders among secondaries is correspondingly small, the reverse of the condition found with primaries.

This general external feeding by the hyperparasitic larvae implies the deposition of eggs directly upon the primary larvae inside their cocoons or puparia. Although this is the usual manner of oviposition, there are numerous interesting exceptions. Those species of the genus (*Chaleis*) *Brachymeria* which are parasitic upon Tachinidae deposit their eggs inside the tachinid maggots before the latter have issued from their hosts, which are various lepidopterous larvae and pupae. Without this adaptation in oviposition the *Brachymeria* would succeed in finding but few of their tachinid hosts, since these usually enter the soil immediately upon emerging, and so are rather well protected throughout the puparial period. No such advantage, however, is derived by species of the ichneumonid genus *Mesochorus* from a similar habit of oviposition; for these attack hymenopterous species that form their cocoons in the open where they are easily accessible. Any benefit that species of *Mesochorus* enjoy from this manner of attack must consist in the advantage that early possession of the primary parasite gives them in the competition with other hyperparasitic forms for those particular hosts. Certain Cynipoidea, represented by species of *Charips* that are hyperparasitic upon aphids, and a species of *Tetrastichus* which is abundantly reared from cocoons of *Apanteles glomeratus* L., also attack the host of the primary in this manner, for the sake of the parasite it may already contain. A better acquaintance with the biology of hyperparasitic species will doubtless reveal a wider occurrence of this habit. None of the secondaries just mentioned can develop as primary parasites upon the hosts attacked; the few observations that have been made indicate that they do not even deposit eggs unless a primary parasite is present within, and then always place their eggs inside the body of the primary.

One of the most interesting types of indirect parasitism among hyperparasites is that exhibited by *Perilampus* as described by Smith (34). The newly hatched planidiumlike larva of *Perilampus* must attach itself to a passing host of one of the parasites upon which it can develop, and must then bore inside in the hope of finding the desired parasite. It does not find its food supply ready at hand, on hatching from the egg, as practically all other parasitic species do. Since only a very small part of the *Perilampus* planidia succeed in locating the larvae of primary parasites in this roundabout manner, an enormous capacity for egg development and deposition by the parent females is required. A habit very similar to that of *Perilampus* has been observed by Clausen (2) in *Schizaspidia*, a member of the closely related family Eucharidae; but in this case the parasite is primary.

FEEDING OF ADULT HYPERPARASITES

The habit with certain parasitic insects, particularly chalcidoids, of feeding at the puncture holes made by the ovipositor has been discussed by various writers, some of the more interesting observations being those recorded by Marchal (24, 25), Howard (17), Doten (8), Johnston (20, 21), and Rockwood (33). In all these cases primary parasites were concerned. But hyperparasites have the same habit, which, as Howard suggested, probably "will be found to be quite widespread." Nearly all the parasites of *Apanteles melanoscelus* treated in this bulletin have been observed feeding at the punctures

made in the cocoons by the ovipositor. This feeding has sometimes been so extensive, in the case of particular individuals, that practically the entire fluid content of the host parasite has been consumed. In these instances the young hyperparasitic larvae, on hatching from the eggs that had been unwisely deposited in the cocoons, found themselves without a supply of food upon which to develop, and necessarily died of starvation. Not infrequently the hyperparasite, after having punctured a cocoon several times and fed at the openings, was observed to leave without depositing an egg. As the primary parasites thus fed upon by the adult hyperparasites were always unable to complete their transformations, this habit of the secondaries must be regarded as increasing their power of destruction. To what extent adult hyperparasites depend upon this manner of feeding for obtaining their nourishment it is impossible to say. A large part of the *Apanteles melanoscelus* cocoons collected in the field and held at the laboratory for the emergence of parasites yielded neither primaries nor secondaries. With a few of the collections the proportion of such cocoons was more than 80 per cent of the number collected. In view of the feeding habit just discussed it appears likely that some of these *Apanteles* had been so heavily fed upon by adult secondaries that they not only had been killed, but no longer contained sufficient food to nourish hyperparasitic larvae to maturity. However, the failure of the cocoons of primary parasites to produce either primary or secondary adults can not be attributed to this cause alone; for the vigorous competition between hyperparasites for the same hosts very often results in the failure of any of the competing individuals to mature; and this competition is usually very extensive.

Doubtless adult hyperparasites are also nourished by other substances than the fluid content of the larvae of their host species. The readiness with which they feed upon a honey or sugar solution in the laboratory leads to the assumption that honeydew and other sweet juices, including sap and nectar, must form a considerable part of their diet. Certainly this must be the case when hosts are scarce.

PARTHENOGENESIS

Parthenogenesis, or reproduction without fertilization, has been so often noted with the parasitic Hymenoptera that it may be regarded as of general occurrence in these groups. All the hyperparasitic species attacking *Apanteles melanoscelus* were found capable of reproducing without previous fertilization, as would be expected. But of particular interest in this connection was the observation that different species of a given genus may differ with regard to the sex of the progeny resulting from parthenogenetic reproduction. One of the two common species of *Hemiteles* reared from *Apanteles* was found to be arrhenotokous, whereas the other is always thelytokous. The two species of *Pleurotropis* and those of *Anastatus* obtained from the *Apanteles* cocoons differ in the same way, one species in each genus always producing males, the other females. Males of the thelytokous species have not been encountered, or at least have not been recognized. It was rather surprising to find as many as four of the species handled in these studies producing females in parthenogenesis, for the parasitic Hymenoptera are considered to be very generally arrhenotokous.

LIFE CYCLE OF APANTELES MELANOSCELUS

Before proceeding to a discussion of hyperparasitism as affecting *Apanteles melanoscelus* it will be well to review the important points in the life cycle of this *Apanteles*. Following is a concise summary of the more important features of the life history of that species. A more detailed account will be found in a bulletin by Crossman (3).

Apanteles melanoscelus is essentially an internal solitary parasite of the larvae of the gipsy moth, *Porthetria dispar* L., although it is sometimes also obtained from the white-marked tussock moth, *Heperocampa leucostigma* S. & A. It passes through two generations upon the gipsy moth, which itself is single-brooded. Adults of the parasite first appear in May, directly after the hatching of the gipsy-moth eggs, and attack the first-stage larvae. The parasitic larvae complete their development in 18 to 20 days, and emerge from the second and third stage *P. dispar* caterpillars to form their cocoons. About seven or eight days later adults emerge, and, after mating, the females attack third-stage larvae of the host species to begin the second generation. From 16 to 20 days afterward, or early in July, the cocoons of this generation of the parasite begin to appear. This is the hibernating form. The mature parasitic larvae remain dormant in these cocoons until the following spring, when they transform to pupae preparatory to becoming adults. Thus, while the cocoons of the first generation are exposed to the attacks of hyperparasites for only a very short period, those of the second generation can be attacked from July until cold weather, when activity of the hyperparasites ceases. These cocoons, furthermore, are largely in exposed situations, on the under side of branches, under loose bark, and in similar places, and so are easily reached by the secondaries.

METHODS EMPLOYED

The field work in connection with these studies consisted of obtaining monthly collections of *Apanteles melanoscelus* cocoons from June to October, inclusive, over a three-year period, from three different localities. Between 200 and 300 cocoons constituted a collection, except in a few instances when it was impossible to obtain so many within a reasonable time. The three localities selected, Pembroke, Mass., Boylston, Mass., and Rye, N. H., were approximately 50 miles apart. One collection of first-generation cocoons and four collections of second-generation cocoons were obtained from each point during each of the three years. These cocoons were isolated and held at the laboratory, at Melrose Highlands, Mass., under outdoor temperatures, for the issuance of *Apanteles* and its parasites. To supplement the records from these collections, data were obtained covering many thousands of cocoons collected in July of each year in localities where *Apanteles* was particularly abundant. These collections have been made annually for some time in connection with the propagation and artificial distribution of *A. melanoscelus*, as discussed by Crossman (3). From all this material it has been possible to obtain a reasonably clear understanding of the relative importance of the various species of hyperparasites that attack *A. melanoscelus*.

All the species that appeared to be of any importance as enemies of this *Apanteles* have been studied more or less in the laboratory.

They have been allowed to oviposit in cocoons of *Apanteles*, and various points in their development and behavior have been determined. It was necessary to have available a considerable number of cocoons that were known to be parasite-free. These were obtained by subjecting gipsy-moth larvae to attack by *Apanteles* and then rearing these caterpillars in covered trays until the *Apanteles* larvae emerged to spin their cocoons.

No difficulty was experienced in holding individuals of the various species of hyperparasites alive and in good condition for a long time. Many were kept for several months. Because many containers were required to care for the various isolated females or pairs, it was desirable that these containers be small and easily handled. The ordinary 4-inch shell vials were found most suitable. These vials were laid on the bottom of shallow trays, and were prevented from rolling about by the use of cardboard frames. A honey solution, consisting of about 40 parts of honey to 60 parts of water, proved to be thoroughly satisfactory as food for these parasites. This was supplied on small strips of white blotting paper. It is unsafe to use colored paper because of the solubility of the dyes. The blotting-paper strips were saturated with the honey solution and placed in the vials on pieces of towel paper, which had been introduced for the purpose of absorbing any excess honey water, thus preventing the vials from becoming sticky inside. The parasites were fed once daily, and the same pieces of blotting paper were used for two feedings. Both the blotting-paper strips and the towel paper were changed every second day. When used longer than this during warm weather they molded, because the honey solution fermented quickly. The vials themselves were renewed about every 10 days in order to keep the quarters in which the parasites were confined perfectly clean. When allowed to remain continually in the light the adult secondary parasites ran about in the vials almost constantly, and of course became weakened more quickly than when kept quiet for part of the time. Accordingly, they were held in darkness for a considerable part of each day. They were found to oviposit almost as readily in darkness as in daylight.

Cocoons which were to be attacked were introduced into the vials at more or less regular intervals and were left for varying periods. When removed they were placed in individual small vials and held for the appearance of the adults or until it was desired to dissect the cocoons for the determination of one point or another. In order to learn how frequently the hyperparasitic larvae molt it is necessary to have particular larvae constantly under observation, since it is practically impossible, in the case of species so small as most of those studied, to be certain of finding all the molt skins by merely dissecting the cocoon after the hyperparasite has completed its development. Certain individuals of species representing the various taxonomic groups concerned in the parasitism of *A. melanoscelus* were carried through their development from egg to adult in the cells on depressed glass slides. The larvae of these particular hyperparasites are external feeders, and so could be constantly observed when held in this manner. Eggs of the secondaries were removed from the cocoons in which they had been deposited and placed upon a cocoon larva of *Apanteles* in one of the glass cells, which was then covered with a piece of thin celluloid sealed down with shellac. These eggs hatched, and the larvae fed to maturity in a perfectly normal manner.

DATA OBTAINED FROM FIELD COLLECTIONS OF COCOONS OF APANTELES MELANOSCELUS

The extent of the hyperparasitism to which *A. melanoscelus* is subject, and the relative paucity of the Apanteles that survive to become adults, as indicated by the field-collected cocoons under observation, were very surprising. A summary of the more important records covering the monthly collections previously referred to is given in Table 1.

TABLE 1.—Summary of records obtained from the monthly collections of *Apanteles melanoscelus* cocoons made from June to October over a three-year period, from three localities

Collection	Total cocoons	Cocoons producing adult Apanteles		Cocoons producing hyperparasites		Cocoons producing neither Apanteles nor hyperparasites	
		Number	Per cent	Number	Per cent	Number	Per cent
First generation.....	2, 164	614	28. 4	1, 143	52. 8	407	18. 8
Second generation No. 1.....	2, 201	597	27. 1	977	44. 4	627	28. 5
Second generation No. 2.....	2, 312	37	1. 6	981	42. 4	1, 294	56. 0
Second generation No. 3.....	2, 224	12	. 5	845	38. 0	1, 367	61. 5
Second generation No. 4.....	2, 008	11	. 5	274	13. 7	1, 723	85. 8

NOTE.—The collections contained 220 to 250 cocoons. Figures given cover nine collections of first-generation cocoons and nine collections of second-generation cocoons for each month from July to October, inclusive, which are numbered, respectively, 1, 2, 3, and 4.

The collections of first-generation cocoons produced the highest proportion of Apanteles, 28 per cent. This may be slightly lower than actually occurs in the field, for most of these cocoons were obtained after a large part of the adult Apanteles of this generation had already emerged, and those, of course, are not taken into account, since only cocoons without exit holes were collected. On the other hand, certainly some of the cocoons from which Apanteles emerged several days after collection would have been parasitized had they remained in the field. Accordingly, 28 per cent is probably not far from the proportion actually produced in nature. The records on the collections of second-generation cocoons show clearly that as the season progresses the chances that given cocoons in the field will ultimately yield Apanteles adults rapidly diminish. The first collections of second-generation cocoons were made within two weeks of the time that the first of these cocoons were being formed and before all the Apanteles larvae had completed their development. In this case the proportion of cocoons producing adult Apanteles was about the same as for the first generation. Both lots of cocoons had been exposed to hyperparasites only a very short time. Less than 1 per cent of collections 3 and 4 of second-generation cocoons, which were obtained in September and October, produced Apanteles adults. The figures for these late collections have particular significance, for they represent more exactly than the data covering the other collections the real condition of the Apanteles cocoons that are to carry this important primary parasite over the winter.

It is possible that the cocoons collected were the more exposed ones, and that these would be most heavily parasitized. On the other hand, the figures on these cocoons do not take into account any dam-

age that would have occurred during the winter from other causes. Furthermore, no cocoons having exit holes (and there were many from which secondaries had already issued) were collected. Strictly, these should be taken into account in computing the proportion of cocoons carrying over living *Apanteles* larvae, and also the proportion yielding hyperparasites. On considering these various phases of the subject it appears that in all probability not more than one-half of 1 per cent of the cocoons formed in July produce adult *Apanteles* the following spring. It is possible that the proportion is frequently even less.

The table indicates that the percentage of cocoons producing neither hyperparasites nor primaries steadily increases as the season progresses. As already suggested, there are probably two principal causes for the failure of cocoons to yield either *Apanteles* or secondaries, namely, excessive hyperparasitism, and the feeding of the adult secondaries upon the *Apanteles* or hyperparasitic larvae within the cocoons. The proportion of such cocoons, as would normally be expected, increases week after week during the late summer and early fall when the hyperparasites are most active and most abundant. That the enormous mortality suffered by the primary parasite, in the case of the collections, is ascribable particularly to hyperparasites, and not in any appreciable degree to low winter temperatures, is indicated by the fact that more than 95 per cent of the cocoons produced at the laboratory and held under the same conditions as those obtained from the field, produced *Apanteles* adults in the spring.

The data on the issuance of *Apanteles* from the many thousands of cocoons collected in July in connection with the regular reproduction work on this species at the laboratory are interesting. Figures are at hand for the collections of 1920 to 1923, inclusive. In 1920 the number of cocoons collected was 11,971; in 1921, 12,081; and in 1923, 29,499. These produced, respectively, 958, 2,650, and 1,290 *Apanteles* adults. In all these cases the cocoons had been in the field from one to four weeks before the collections were made. As a result of being exposed to hyperparasites for this period, only 9 per cent of the total number of cocoons taken in those years yielded adults of the primary species. In 1922 the cocoons were collected very early, as soon as possible after they were formed; consequently 15,866 cocoons of the 38,855 collected that year produced *Apanteles*. Unfortunately, complete figures on the numbers yielding hyperparasites are not available.

In a review of the above discussion the following points are particularly impressive: (1) The first-generation *Apanteles* cocoons are relatively lightly parasitized; (2) during their long period of exposure the *Apanteles* of the second generation have a steadily diminishing chance of becoming adults, and probably not more than one-half of 1 per cent of the cocoons formed in July produce adults of the primary species the following spring; (3) an extremely high proportion, probably close to 50 per cent, of the total number of second-generation cocoons formed will yield neither primaries nor secondaries.

It is quite apparent that *A. melanoscelus* would find it difficult to survive, or at least would be unable to maintain its effectiveness as an enemy of the gipsy moth, if it did not have two generations annually. On the other hand, if not severely checked during the second generation, the species would multiply excessively. The

hyperparasites must be considered as very largely responsible for the maintenance of the proper relationship between *A. melanoscelus* and its host. And indirectly they affect, of course, the relationships between the gipsy moth and its other parasites as well.

BIOLOGY OF THE HYPERPARASITIC SPECIES CONCERNED IN THE PARASITISM OF APANTELES MELANOSCELUS

Some 35 hyperparasitic species were reared from *A. melanoscelus* cocoons; but many of these are evidently of little or no significance as enemies of this primary parasite. More than 90 per cent of the hyperparasites obtained comprised the following 14 species, which are listed in the order of their apparent relative importance.

<i>Eurytoma appendigaster</i> (Swed.)	<i>Hypopteromalus tabacum</i> Fitch
<i>Dibrachys boucheanus</i> (Ratz.)	<i>Habrocytus dur</i> Girault
<i>Hemiteles tenellus</i> (Say)	<i>Hemiteles fulvipes</i> Grav.
<i>Dimmockia incongruus</i> (Ashm.)	<i>Eupelminus saltator</i> (Lindm.)
<i>Gelis bucculatricis</i> (Ashm.)	<i>Dimmockia pallipes</i> Mues.
<i>Gelis apantelis</i> Cush.	<i>Pleurotropis tarsalis</i> (Ashm.)
<i>Eupelmus spongipartus</i> Foerst.	<i>Pleurotropis nawati</i> (Ashm.)

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tertiary.

Among the species reared in the course of this study several have been found to be apparently new to science. These have recently been described (5, 27).

The various species of hyperparasites which the writers have reared from *A. melanoscelus* will be briefly discussed, with the purpose of bringing out certain phases in their behavior and biology. They have been arranged according to taxonomic position.

ICHNEUMONIDAE

CRYPTINAE

HEMITELES TENELLUS (SAY)

(Fig. 1)

Hemiteles tenellus is one of the most common of all our hyperparasites, and has been abundantly reared from the cocoons of many parasitic species. In literature it has been mentioned under a great variety of names, the synonymy of which has been summarized by Cushman and Gahan (6). In addition to parasitic forms, like species of *Apanteles*, *Meteorus*, *Rogas*, *Macrocentrus*, *Campoplex*, *Hyposoter*, *Spilopteryx*, and many other Ichneumonoidea, its host list includes *Coleophora*, *Bucculatrix*, and certain Tenthredinidae, upon which it is occasionally a primary parasite. There can be no doubt, however, that its importance as a secondary greatly exceeds its value as a primary.

Hemiteles tenellus is a very sturdy species and is easily handled in the laboratory. The eggs, which are comparatively large, are deposited singly within the cocoon of *Apanteles* but on the outside of the body of the larva. Usually the *Apanteles* larva is pierced by the ovipositor; but the purpose of this is evidently to cause some of the body fluids to exude from the cocoon upon the withdrawal of the ovipositor, so that the hyperparasite may then feed at the puncture hole. The ovipositor may be inserted and withdrawn many times before an egg is deposited: in fact, sometimes no egg is depos-

ited at all, and very frequently so much of the fluid content of the *Apanteles* is appropriated by the adult *Hemiteles* that only a shriveled mass remains, which is entirely inadequate for the nourishment of a *Hemiteles* larva. On one occasion a single female of this species made 47 punctures in one cocoon, but deposited only one egg. Often, however, several eggs are placed in a single cocoon during the course of repeated insertions of the ovipositor, even when other cocoons are available; but never does more than one larva mature in such cases. Because of their large size only a few fully developed eggs are present in the uterus at one time, and evidently more than six to eight eggs are rarely deposited within a 24-hour period. In the laboratory the largest number of eggs obtained from one female on one day was 10, and this only on a single occasion,

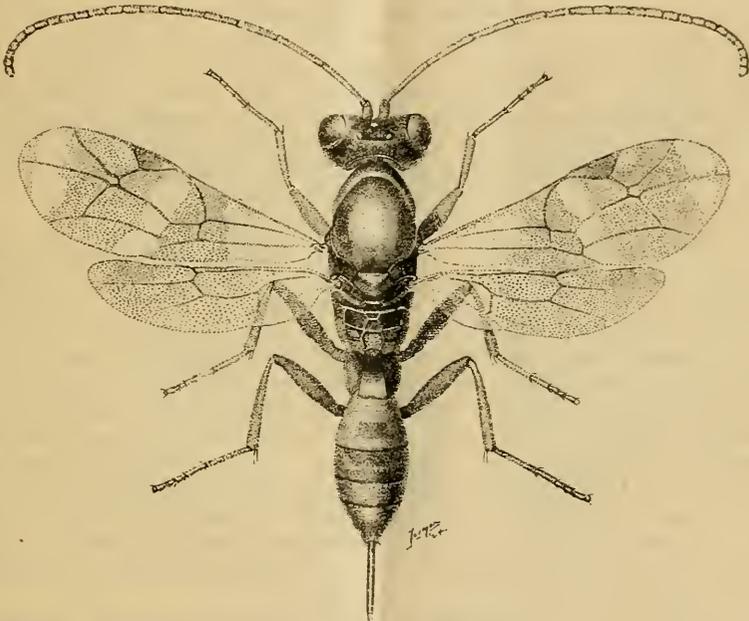


FIG. 1.—*Hemiteles tenellus*, female

following the failure of this parasite to deposit any eggs during the two days immediately preceding. Usually only from one to three eggs per day were obtained, and in the case of all the *Hemiteles* observed there were many days interspersed upon which no eggs were deposited. The largest total number of eggs laid by one female in the laboratory was 76, and this over a period extending from May 11 to July 1.

The egg hatches after about 48 hours and the larva feeds externally upon the *Apanteles* within the cocoon. There are five larval stages. This was determined by carrying through individual hyperparasites, from eggs to adults, in cells on depressed slides. According to these observations, the first stage required two days, the next three stages about one day each, and the fifth stage an average of seven days, although feeding in this stage ceased at the end of a day and a half. Thus *Hemiteles* became full grown after about six or seven days

of feeding. The interruptions in feeding at the times of molting were very brief, usually of only two or three hours' duration. On an average $7\frac{1}{2}$ days were spent as a pupa, bringing the total period from egg to adult, in the case of the summer generations, to about 22 days. The artificial method of carrying the parasites through the immature stages apparently had no effect upon the rapidity of development, for in the case of a large number of individuals which were allowed to develop normally within *Apanteles* cocoons, the total period from egg to adult ranged from 15 to 30 days, depending principally upon temperature.

Hemiteles tenellus is one of the first of the hyperparasites which attack *Apanteles melanoscelus* to appear in the spring, sometimes emerging from overwintering cocoons as early as April 20. The number of generations annually varies from one to four, with three being the most common number and with four being much more common than one. There is, however, much irregularity in this, even among the progeny of a single parent. In numerous cases where several cocoons were attacked by the same individual, some produced adult *Hemiteles* after 18 to 24 days to begin another generation, while others did not yield adults until the following spring. The species hibernates as a mature larva within the cocoon of its host.

Females are invariably produced in parthenogenetic reproduction. In the laboratory several pure lines of females have been obtained through 12 generations, over a period of three years. The male is unknown. In the course of the rearing of many thousands of parasites from field-collected cocoons of *A. melanoscelus* nothing has been obtained that could be the male of this species, although females have always been found in large numbers. Males of the European *Hemiteles areator* (Panz.), which is not clearly distinguishable from *tenellus* morphologically, and of which *tenellus* has sometimes been regarded as a subspecies or variety, occur abundantly in museum collections. Having the opportunity, during the summer of 1924, to determine the result of parthenogenetic reproduction with *H. areator*, the writers found that unfertilized females produce males. It is evident from this disparity in the biology of the two forms that they are quite distinct.

The writers have obtained *H. tenellus* with remarkable regularity from all their collections of cocoons and usually in considerable numbers. The fact that it usually has several generations annually and can develop upon a great variety of hosts, its ruggedness, and its characteristic of producing females in parthenogenesis combine to make this hyperparasite one of exceptional importance.

HEMITELES FULVIPES GRAVENHORST

(Fig. 2)

Like *H. tenellus*, *H. fulvipes* attacks a large number of different primary parasites. It agrees with that species also in nearly all details of its biology. The eggs and the larval instars are indistinguishable; the period of larval development, the number of generations annually, and the form in which hibernation occurs all agree. In one particular, however, *H. fulvipes* differs decidedly from *H. tenellus*: In parthenogenetic reproduction males are always produced, whereas the progeny of unmated females of *H. tenellus* are invariably females.

Although frequently reared from cocoons of *A. melanoscelus*, *H. fulvipes* is by no means so important an enemy of this *Apanteles* as *H. tenellus*. In the foregoing list it has been included among the 14 hyperparasites which are most abundantly reared from that species, but it falls well down in the list.

HEMITELES APANTELIS CUSHMAN (6)

Hemiteles apantelis was only rarely encountered as a parasite of *Apanteles melanoscelus*; according to the observations of the writers, at least, it is at present of no importance as an enemy of this primary. It is included here, however, in order to record its occasional occurrence in this rôle. It is possible that under certain conditions it may

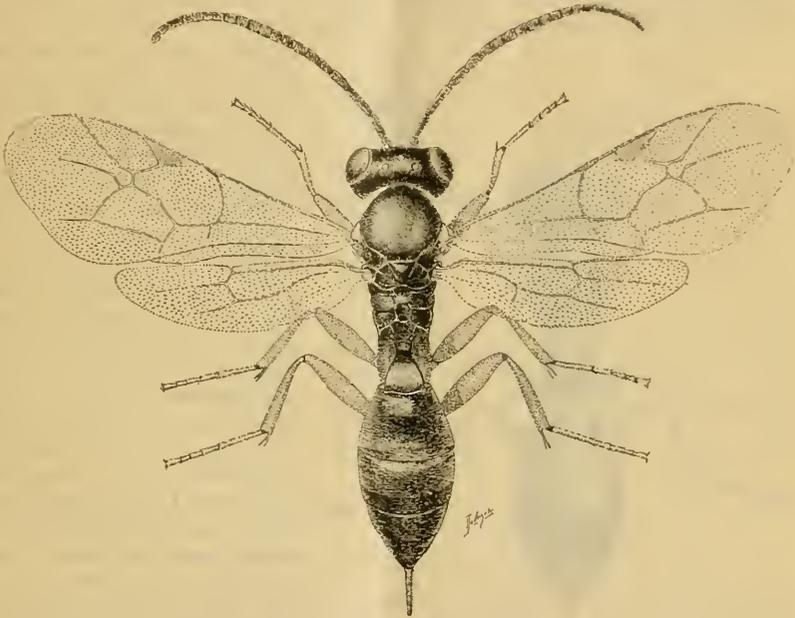


FIG. 2.—*Hemiteles fulvipes*, female

become much more destructive. There is usually but a single generation annually, which hibernates in the form of full-grown larvae. Cocoons attacked as early as May 20 to June 15 did not produce adults of the hyperparasite until May of the following year. In parthenogenetic reproduction males are produced.

ACROLYTA EMPRETIÆ ASHMEAD

Only a few specimens of *Acrolyta empretiæ* have been obtained from cocoons of *Apanteles melanoscelus*. In biology it exactly resembles *Hemiteles fulvipes*. Adults appear in May and attack the cocoons of various species of *Apanteles*. There are several generations annually, development from egg to adult requiring only from 16 to 20 days. Like all the species of *Hemiteles*, it is a solitary parasite, and passes the winter as a mature larva within the host cocoon. The progeny of unfertilized females are males.

GELIS SPECIES

The writers have found five species of (*Pezomachus*) *Gelis* parasitizing *Apanteles melanoscelus*. They are *Gelis bucculatricis* (Ashmead) (figs. 3 and 4), which has been obtained in especially large numbers, *G. urbanus* (Brues), *G. apantelis* Cushman, *G. nocuus* Cushman, and *G. inutilis* Cushman. The last three were found by Cushman to be new and have been described by him (5). Like many species of Hemiteles, the various species of *Gelis* are not at all specific as regards host selection. In addition to attacking primary parasites of numerous different types, they sometimes become primary themselves, developing within spider egg cocoons and in the cases or cocoons of certain Lepidoptera, like *Coleophora* and *Bucculatrix*.

The species reared by the writers from *A. melanoscelus* have two or three generations annually, with no regularity in this respect, however,

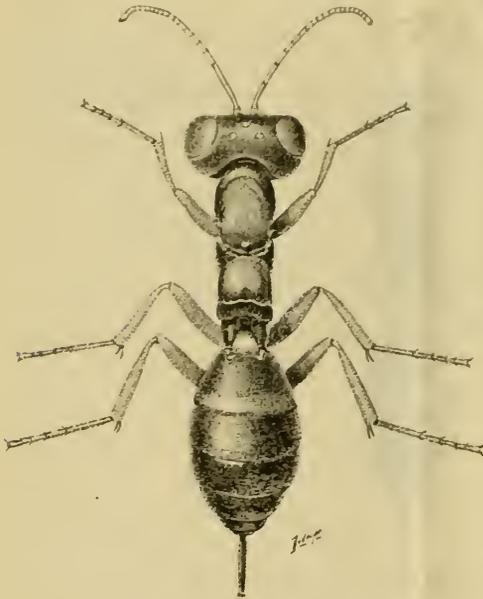


FIG. 3.—*Gelis bucculatricis*, female

in any particular species; and in general habits and life history the five species are practically identical. All of them hibernate as mature larvae in the *Apanteles* cocoons and emerge as adults during the month of May. They appear to mate more readily under laboratory conditions than most ichneumonoids. Whether fertilized or not, the females oviposit freely in cocoons exposed to them. The eggs, scarcely distinguishable from those of species of Hemiteles in size, shape, and general appearance, are deposited externally upon the *Apanteles* larvae within the cocoons; and they hatch in about two days. The period of larval growth is

very short, the host being completely consumed within four to six days after the hatching of the egg. In this short space of time the hyperparasitic larva passes through five stages. In the case of the summer generations only a few days are spent as quiescent mature larvae before pupation; and the pupal period averages 7 to 10 days. The time consumed in developing from egg to adult is normally about 18 days, with 14 days the minimum and 24 days the maximum observed. With the hibernating generation the fully developed larvae remain in the host cocoons from August until the following spring.

According to the writers' observations, the males of *apantelis*, *nocuus*, and *inutilis* are always winged, whereas in *urbanus* and *bucculatricis* both winged and wingless males occur. In all five species males are always produced in parthenogenetic reproduction,

and in the case of *bucculatricis* and *urbanus* individual virgin females, as well as individual fertilized females, were found to produce both the winged and the wingless males. There appears to be no regularity in the appearance of either male form of those species, whether or not the parent has mated.

G. bucculatricis and *G. apantelis* have been reared in much larger numbers than the other species, but all of them have occurred more or less abundantly among the hyperparasites obtained from collections of *Apanteles* cocoons, and combined they are certainly of major importance in retarding the increase of this primary.

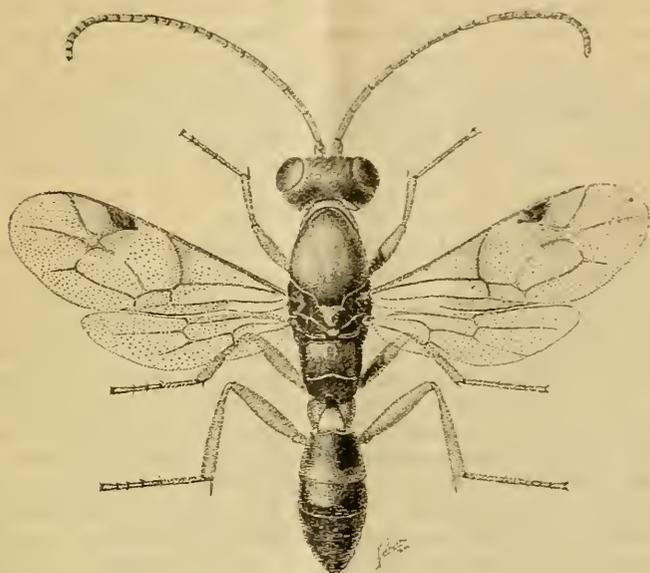


FIG. 4.—*Gelis bucculatricis*, winged male

THYSIOTORUS TRIANGULARIS (CRESSON) (?)

This species, which has been doubtfully determined as *triangularis* by Cushman, is merely mentioned here among the hyperparasites attacking *A. melanoscelus*. It has been reared from only a very few cocoons, and up to this time at least has been of no consequence as an enemy of that parasite.

EPHIALTES (ITOPLECTIS) CONQUISITOR (SAY)

Two very small male specimens of this species have been reared from cocoons of *Apanteles melanoscelus*. This parasitism was doubtless purely accidental and is of no importance, but it is mentioned here because *Itoplectis conquisitor* has not previously been recorded as having been reared from any species of *Apanteles*. It is normally primary, being an important parasite of various Lepidoptera, including such common injurious forms as *Malacosoma americana* Fab., *Cacoecia cerasivorana* Fitch, *Thyridopteryx ephemeraeformis* Haw., and *Hemerocampa leucostigma* S. & A. Not infrequently, however, it has

been reared as a hyperparasite. Fiske (9) has recorded it from several primary parasites of *Malacosoma americana*.

OPHIONINAE

MESOCHORUS VITREUS WALSH

Species of this genus have often been reared from the cocoons of various Braconidae and Ichneumonidae, sometimes in large numbers; but the single species obtained from *Apanteles melanoscelus* at the gipsy-moth laboratory has appeared very infrequently. Despite its unimportance as an enemy of this *Apanteles*, however, its unusual habits and manner of development deserve some comment. Gatenby (12) has called attention to the indirect manner of attacking its host exhibited by *Mesochorus*; but he did not actually observe oviposition, finding the parasites exceedingly timid under confinement. His statement that the egg of *Mesochorus* is deposited within the body of the primary parasite while the latter is still inside its host probably holds for all the species of this little known group, the *Mesochorini*. This manner of attack was observed in the case of the species parasitizing *Apanteles melanoscelus*. The following statements briefly describe the procedure as noted in several instances. When a gipsy-moth larva, which had been attacked by *Apanteles* 8 or 10 days before, was introduced into a vial containing a female of *Mesochorus*, the hyperparasite instantly became greatly excited. Her wings, which were spread and slightly elevated, vibrated intensely and continuously. In a few moments she mounted the caterpillar and at once inserted her ovipositor in one of the posterior segments. After some probing about inside the larva the ovipositor was finally inserted to its full length, held there quietly for a moment or two, and then withdrawn. There were several more insertions of the ovipositor in the various parts of the body of the same caterpillar, the parasite remaining on the larva 8 or 10 minutes. Throughout the entire procedure the wings and antennae of the hyperparasite kept up an incessant vibration. Dissection of the caterpillar and of the *Apanteles* larva inside it showed that a very tiny egg had been deposited within the body of the immature *Apanteles* larva.

The early development of the *Mesochorus* is slow, the *Apanteles* being permitted to complete its growth, and to emerge from its host and form its cocoon before being destroyed by the hyperparasite. This is one of the comparatively few secondary parasites that are endoparasitic.

CHALCIDOIDEA

CHALCIDIDAE

HALTICHELLA XANTICLES WALKER (?)

This species of *Haltichella*, doubtfully determined as *xanticles* by Gahan, has been occasionally reared from cocoons of *Apanteles melanoscelus* in Massachusetts, but only in very small numbers. It appears to be of little or no significance as an enemy of that primary. The small amount of laboratory work carried on with it indicated that *Apanteles* is not an especially desirable host; for only 5 out of 34 cocoons exposed individually for periods of two to four days were attacked. There are evidently two, and sometimes three, generations

annually. From 30 to 40 days are required for development from egg to adult, in the case of the summer generations. Hibernation occurs in the mature larval form, and adults appear about the middle of June.

SPILOCHALCIS TORVINA (CRESSON)

On a very few occasions the writers have obtained this species from cocoons of *A. melanoscelus*. Its very rare appearance indicates that it is of no consequence as an enemy of this *Apanteles*. Sufficient material was not available to permit laboratory studies of its life history.

EUSAYIA DEBILIS (SAY)

Even less frequently reared than the preceding species, *Eusayia debilis* has been of no importance whatever in preventing the increase of *Apanteles melanoscelus*. It is included here merely to record its occasional appearance among the hyperparasites attacking that primary.

CALLIMOMIDAE

MONODONTOMERUS AEREUS WALKER

This hyperparasite is of major importance as an enemy of certain Tachinidae. It appears to attack hymenopterous primary parasites much less often, and has been very seldom obtained from cocoons of *A. melanoscelus* collected in the field. It is discussed in some detail because of certain interesting traits which it exhibits.

In the laboratory it has frequently been bred upon *Apanteles*, as well as upon *Meteorus* and *Spilocryptus*. There appear to be normally two generations annually, but the writers have carried the species through the full year with only one generation. The females on emerging from their winter quarters are very slow to oviposit. It was found by dissection that fully formed eggs do not occur in the reproductive system until two or three weeks after emergence. Development from egg to adult, however, is very rapid. The eggs hatch in about 2 days, and the entire larval period covers only 7 to 10 days, while the pupal stage is as long as the combined periods spent as egg and as larva, or approximately 9 to 13 days. Approximately 20 to 25 days are required for development from egg to adult. Like most hyperparasitic species, the larvae feed externally upon the primary parasite. Usually they are gregarious, several developing upon one host. As many as 24 very small adults have been obtained from a single field-collected puparium of *Compsilura concinnata* Meig., but usually the number emerging from such puparia ranges from 6 to 14. From the much smaller *Apanteles* cocoons more than two adults have rarely been obtained.

The females of the overwintering generation mate in the early fall and hibernate as adults. In several cases females issuing from host cocoons or puparia as early as July 15 have been successfully hibernated. No males have ever been found going over the winter. The brown-tail moth seems to have a particular attraction for this species: and the winter webs of the hibernating gregarious brown-tail moth larvae are used to a considerable extent by the female *Monodontomerus* for winter quarters. However, at the gipsy-moth laboratory there is a record of a specimen having been found hibernating in a

bird's nest taken in the field; and the species probably does hibernate in various protected places. Females have been successfully carried through the winter in an outdoor cage at the laboratory by placing them in large glass vials containing crumpled dried leaves.

The attraction of the brown-tail moth is further manifested by a decided preference that seems to be exhibited by ovipositing females for brown-tail moth parasites. The species is reared in large numbers from the tachinids that attack that host and is much more frequently obtained from the hymenopterous parasites of the brown-tail moth than from other Hymenoptera. In Europe it also seems to attack extensively a tachinid that forms its puparia within the pupae of the gipsy moth. The injury caused to *Apanteles melanoscelus* is almost negligible.

EURYTOMIDAE

EURYTOMA APPENDIGASTER (SWEDERUS)

(Fig. 5)

This European species of *Eurytoma* has been the most abundant of the hyperparasites of *Apanteles melanoscelus* encountered, although not greatly surpassing in importance either *Hemiteles tenellus* or *Dibrachys boucheanus*. It has been obtained in large numbers from practically all of the collections of cocoons made by the writers.

In the New England States this species has either one or two generations annually, two being apparently the more common. The adults of the overwintering brood emerge from their host cocoons over a period of several weeks during the latter part of May and early June, or shortly before the first-generation cocoons of *A. melanoscelus* can be found in the field. A partial generation of *Eurytoma* develops on these cocoons; but apparently a large proportion of the females live until the more abundant second-generation cocoons appear, and attack these as well. The adults are exceedingly hardy, and doubtless live for a long time in the field; in the laboratory they have been kept alive for several months. The first-generation cocoons attacked almost invariably produce adults the same season; but a large majority of those of the second generation that are parasitized carry the *Eurytoma* over the winter. The species hibernates as a mature larva.

In order to obtain some idea of the number of eggs that may be deposited, five females, all of which emerged on May 31, were continually supplied with cocoons of *Apanteles* throughout their life. Three of these failed to oviposit even once though cocoons were furnished them every day for two months. Of the remaining two, one deposited 111 eggs over a period from June 18 to September 20, and the other laid 163 eggs from June 12 to September 28. Females of this species have been observed to feed extensively at the puncture holes made by the ovipositor. Very often no oviposition occurs, the punctures being apparently made for the sole purpose of feeding.

Like the majority of hyperparasites, this species is ectoparasitic. The egg is deposited inside the cocoon but external to the host larva or pupa, and is not attached either to the *Apanteles* larva or to the cocoon. It is unusually striking in appearance because of the minute, closely set, blackish spines which cover it, and also because of the curious, usually folded, stalk at the posterior end, and the short deli-

cate flagellum arising from the anterior end. Very often several eggs are deposited in one cocoon, but the species is strictly solitary with respect to development, and never more than one individual matures in such cases. About two days are required for the egg to hatch. The rapidity of the development of the larva is indicated by the following quotation taken from the notes upon one of the individuals which were carried through from egg to adult in the cells on depressed glass slides:

August 26—Egg has hatched.

August 27, 3 p. m.—First stage molt skin removed and mounted.

August 28, 10 a. m.—Second stage molt skin removed and mounted.

August 29, 8 a. m.—Third stage molt skin removed and mounted.

August 30, 8 a. m.—Fourth stage molt skin removed and mounted.

September 1, 2 p. m.—Meconium has been cast.

September 2, 7 a. m.—Pupa has been formed; fifth stage molt skin removed and mounted.



FIG. 5.—*Eurytoma appendigaster*, female

The pupal stage averages 10 to 14 days, making a total period for development from egg to adult normally of from 18 to 24 days, in the case of the summer generation. The hibernating brood spends nearly 10 months as a mature larva.

We have sometimes found *E. appendigaster* rather extensively parasitized by two species of *Pleurotropis*, which are discussed later.

EUPELMIDAE

EUPELMUS SPONGIPARTUS FOERSTER

(Fig. 6)

The recorded hosts of various species of *Eupelmus* include many types of insects, such as numerous species of *Cynipidae* and of the eurytomid genus *Harmolita* among the Hymenoptera; eggs of certain Orthoptera, particularly Mantis eggs; Lepidoptera like Cole-

ophora; species of the coleopterous genus *Bruchus*; and in the Diptera, *Phytophaga destructor* (Say), the Hessian fly. Phillips and Poos (29) found that *Eupelmus allynii* French might develop as either a primary or a secondary parasite of the joint worm, *Harmolita tritici* (Fitch). The species considered here, which is of European origin, is recorded as principally parasitic on Cynipidae in Europe and probably attacks such species here to some extent. Although obtained more or less regularly from collections of *Apanteles melanoscelus* cocoons, it is usually not a particularly serious hyperparasite. Occasionally, however, it becomes very destructive.

It is a solitary species, so far as larval development is concerned, never more than one individual maturing within a cocoon, although



FIG. 6.—*Eupelmus spongipartus*, female

several eggs may have been deposited; and in New England it passes through not more than two generations, usually only one, annually. The eggs are deposited inside the *Apanteles* cocoon, but only occasionally are they placed directly upon the *Apanteles* larva which is resting there. Much more frequently they are found to lie just inside the inner wall of the cocoon, firmly held in place by a delicate fibrous mass, which must have been deposited by the parasite at the time of oviposition, for it can be readily pried loose with a needle, coming off with the egg. Phillips and Poos (29) observed the same curious type of fibrous structure usually supporting the eggs of *Eupelmus allynii* against the inner wall of the host cell or puparium. When the adult emerges the same season that the egg is deposited the period required for development from egg to adult

ranges from 25 to 38 days. According to observations made upon certain individuals carried through their development in glass cells, between 3 and 4 days are passed in the egg, about 48 hours in each of the first four larval stages, from 4 to 7 days in the last larval stage, and 12 to 14 days in the pupal stage. When there is but one generation annually about 11 months are spent in the host cocoon, nearly all of this period as a resting mature larva, which is the hibernating form.

Unfertilized females deposit eggs quite as readily as those that have been mated. The progeny resulting from parthenogenetic reproduction are entirely males.

EUPELMINUS SALTATOR
(LINDEMANN)

(Fig. 7)

The biology of this species has been discussed in detail by McConnell (23), who studied it particularly in its rôle as a primary parasite of the Hessian fly. He also states that specimens reared by Phillips from the galls of various species of *Harmolita*, the joint worms, have been identified as this species. That it is actually primary on the Hessian fly has been demonstrated by McConnell by breeding it experimentally upon puparia known to have been free from other parasites. The writers have definitely determined that it is frequently hyperparasitic by rearing hundreds of specimens from field-collected cocoons of *Apanteles melanoscelus*. They have also bred it in the laboratory upon this primary parasite.

As a parasite of *Apanteles* in New England, *Eupelminus saltator* seems in general to have three generations annually, although there is some variation in this. The first adults appear about the end of May or the first of June. The first-generation cocoons of the *Apanteles*, which are formed soon afterward, are sometimes extensively parasitized; and the female hyperparasites emerging from these cocoons attack the second brood of *Apanteles*. Normally 24 to 30 days are required for development from egg to adult, and there are

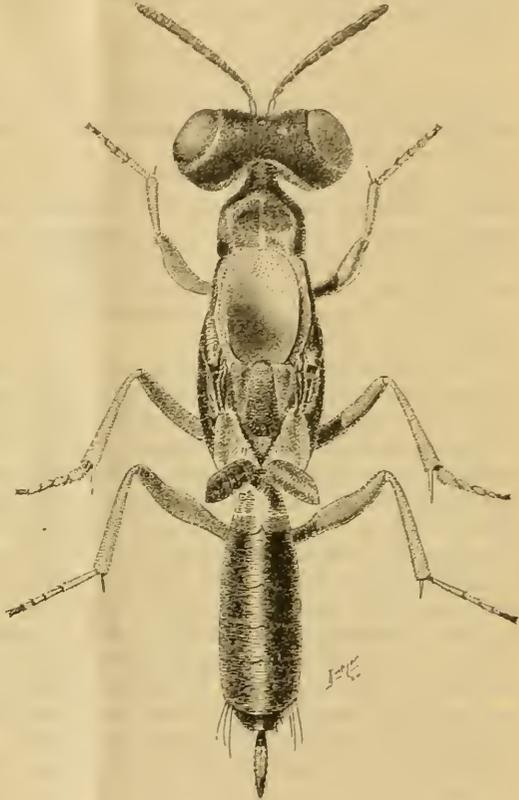


FIG. 7.—*Eupelminus saltator*, female

usually two complete generations upon the second-generation *Apanteles* before the overwintering form appears. The species hibernates as a mature larva within the host cocoon. Only one specimen matures on one host even though several eggs be deposited.

Like McConnell, the writers have found *E. saltator* to be thelytokous in parthenogenetic reproduction. In fact, they have not recognized the male of this species among the hyperparasites of *Apanteles melanoscelus*.

ANASTATUS BIFASCIATUS (FONSCOLOMBE)

Although essentially a primary parasite of the eggs of the gipsy moth, this *Anastatus* is occasionally reared from cocoons of *Apanteles melanoscelus*, in which case it is a secondary parasite. The injury resulting from this hyperparasitic habit is of no serious consequence because of the relatively small number of cocoons attacked. Only about 25 instances of parasitism of field-collected *Apanteles* cocoons have been noted. It is briefly discussed here only because its behavior as a hyperparasite represents another instance of the occasional departure of a parasitic insect from its normal habits, as regards host selection.

For an account of the life history and biology of this species as an egg parasite the reader is referred to a recent paper by Crossman (4), where this subject is discussed in considerable detail. In the study of the species as a hyperparasite specimens obtained from *Apanteles* cocoons were found to attack quite freely the eggs of the gipsy moth, and individuals reared from gipsy-moth eggs readily attacked *Apanteles* cocoons. Usually but one *Anastatus* develops upon an *Apanteles* larva, and the resulting adult is much larger than specimens obtained from gipsy-moth eggs, because of the greater amount of food available for the development of the larva. There is normally but one generation annually, just as when the species is primary, about 11 months of the year being spent as a resting mature larva within the host cocoon. However, cocoons that were attacked late in April by females that had been caused to emerge prematurely by holding parasitized gipsy-moth eggs in a warm room, produced adults the same season, the period from egg to adult being from 40 to 100 days.

ANASTATUS PEARSALLI ASHMEAD

Originally described as a parasite of the eggs of *Smerinthus*, and probably normally parasitic on lepidopterous eggs of that type, this species has also been reared from *Apanteles melanoscelus* cocoons, and in slightly larger numbers than the preceding species, although likewise of little significance as an enemy of that primary parasite. The adult closely resembles *bifasciatus*, and the immature stages are practically indistinguishable.

A cocoon of *A. melanoscelus* will maintain but a single *Anastatus*, although several eggs are sometimes placed in one cocoon. Certain females were found to oviposit very freely, whereas others would not attack any of the cocoons presented to them. It appears that the ovipositor is always inserted into the *Apanteles* larva inside the cocoon, and that upon its withdrawal the egg is left attached at

this puncture, for the eggs were always found fastened to the *Apanteles* larva by the end of the long flexible stalk with which they are provided and the point of attachment was invariably a puncture hole. The egg hatches after 3 or 4 days, and the parasitic larva passes through five larval stages, the feeding period covering 10 to 15 days. From 3 to 4 weeks are passed as quiescent mature larva and as pupa, in the case of those individuals that will produce adults the same season, thus making the total period spent in the cocoon about 40 to 50 days. Usually, however, there is but a single generation annually, 11 months or more being spent in the host cocoon. Like *bifasciatus*, this species hibernates as a mature larva. The two species of *Anastatus* are the last of the hyperparasites attacking *Apanteles melanoscelus* to appear in the spring, emerging about the middle of July.

Anastatus pearsalli is another of the comparatively small number of parasitic Hymenoptera that always produce females in parthenogenesis. In this respect it differs from the preceding species, which is arrhenotokous.

ENCYRTIDAE

SCHEDIUS KUVANAE HOWARD

Schedius kuvanae, imported from Japan and established in the New England States as an aid in the control of the gipsy moth, is another egg parasite which has been reared in small numbers from cocoons of *Apanteles melanoscelus*. Its value as a primary parasite of the eggs of the gipsy moth is not materially lessened by its behavior as a hyperparasite, for the number of *Apanteles* destroyed is relatively so small as to be almost negligible. This hyperparasitism by *Schedius* is doubtless purely accidental. It is interesting, nevertheless, because it shows the adaptability of the larva to the conditions in which it finds itself, and further emphasizes the fact that parasitic Hymenoptera are rarely absolutely restricted to one or another particular host.

Specimens emerging from either eggs of the gipsy moth or from field-collected cocoons of *A. melanoscelus* attacked *Apanteles* cocoons readily in the laboratory. But they often experienced difficulty in piercing the tough cocoon, and exhibited a distinct preference for gipsy-moth eggs. When parasitic upon *Apanteles* the species is gregarious, from 6 to 17 individuals maturing in a single cocoon; and about 30 days are required for development from egg to adult. Several generations a year upon *Apanteles* are possible. The details of the life history of this species as an egg parasite have been published by Crossman (4) and need not be discussed here. In the case of cocoons parasitized in the laboratory, the adults were sometimes unable to cut an exit opening and died without emerging. This indicates the unsuitability of *Apanteles* as a host for *Schedius*.

PTEROMALIDAE

DIBRACHYS BOUCHEANUS (RATZBURG)

(Fig. 8)

This cosmopolitan species attacks a great variety of primary parasites and very rarely itself acts as a primary parasite. At the gipsy-moth laboratory it has been reared in enormous numbers from *Apanteles melanoscelus*, from numerous other species of *Apanteles*, from

various species of *Meteorus*, *Rogas*, *Hyposoter*, and *Campoplex*, in a few instances from tachinid puparia, and in one case from the mud cells of a psammocharid wasp upon which *Dibrachys* had been a primary parasite. Evidently it is occasionally also a tertiary, having been recorded by Ratzeburg (52) as probably parasitic on the hyperparasite *Hemiteles socialis* Ratz., and having been bred at this laboratory upon a species of *Gelis* which had developed upon *A. melanoscedus*. Because of its wide host range, it can maintain itself in large numbers, although one or another of the parasites on which it preys be periodically greatly reduced. Accordingly, *Dibrachys* can



FIG. 8.—*Dibrachys boucheanus*, female

be obtained in abundance year after year, without noticeable periodic recessions. It has proved to be one of the three most serious parasites of *A. melanoscedus*.

Although of small size, it appears to be very hardy. In the laboratory specimens have been kept alive for two or three months. Despite its small size, and contrary to Tothill's assumption (36), it is a prolific species. Under laboratory conditions four females deposited, respectively, 235, 255, 375, and 389 eggs over a period of approximately two months. The largest number laid on any one day by a single female was 29. It is likely that under natural conditions even more eggs may be deposited. Unfertilized females oviposit as readily as those that have mated, but the result of such reproduction is always males. Nearly always several eggs are placed in the same host cocoon, and as many as 14 individuals have been found to mature upon a single *Apanteles*, the species being normally gregarious in the larval stage. Females have not been observed to deposit more than three eggs at one insertion of the ovipositor, but the same cocoon is usually attacked more than once. There is much variation in the size of the adults in consequence of the varying number developing within a cocoon. The larvae feed externally upon the *Apanteles* larva, like most hyperparasites, and pass through five larval stages,

as determined by observations upon specimens which were carried through their development in glass cells. The period from the deposition of the egg to the emergence of the adult from the host cocoon was found to range from 17 to 34 days, the length of this period being largely dependent on the temperature. After an egg stage of 2 to 5 days, from 5 to 8 days were required for the feeding period, and the rest of the time spent in the cocoon was passed as resting fifth-stage larvae and as pupae. In the case of specimens that were held under constant observation none of the larval instars, except the last, covered more than 24 hours. After the cessation of feeding the larva remains quietly in the last stage from 6 to 14 days before transforming to a pupa, and the pupal period covers 5 to 12 days.

There are several generations annually, as many as five being produced at the laboratory under outdoor temperatures. It was noted that cocoons attacked prior to September 1 usually produced adults of the hyperparasite the same season, whereas those attacked after that date normally carried the full-grown hibernating larva over the winter.

Its reproductive capacity, its gregarious habit, and its characteristic of passing through several generations a season combine to make this species a hyperparasite of exceptional importance.

COELOPISTHIA SCUTELLATA MUESËBECK (27)

In the experience of the writers this species has not been of major importance as a parasite of *Apanteles melanoscelus*, but its general similarity in biology to the closely related *Dibrachys boucheanus* suggests that it may, under the proper conditions, become a serious enemy of this *Apanteles*.

Like *Dibrachys*, it is a gregarious ectoparasite on the *Apanteles* larva or pupa, and the eggs and larvae of the two hyperparasites are practically indistinguishable. About 25 to 30 days are required for development from egg to adult, except in the hibernating generation, while the actual feeding period of the larva covers only 7 to 9 days. There are from one to three generations annually, there being considerable irregularity in this, as has been noted with most multiple-brooded hyperparasitic species; and hibernation occurs in the form of full-grown larvae. The adults of the hibernating generation appear in early June. Like most of the hyperparasites discussed, this species also produces males in parthenogenesis.

HABROCYTUS DUX GIRAULT

Urbahns (37) has discussed, in some detail, the life history and habits of *Habrocytus medicaginis* Gahan as a primary parasite of the alfalfa-seed chalcid, *Bruchophagus funebris* Howard; and Pierce, Cushman, Hood, and Hunter (31), and Wellhouse (38) have recorded species of this genus as primary parasites of weevil larvae. In general, however, the species of *Habrocytus* are probably hyperparasitic, attacking various braconid and ichneumonid cocoons. Although not obtained in great abundance, most of the collections of *Apanteles melanoscelus* cocoons have produced *Habrocytus dux* in some numbers. It must be included among the more important parasites of that primary.

The adults appear about the middle of May and pass through two, and sometimes three, generations annually, the summer generations requiring approximately three weeks for development from egg to adult. The larvae are ectoparasitic within the host cocoon, and always solitary, only one maturing on an *Apanteles*. Hibernation occurs in the form of full-grown larvae in the *Apanteles* cocoon. When reproducing parthenogenetically the species produces males.

HYPOPTEROMALUS TABACUM (FITCH)

The species of this genus are apparently always hyperparasitic, and are sometimes very destructive parasites of Braconidae. *Hypopteromalus tabacum*, a widely distributed North American form, has appeared commonly among the species reared from *Apanteles melanoscelus*, although it does not rank with *Eurytoma appendigaster*, *Hemiteles tenellus*, *Dibrachys boucheanus*, or *Dimmockia incongruus* in point of abundance. In the laboratory the writers have found it to oviposit much more readily than the closely related *Habrocytus* in *Apanteles* cocoons, but field collections of cocoons indicate that there is little difference in effectiveness between the two.

Adults emerge late in May and sometimes parasitize the first brood of *Apanteles* quite extensively. The larva develops as a solitary ectoparasite within the cocoon and matures rapidly; only 14 to 23 days elapse between oviposition and the emergence of the adult. Despite this rapid development, however, there are in general only two generations annually. Second-generation *A. melanoscelus* cocoons which are attacked in July usually carry the species over the winter in the form of full-grown larvae.

HYPOPTEROMALUS INIMICUS MUESEBECK (27)

This species has been obtained only in relatively small numbers, and up to the present time has been of but minor importance in checking the increase of *Apanteles melanoscelus*. In habits and life history it agrees with *Hypopteromalus tabacum*.

EUPTEROMALUS NIDULANS (FOERSTER)

Kurdiunov (22) has shown that the species discussed under the name *Pteromalus egregius* Foerster by Howard and Fiske (19) is *Eupteromalus nidulans* (Foerster). Although during the height of the brown-tail moth epidemic in New England it was abundantly found acting as a primary parasite of the small hibernating caterpillars of that pest, this species appears at present to be more commonly hyperparasitic, developing within the cocoons of various Braconidae. The writers have never obtained it in large numbers from *Apanteles melanoscelus*, however. In fact, during the years that the hyperparasites of this *Apanteles* have been closely observed, it has been one of the least important among these species. It seems to prefer for oviposition cocoons that are more delicate and of finer texture than those of *A. melanoscelus*. *A. lacticolor* Viereck, the brown-tail moth parasite, is attacked to a considerable extent in the field. And in the laboratory the writers have been more successful in breeding it upon cocoons of *A. glomeratus* L., *A. hyphantriae* Riley, and *A. euchaetis* Ashm. than upon those of *A. melanoscelus*.

The period from egg to adult requires only 13 to 18 days and there are several generations annually. Like the other pteromalids discussed above, this species is ectoparasitic within the host cocoon and hibernates as mature larvae, the adults of the overwintering generation appearing in May.

ELASMIDAE

ELASMUS ATRATUS HOWARD

This species has been one of the rarest among the hyperparasites of *Apanteles melanoscelus*, having been obtained from only a very few cocoons. It has been recorded by Howard (15) as an abundant parasite of *A. hyphantriae*, and (16) as an occasional parasite of *A. delicatus* Howard, the tussock moth parasite. In the former paper other species of *Elasmus* are mentioned as sometimes primary on Lepidoptera, such as *Tischeria* and *Aspidisca*; and it is probable that *atratus* will also attack hosts of that type. *A. melanoscelus* cocoons appear to be too thick and tough to be readily pierced by the ovipositor of this species. Females of *E. atratus* were very often observed in the laboratory attempting oviposition in these cocoons, but very rarely were they successful.

In hibernating as a pupa within the host cocoon, *Elasmus* differs from most hyperparasites and agrees with the two species of *Dimmockia* mentioned below.

EULOPHIDAE

DIMMOCKIA INCONGRUUS (ASHMEAD)

(Fig. 9)

Reared regularly from nearly all collections of *Apanteles melanoscelus* cocoons of both generations, *Dimmockia incongruus* is often obtained from this host in enormous numbers; it has also been reared from various Braconidae and Ichneumonidae, and more rarely from Tachinidae. A large number of adults may be obtained from a relatively small number of cocoons, for this species is gregarious in the larval stage, sometimes as many as a dozen, or even more, individuals maturing within a single host cocoon. Counts covering several hundred parasitized cocoons gave an average of six adults per cocoon. A gregarious parasite of this character is able to maintain itself in considerable abundance on a relatively small number of hosts.

Observations over several years have shown that *D. incongruus* passes through not more than two generations annually, and that often there is but one. This is in rather marked contrast with the habit of *Dibrachys boucheanus*, the other very common gregarious parasite of *Apanteles melanoscelus*. Progeny of the same individual sometimes issue in part the same season and in part the following year, the same irregularity in the number of generations existing which has been observed with most other hyperparasites. When there are two generations the first requires only 11 to 23 days for development from egg to adult, with an average of 16 days, whereas the second covers 10 months or more. The female usually deposits several eggs at one insertion of the ovipositor; this was determined by dissecting cocoons which had been closely observed and had been allowed to be attacked only once. The eggs, which are placed any-

where on the body of the primary within its cocoon, hatch after 2 or 3 days. The larvae feed externally and complete their growth in 4 or 5 days; and after 2 to 4 days spent quietly as full-grown larvae, they enter the pupal stage. If the adults are to emerge during the same season, the pupal period covers normally 3 to 12 days; if they are not to issue until the following spring, approximately 10 months are spent as pupae, for, unlike most chalcidoid secondaries, this species hibernates as a pupa. Cocoons of *A. melanoscelus* attacked as early as June 3 have been found to carry *Dimmockia* through the winter, producing adults early in June of the following year, a full year after the eggs were deposited.

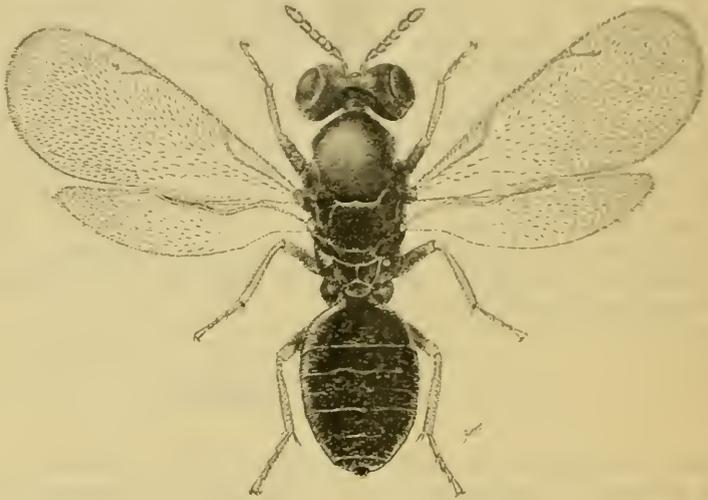


FIG. 9.—*Dimmockia incongruus*, female

DIMMOCKIA PALLIPES MUESEBECK (27)

This species has been reared much less abundantly than *Dimmockia incongruus*, but it is, nevertheless, of some importance as an enemy of *Apanteles*. The immature forms are inseparable from those of *incongruus*, and in all details of life cycle and biology the two species appear to agree perfectly.

CIRROSPILUS SPECIES

Several species of the genus *Cirrospilus* have been obtained from cocoons of *Apanteles melanoscelus*, but in very small numbers. They are *C. cinctithorax* (Gir.), *C. flavicinctus* Riley, *C. marylandi* (Gir.), and *C. coptodiscae* (Gir.). Their principal hosts are apparently the larvae of small lepidopterous leaf miners belonging to such groups as *Coptodisca*, *Coleophora*, and *Bucculatrix*, and they may be only occasionally secondary. However, too little is known of their habits to permit aligning them definitely with either primaries or secondaries. The above species are listed here only to record their occasional occurrence among the parasites of *A. melanoscelus*.

PLEUROTROPIS TARSALIS (ASHMEAD)

This species differs from all the other hyperparasites treated in this bulletin, except *Pleurotropis nawaii*, which is considered next, in its unusual habit of being essentially a tertiary parasite. The writers have had no difficulty in breeding it in the laboratory as a secondary on *Apanteles melanoscelus*; but in the field it has appeared of little importance in this rôle, occurring most frequently as a tertiary. Several hundred cocoons from which *Pleurotropis* emerged were dissected to determine to what extent the species had been secondary and to what extent tertiary. It was found that in 97 per cent of these cocoons *P. tarsalis* had developed as a parasite of the secondaries *Eurytoma*, *Dibrachys*, *Dimmockia*, *Eupelmus*, *Hemiteles*, and *Habrocytus*, and in only a very few instances as a parasite of *Apanteles*. However, if certain conditions should bring about a decided reduction in the secondary parasitism of *A. melanoscelus*, it is very probable that *Pleurotropis* would be more often found acting as a true secondary than as a tertiary.

The female places its eggs inside the larva or pupa of the parasite attacked, whether that host be a primary or a secondary, and the *Pleurotropis* larva develops as an internal parasite, entirely consuming the contents of the host individual and leaving only the larval or pupal shell, within which it pupates. Except in rare instances it is solitary, only one maturing within a host irrespective of the size of the latter, and whether this host is a primary or a secondary. As is the case with most hyperparasites, the progeny of unfertilized females are males.

The writers have found the species to have either one or two generations annually. When adults emerge the same season that the eggs are deposited, about 28 to 40 days are required for development from egg to adult. Of this period about 2 days are spent in the egg, 8 to 12 days as a larva, and the remaining time as a pupa.

The writers have repeatedly observed that when one or two larvae or pupae of a gregarious secondary, like *Dibrachys* or *Dimmockia*, are parasitized by *Pleurotropis*, any unparasitized individuals in that cocoon fail to emerge, although they frequently reach the adult stage. It is difficult to understand the reason for this, since the tertiary larvae inside their particular hosts can hardly exert any influence upon the unparasitized secondaries in the same cocoon. It is curious that the unparasitized individuals should nearly always succeed in transforming to adults and yet fail to cut their way out of the cocoon.

PLEUROTROPIS NAWAII (ASHMEAD)

(Fig. 10)

This Japanese and European species of *Pleurotropis* has been commonly reared from cocoons of *Apanteles melanoscelus*. Like *Pleurotropis tarsalis*, it acts chiefly as a tertiary parasite. It also resembles that species in life history and biology, except in two features; it hibernates as a pupa instead of as a larva within the shell of its host, and whereas *tarsalis* produces males in parthenogenesis, this species is always thelytokous. This last characteristic should make it more valuable than *tarsalis* as a tertiary parasite. But the two species have been reared in approximately equal numbers.

SYMPLESIS MASSASOIT CRAWFORD

Symplesis massasoit was only very rarely reared from cocoons of this *Apanteles*, and this parasitism must be considered purely accidental. The species of *Symplesis* are probably largely primary parasites of dipterous leaf miners.

COLEOPTERA

CLERIDAE

HYDROCERA VERTICALIS SAY

On several occasions the writers have secured from isolated *Apanteles* cocoons larvae of this species of the family Cleridae, kindly identified by A. G. Böving, of the Bureau of Entomology. The conditions under which these specimens were obtained indicate that the coleopterous larva developed as a true hyperparasite either upon the larva of *Apanteles melanoscelus* or on a larva of a secondary parasite within the *Apanteles* cocoon.



FIG. 10.—*Pleurotropis nawaii*, female

SUMMARY

Hyperparasitism is of very general occurrence. Practically all species of primary parasites are subject to attack, although the extent to which a given species may be parasitized depends to some extent upon its particular habits and biology. Secondary parasites often greatly retard the increase of valuable primary parasites and may seriously interfere with the successful establishment of the latter in a new country.

The vast majority of hyperparasites are Hymenoptera. They belong principally to the Chalcidoidea and the Ichneumonoidea. Very few Diptera and Coleoptera are known to act as secondary parasites.

As regards host selection, hyperparasites are in general much less discriminative than primary parasites. This is obviously a

decided advantage, for they are able to maintain themselves in large numbers irrespective of the periodic fluctuations of particular primaries. The difficulty of establishing primary parasites in new localities is greatly increased because of this, for the secondaries native to the country in which it is desired to establish the primaries will attack the latter as readily as they do native species.

The larvae of hyperparasites, for the most part, feed externally upon their hosts, which are usually protected within cocoons or puparia. There are some interesting exceptions, however, including such widely different forms as *Mesochorus*, *Charips*, and *Pleurotropis*, representing respectively the Ichneumonoidea, the Cynipoidea, and the Chalcidoidea.

The habit of adult secondaries of feeding at the puncture holes made by the ovipositor is very general and is doubtless responsible for much destruction of primary parasites. Eggs are not always deposited, indicating that insertion of the ovipositor is often for the sole purpose of making an opening at which the secondary can feed.

Probably without exception hyperparasites can reproduce without fertilization, and in the case of nearly all species males are the result of such reproduction. With a relatively small number of forms, however, females are produced in parthenogenesis. Four species, *Hemiteles tenellus* Say, *Anastatus pearsalli* Ashm., *Eupelminus salinator* (Lindm.), and *Pleurotropis nawai* (Ashm.) among the parasites attacking *Apanteles melanoscelus* were found to be thelytokous.

About 35 species of hyperparasites have been reared from cocoons of *A. melanoscelus*. Fourteen of these are responsible for more than 90 per cent of the total parasitism, and four species, *Eurytoma appendigaster* (Swed.), *Dibrachys boucheanus* (Ratz.), *Hemiteles tenellus* (Say), and *Dimmockia incongruus* (Ashm.), destroy many more *Apanteles* than all the other species combined.

Extensive collections of *Apanteles melanoscelus* cocoons, which have been held for the issuance of primaries and secondaries, indicate that from 25 to 30 per cent of the first-generation cocoons produce adult *Apanteles*, while less than 1 per cent of the second-generation cocoons, which are formed in July and must carry the species over the winter, produce adults of the primary the following spring. Fifty per cent or more of these cocoons yield neither primaries nor secondaries, as a result of the extensive feeding of the adult hyperparasites and the very strenuous competition between the secondaries for the same individual hosts.

Individuals of several species of secondaries were carried through their entire development from egg to adult in glass cells to determine the number of larval stages, the rapidity of larval growth, and the length of the periods spent in the egg, as larva, and as pupa. In the case of all the species observed, which included the ichneumonids *Hemiteles tenellus* and *Gelis bucculatricis* Ashm.; a eurytomid, *Eurytoma appendigaster*; two eupelmids, *Eupelmus spongipartus* Foerst., and *Anastatus pearsalli*; a pteromalid, *Dibrachys boucheanus*; and a culophid, *Dimmockia incongruus*, there were five larval stages. The feeding period is nearly always very short, rarely more than 36 hours being spent in any of the larval stages except the last; in the last stage, too, feeding ends after from 24 to 48 hours, but several days are usually spent as a resting larva before pupation.

All the hyperparasites obtained from *Apanteles melanoscelus*, with the exception of the two species of *Pleurotropis*, were found to be

essentially secondary, although nearly all may sometimes be accidentally tertiary. *Pleurotropis tarsalis* and *Pleurotropis nawaii*, however, were tertiary in nearly all cases and sometimes appear to exert a considerable check upon the increase of certain secondary parasites.

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UNITED STATES DEPARTMENT OF AGRICULTURE



DEPARTMENT BULLETIN No. 1490



Washington, D. C.



July, 1927

DEFECTS IN TIMBER CAUSED BY INSECTS

By THOMAS E. SNYDER, *Entomologist, Forest Insect Investigations, Bureau of Entomology*

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INTRODUCTION

It is extremely difficult to estimate the losses due to defects in timber caused by insects. Where the grade of lumber is lowered, the loss may be ascertained by the reduction in the grade, because of the number or size of the holes caused by insects. However, where entire large oak or spruce trees are left to rot in the forest,

because the wood has pinholes in it and hence is not suitable for high-grade cooerage or airplane stock, the loss is greater, but perhaps more intungible. Where such timber is accessible and there are suitable markets, it need not be an entire loss, but could be used for lower-grade products. Closer utilization is of prime importance in the prevention of waste in the conservation of our forest resources.

Better methods of manufacture and the use of forest products, and the elimination of waste, as advocated by the Federal Forest Products Laboratory at Madison, Wis., and the Bureau of Standards of the Department of Commerce, will go far in helping to relieve the great timber shortage, which is especially serious in the case of the hardwoods.

The purpose of this bulletin is briefly to describe and illustrate, from the viewpoint of the entomologist, for the benefit of graders, inspectors, manufacturers, or utilizers of timber products, the principal types of defects in timber caused by insects, the causes of these defects, and, where possible, the mode of applying recommended methods to prevent the damage and loss. The Forest Service has already published a circular on grading lumber (39).¹

Wood-boring insects not only destroy a considerable quantity of forest products, but also cause the loss of the labor expended during the process of their manufacture. The trees from which these products were cut are a loss, and additional trees must be taken from the forest to replace them. To this loss must be added percentages of the cost and upkeep of lumber camps, machinery, equipment, logging railroads, wages and keep of men and animals in the woods, storage in the mill pond, sawing, drying, finishing, and piling at the mill.

The direct money loss caused by insects to cut timber and lumber assumes an enormous aggregate—greater proportionately than that caused by insects to living timber. To the money loss of production costs must be added the loss of time necessary to properly season the wood.

Of course, damage to seasoned finished wood products causes relatively greater loss than does damage to crude forest products. Where the products are damaged after being put in place, the cost of replacement involves additional loss of labor and time, as well as the cost of the original and replaced products, a loss far greater than the value of the raw products. Often such replacement charges should be charged to both wood-destroying fungi and wood-boring insects and not to one agency alone, as frequently there is a close relationship between these forms of life in the destruction of timber. However, in many cases wood-destroying fungi alone are responsible for the destruction.

It has been demonstrated in practice that a large percentage of the \$45,000,000 annual loss (37) caused by wood-boring insects in the past can be prevented in the future. The increased prices of lumber and all other forest products make it even more essential that all avoidable waste caused by insect defects should be eliminated in the interest of conservation.

¹ Reference is made by italic numbers in parentheses to "Literature cited," page 44.

In order to accomplish this saving it is necessary for manufacturers of wood products to utilize all available information that has been obtained from experiments carried on for many years by the Bureau of Entomology, especially the results of scientific research on the specific causes of the different types of insect defects and methods of preventing them. Data contained in earlier bulletins by experts of this bureau, as well as new and unpublished data, have been used freely in this bulletin. The published articles by Hopkins (23, 24, 25, 26, 27, 28, 29, 30, 31, 32, 33, 34, 35), Burke (6, 7), Webb (50, 51), Craighead (9, 10, 11, 12, 13, 14), Snyder (43, 44, 45, 46, 47), and St. George (41) were the source of much information. The pioneer investigations and publications of Doctor Hopkins, former forest entomologist of the Department of Agriculture, in reality form the basis for this bulletin. Doctor Hopkins's investigations have done much to prevent waste and losses due to insects. References to these and many other publications are to be found in Chamberlin (8).

Timber inspectors and graders should be able to determine from the defect in the wood whether it was caused by insects working in (1) the living tree; (2) the freshly felled, green saw log or bolt, with or without the bark on; (3) the green, unseasoned lumber; or (4) seasoned rough or finished product.

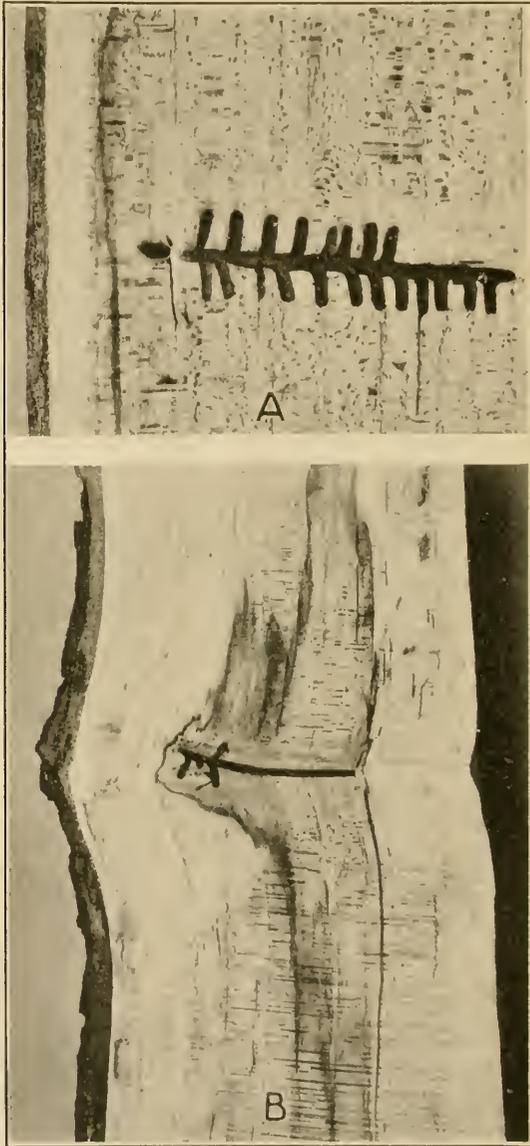


FIG. 1.—Black holes in white oak made by *Cortlylus columbianus*. A, slightly enlarged; B, slightly reduced

The rejection of timber with insect defects caused in the tree, log, or green lumber before the wood is dry or seasoned is often an avoidable loss, because the insects are no longer working in the wood. This type of insect defect is analogous to "pecky cypress" caused by a fungus. Even though the defects are such that they materially affect the strength of the wood or otherwise unfit it for the special

use intended, there are still many purposes for which it can be used. The grade may be merely lowered, according to the number and size of the holes; or the defect may unfit the wood for special uses, owing to unsightly appearance, likelihood to cause leaks (as for barrel staves and heads for tight cooperage), or weakening (as for high-grade airplane stock). Much waste can be avoided by utilizing such defective timber for other uses and in lower grades than originally intended.

Damaged implement or vehicle stock and other material in which great structural strength is required can be used for less exacting purposes, the defect being plugged and painted over; while low-grade lumber with wormholes but no living worms or decay can be used as the base for veneer if the holes are not large enough to cause depressions in the face veneer. On the other hand, the acceptance of material infested by powder-post beetles may lead to serious results through a break at a critical moment.

Special reference is made in this bulletin to the protection

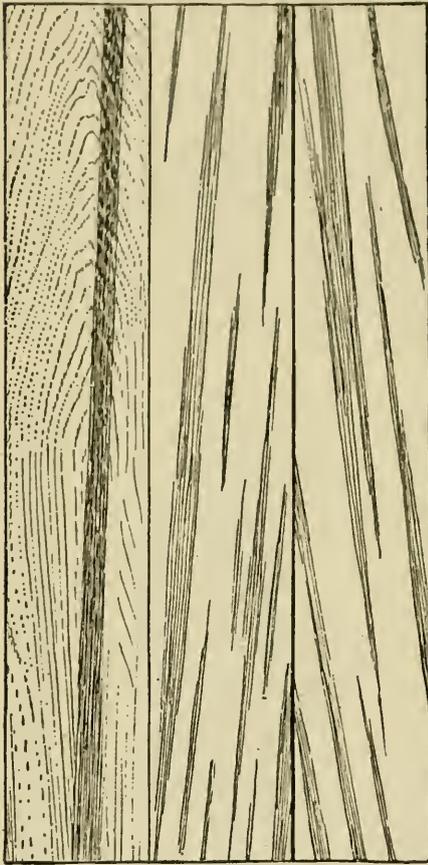


FIG. 2.—"Calico poplar," a defect caused by an ambrosia beetle (*Corthylus columbianus*). (25)

and conservation of both crude and finished wood products, such as lumber, bolts, cooperage stock (finished and unfinished), agricultural-implement handles, tent poles, vehicle parts, timber for shipbuilding, oars, airplane stock, and other high-grade products.

TYPES OF INSECT DEFECTS; DEFINITIONS

The principal types of defects caused by insects may be classed in three definite groups, namely, pinholes, grub holes, and powder post. (Table 1.) The terms for these defects are those generally used by the loggers in the woods and the sawyers and graders at the mill.

PINHOLES

Pinholes are small, round, usually open holes ranging from one one-hundredth to one-fourth of an inch in diameter; they are made either by ambrosia beetles or timber worms. Pinholes caused by ambrosia beetles are of two types: (1) Pinholes caused by adult beetles boring into the trunks of growing trees for the purpose of laying eggs and rearing their young, or by larvae, which also may burrow in the wood; (2) pinholes made by adult beetles or larvae in freshly felled green saw logs (with or without the bark on), bolts, and green or partly seasoned lumber.

In commercial grading rules for various species of timber pinholes constitute a standard defect (considering only wormholes), but are sometimes recognized as "equivalent defects," that is, equivalent

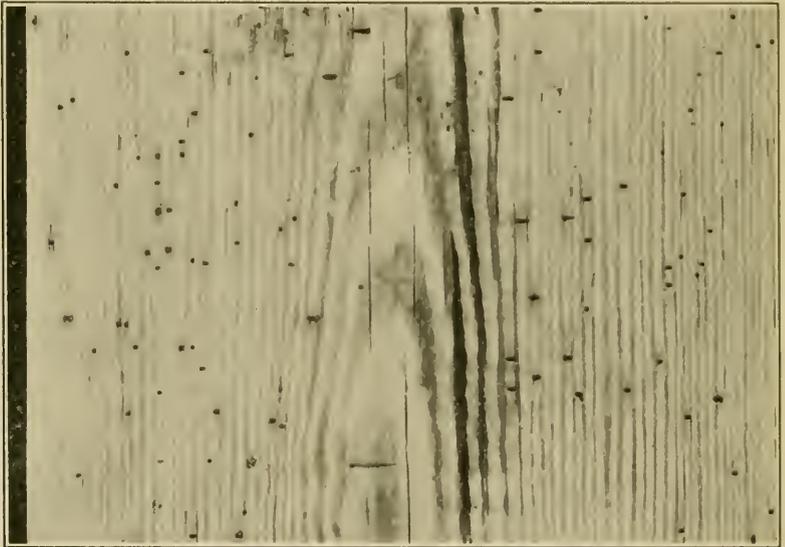


FIG. 3.—Work of ambrosia beetles in both sapwood and heartwood of southern yellow pine

to other defects, such as knots. This grade in certain hardwoods is termed "sound wormy" and is of that class of defects in timber or lumber in which the insects are no longer present and hence no further damage results to the timber.

GRUB HOLES

Grub holes or the larger wormholes are oval, circular, or irregular holes three-eighths of an inch to 1 inch in diameter, produced by adult insects (1) boring into or laying eggs in the trunks of living trees, or (2) boring into green, recently felled logs for the purpose of laying eggs or rearing their young; the young or larvae cause most of the injury to the wood, which serves as both food and shelter.

Grub holes may also be classified as standard defects.

POWDER POST

Powder post is that class of defects in which the larvae of insects reduce the wood fibers of seasoned or partially seasoned wood to a powderlike condition by boring through the wood, which is both their shelter and their food.

Powder post occurs only in the seasoned or partially seasoned sapwood or heartwood of both hardwoods and softwoods. Logs, bolts, timbers, lumber, and crude or finished products are attacked. The infested wood is always more or less filled with fine or coarse powdery or granulated boring dust and is called powder-posted. This type of injury is dangerous, since the grubs continue their destructive work in the wood and also infest other timber near by.

DEFECTS CLASSED AS PINHOLES

The term "pinholes" undoubtedly originated with stave makers and coopers, from the fact that such holes are often plugged with small wooden pins. Pinholes are small, round holes one one-hundredth to one-fourth of an inch in diameter in both the heartwood and sapwood of hard (broad-leaved) and soft (coniferous) living trees, green, moist saw logs, bolts, green timbers, or green piled lumber. These holes are made by either ambrosia



FIG. 4.—Pinholes caused by the pine-wood stainer (*Gnathotrichus materiarius*)



FIG. 5.—Pinholes in sapwood Douglas fir made by *Xyloterus* sp.

beetles or timber worms. In the former case (where caused by ambrosia beetles) the holes are made by both the small, slender, cylindrical, adult beetles, and, after hatching within the wood, by their

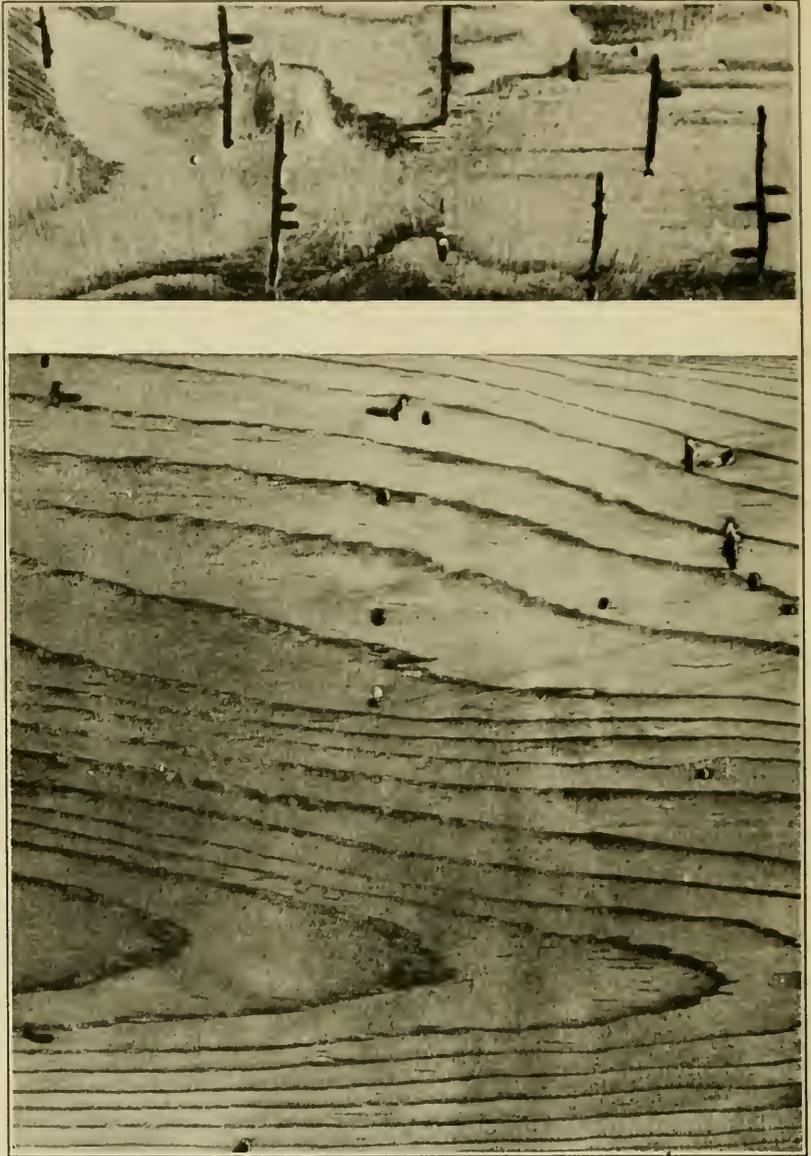


FIG. 6.—Pinholes made by the spruce timber beetle (*Xyloterus bivittatus*) in red spruce, West Virginia

larvae or young. In the latter case the injury is caused entirely by the larvae or grubs (young) of beetles or the so-called timber worms.

The larvae of some types of ambrosia beetles excavate side galleries at right angles to the gallery made by the adult, which tunnels into the wood to deposit eggs; other types excavate no side galleries. Some holes are clear; others are stained black by the action of fungi, some of which the beetles cultivate for food in their

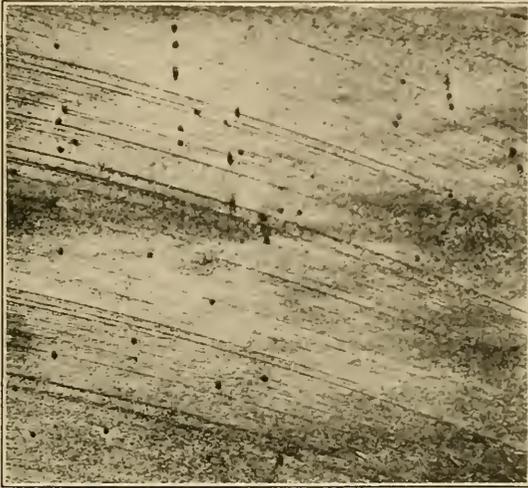


FIG. 7.—Pinholes caused by ambrosia beetles in heading and tight cooperage in South Carolina

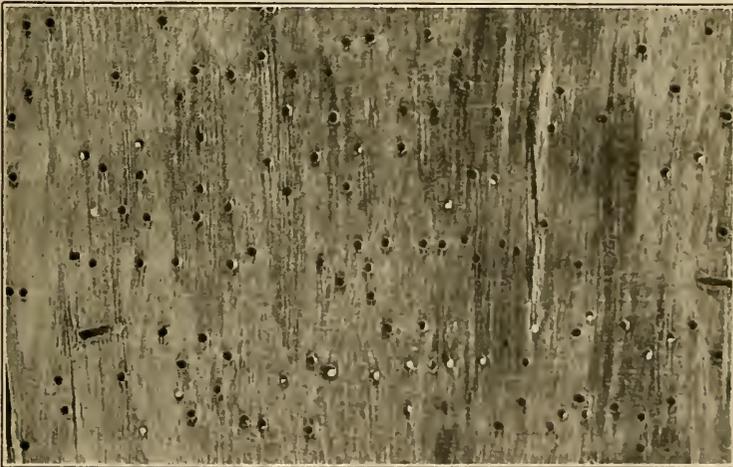


FIG. 8.—Pinholes in green hickory lumber caused by an ambrosia beetle (*Xyleborus xylographus*)

galleries. Injury to green heartwood stock and to partly seasoned stock of such woods as hickory and cypress in many cases does not produce the stain.

These holes are always open (never filled with dust), and are either clear or black and associated with discolored streaks or stains

in the surrounding wood. In the latter case, the injury is caused by the larvae or grubs (young) of the beetles.

PINHOLE DEFECTS FORMED IN LIVING TREES; A NONPREVENTABLE LOSS

When pinhole defects occur in the living tree, it is of course impossible for the lumberman to prevent the injury, since the holes

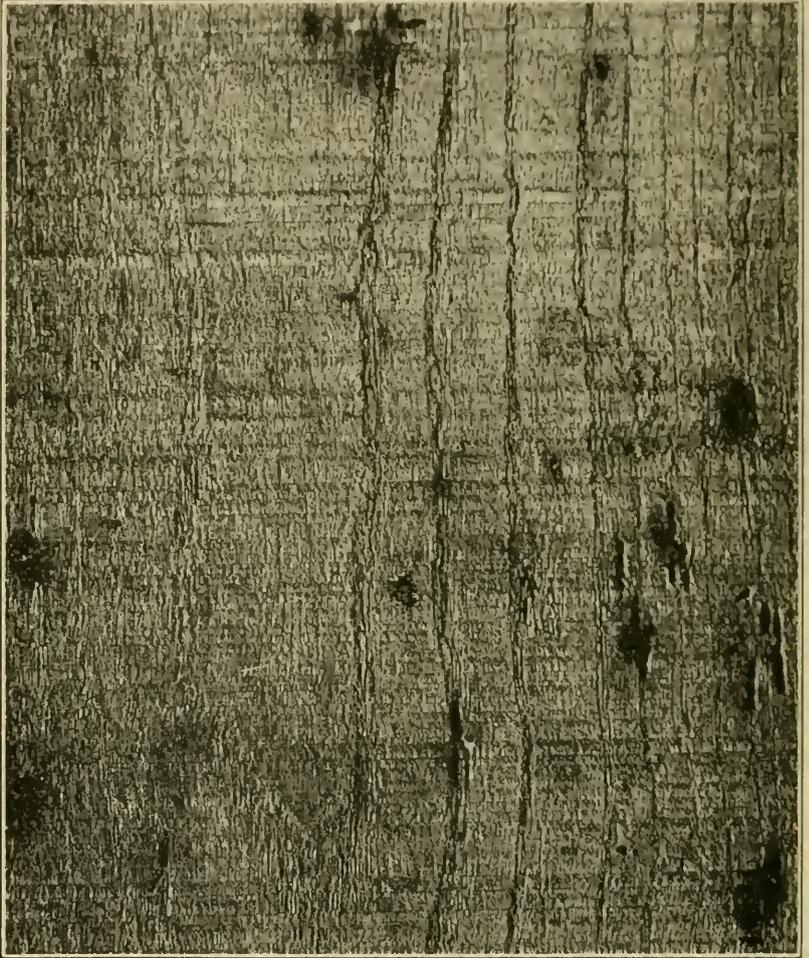


FIG. 9.—Pinholes with short stain streaks made in green ash lumber by *Platypus compositus*

have been made periodically, and often many years before the tree was cut. The dates when the injury was done can be determined by counting the annual rings of tree growth. Usually the wood surrounding pinholes of this type is stained.

PINHOLES IN LIVING TREES CAUSED BY AMBROSIA BEETLES

Pinholes are uniform in size, one-eighth of an inch in diameter or smaller (to one twenty-fifth inch), either darkly stained or un-

stained, or with short streaks in the surrounding wood; these holes run deeply in every direction in an irregular manner through the wood, and it is difficult to determine their extent from the surface. They are termed "pinholes," "shot holes," or "black holes" (36). Such holes occur in both the sapwood and heartwood of softwoods and hardwoods, but are more common in the sapwood.

One of the commonest defects (fig. 1) is caused in living trees by an ambrosia beetle,² and the holes are known as "black holes," "spot worm," "steamboats," "grease spots" (West Virginia), and "flag worm" (Arkansas). The holes usually occur in the best part of the wood, either one in a place, or two or more in a row. This defect is so prevalent in mature white oak and other oaks that it is often difficult to find a tree the wood of which is entirely free from it; in yellow poplar the defect is not so common. When the defect does occur in whitewood or yellow poplar the accompanying long, black, greenish or bluish streaks give a calico effect, and the wood is called "calico poplar" (fig. 2) (23, 27). The same defect occurs in beech, birch, basswood, maple, and elm in West Virginia, elm and oak in Michigan, oak in Arkansas, and chestnut in Tennessee.

Calico poplar and oak might be used, when available in sufficient quantity, as a special grade for interior natural-wood finish, as the effect is pleasing.

Thus the apparently limited quantity could be utilized without having its value depreciated much below that of the first and second grades.

This defect causes a serious loss to stave and shingle stock. In Arkansas from 30 to 40 per cent of white oak Bourbon whisky-barrel-stave stock and staves has often been left to rot in the woods on account of injury by the oak timber worms and ambrosia beetles.

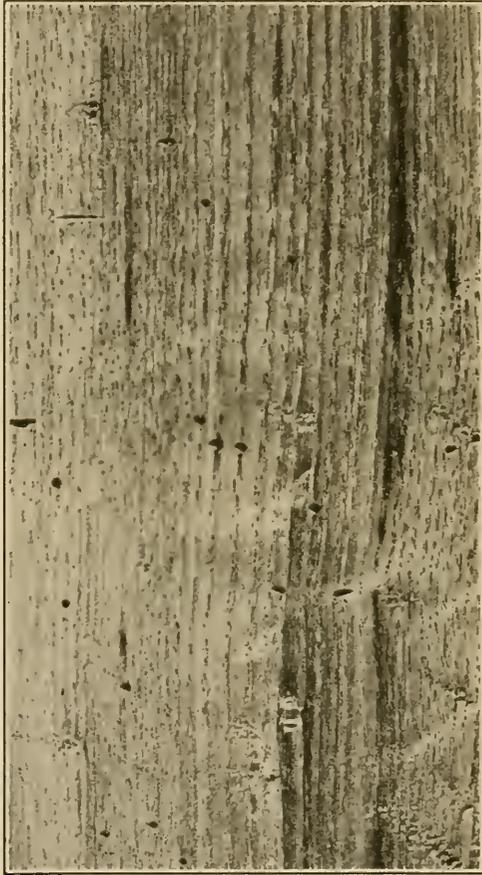


FIG. 10.—Pinholes made by *Xyleborus* sp. in green chestnut board, after piling

² *Corthylus columbianus* Hopkins.



FIG. 11.—Pinholes in the sapwood of high-grade cypress blocks; end view of logs in freight car; wood completely riddled by ambrosia beetles (*Platypus compositus* and *Xyleborus* sp.)

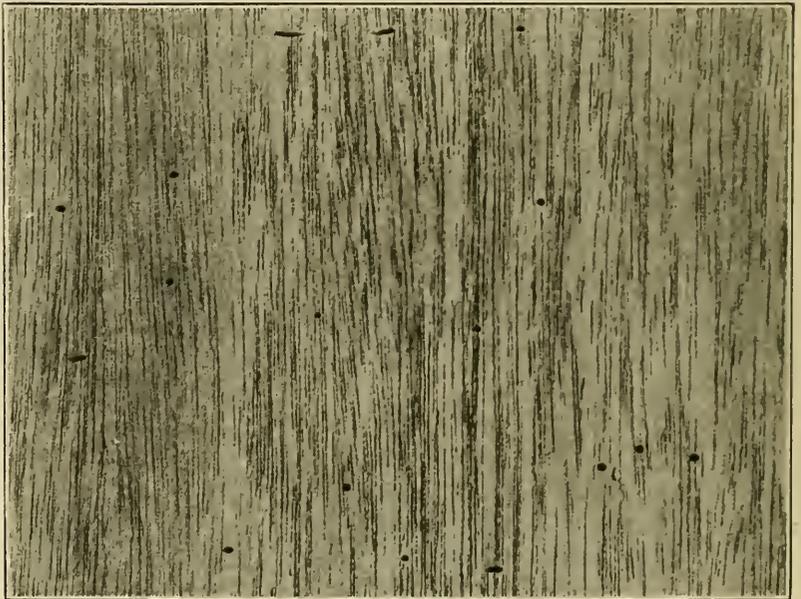


FIG. 12.—Pinholes caused by ambrosia beetles (*Xyleborus* sp.) in mahogany fitches

A loss of \$5 to \$20 per thousand feet of timber is a conservative estimate. This defect is classed as "wormholes, no living worms or decay," and can not be prevented in the tree, but of course similar defects in the green stock can be prevented by proper handling.

Pinholes one twenty-fifth to one-eighth of an inch in diameter in both heartwood and sapwood of hardwoods and softwoods (figs. 1, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, and 14) are caused by similar beetles.³

The defects caused by these pinholes and stains (discolored streaks and patches) (figs. 1, 2, 3, 4, 6, 9, and 13) reduce the grade of timber and its full strength, unfitting it

for structural timber, wagons, agricultural implements, tight cooperage

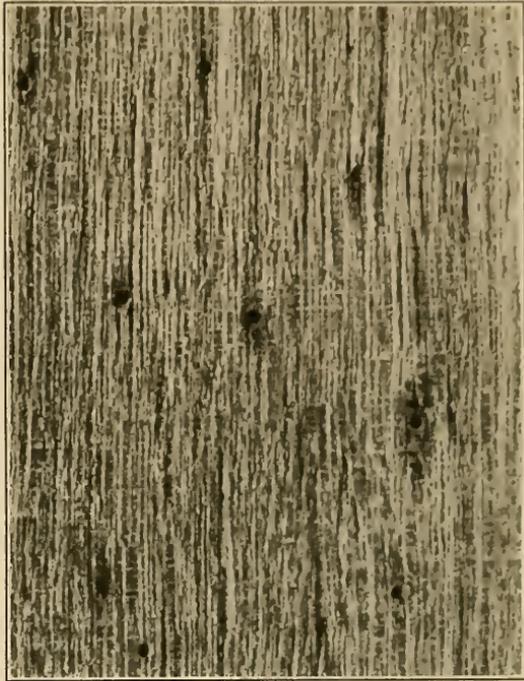


FIG. 13.—Pinholes caused by ambrosia beetles (*Xyleborus* sp.) in imported greenheart (*Nectandra rodioei*)



FIG. 14.—Pinhole damage by ambrosia beetles (*Xyleborus grenadensis*) to Hura wood (Rakuda) imported from Central America

logs at the mills in Illinois was due to such defects. In some cases millions of feet of timber have been reduced 10 to 25 per cent or more in value by pinhole defects. In deadened standing cypress in the Gulf States, pinhole injury can be prevented by girdling the trees in March, April, October, and November (28), but from August to September is apparently the most effective season.

³ Platypus, Monarthrum, Xyleborus.

PINHOLES IN LIVING TREES CAUSED BY TIMBER WORMS

Pinholes or wormholes in the heartwood of chestnut and red oak, one one-hundredth to one-fourth of an inch in diameter, open, clear, not stained, but lined with a substance about the color of the wood, a large number of holes in a given space, are made by timber worms hatching from eggs laid in or near scars. The holes made by the grubs are not of uniform size; they may extend several feet through the wood. (Fig. 15.)

This defect, due to the chestnut timber worm,⁴ is one of the most common and serious defects in chestnut timber throughout its range. It is rare to find chestnut trees, logs, or telephone or telegraph poles free from this defect, and practically every tree of merchantable

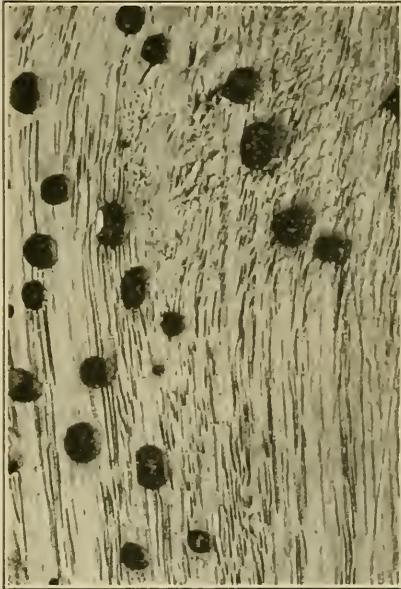


FIG. 15.—Holes caused by the chestnut timber worm (*Melittomma sericeum*), which causes the defect classed in the grade "sound wormy chestnut"

size is more or less affected. There is a very low percentage of "clear" chestnut, the remainder being "wormy" and reduced to the lower grades. This defect is a "sound wormy" injury and can not be prevented. Unfortunately the chestnut is rapidly becoming extinct as a commercial tree, owing to the chestnut blight fungus.

Wormy chestnut and oak wood can be used wherever structural strength is not necessary. They are especially suitable as the base for veneer in manufacturing pianos, caskets, coffins, automobile running boards, and the lower grades of building lumber, because of the comparatively reasonable price at which this grade of lumber can be bought. Much timber that would otherwise be wasted can be thus utilized. There is, however, a limit to the size of the holes admitted.

Similar pinholes or wormholes one one-hundredth to one-eighth of an inch in diameter in oak timber (fig. 16) are caused by the oak timber worm.⁵ This defect is especially serious in large mature white oak trees. The holes occur in large numbers in a given space and extend in all directions through the solid heartwood. This insect usually affects the wood of the finest old, mature, or over-mature trees, sometimes causing defects which result in the discarding of entire trees for such uses as tight barrel staves. This defect is classified under the term "wormholes, no living worms or decay," and can not be prevented when occurring in living trees, although losses can be lessened by clean forest management; that is, removal

⁴*Melittomma sericeum* Harris.

⁵*Eupsalis minuta* Drury.

of old dead and dying snags, stag-headed trees, and trees badly fire-scarred. From 20 to 25 per cent of oak lumber may be wormy from this cause. A loss of 15 to 20 per cent of the product is considered low.

Pinholes or wormholes one-eighth to three-sixteenths of an inch in diameter, few to many grouped in a given space, accompanied by a staining of the wood, or all more or less connected by irregular blackened streaks, in oak, maple, tupelo gum, beech, and other hardwoods, are similar to those caused by the oak timber worm. This defect is caused by tenebrionid timber worms.⁶ The insect lays its eggs in the living tree near a scar or wound, and many larvæ working together excavate irregular cavities and longitudinal burrows sometimes a foot in length. This defect is fairly common throughout Pennsylvania, Maryland, and Virginia and is classed as "wormholes, no living worms or decay." Although the losses can be greatly lessened by clean forest management, they are not preventable from the lumberman's standpoint.

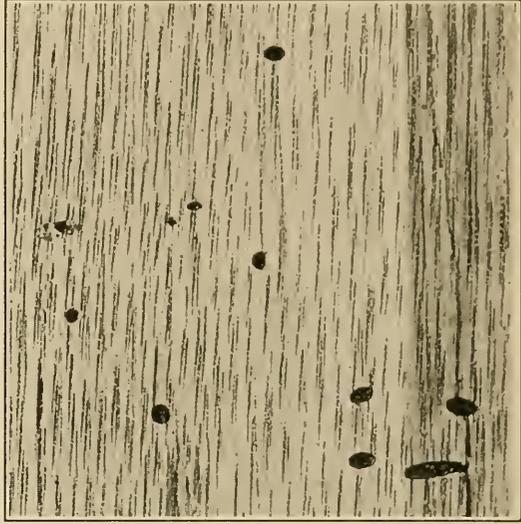


FIG. 16.—Pinholes caused by the oak timber worm (*Eupsalis minuta*), which causes the defect classed in the grade "sound wormy oak"

PINHOLE DEFECTS FORMED IN WOOD AFTER THE TREES ARE FELLED; A PREVENTABLE LOSS

Pinholes in felled timber are similar to those caused in living trees by ambrosia beetles and timber worms. Such holes are less than one-eighth of an inch in diameter and open, either darkly stained or unstained, or with dark streaks in the surrounding wood.

PINHOLE IN FELLED TREE" CAUSED BY AMBROSIA BEETLES

In sapwood or heartwood of white oak, chestnut, yellow poplar,⁷ birch, beech, and sweet gum the pinholes caused by ambrosia beetles are about one-twelfth of an inch in diameter, open, usually isolated, and always accompanied by long, discolored streaks in the surrounding wood. Lumber with such defects is rejected for the higher grades.

⁶ *Strongylus* spp.

⁷ The adult of *Corthylus columbianus* Hopkins causes pinholes in hardwoods with which discolored streaks are associated.

In Arkansas a 2 per cent loss of the product of green or newly manufactured white-oak Bourbon whisky-barrel staves occurred at one operation.

Pinholes one twenty-fifth to one-eighth of an inch in diameter occur in the sapwood of both hardwoods and softwoods (figs. 3, 4, 5, 7, 8, 9, 10, 12, 13, 14); in hardwoods usually the wood is not stained; but in freshly cut green hardwoods the wood may be stained. A few to a large number of holes occur in a given space; often every



FIG. 17.—Pinholes in yellow birch caused by the sapwood timber worm (*Ilyecoccus lugubris*). (Drake)

square inch of wood is penetrated. These common pinhole defects in recently felled green logs or bolts (with or without the bark) and closely piled green timber and lumber are caused by ambrosia beetles⁸ (figs. 4 and 5). There are two types of galleries made by these beetles—one, a long, winding main gallery and usually no staining of the wood, and the other, a series of short side galleries at right angles to this main gallery (figs. 1 and 6), the gallery usually being accompanied by a staining of the wood. Unlike holes made by the timber worms, which increase with the growth of the worms, these holes are more or less uniform in size.

PINHOLES IN FELLED TREES CAUSED BY TIMBER WORMS

Pinholes caused by timber worms in the heartwood of chestnut⁹ and oak¹⁰ can be recognized as follows: Holes from one one-hundredth to one-fourth of an inch in diameter; open and not stained; a large number to a given space.

Such holes may be a serious defect in square timbers used in structures the woodwork of which is exposed to the weather. Care should be exercised in utilizing wormy oak in structural work where strength is required, or in vehicle, ladder, or implement stock. It should be

⁸ *Gnathotrichus* and *Xyloterus*.

⁹ The larvae of *Aclittonna sericeum* Harris cause wormy chestnut and oak; the eggs are laid under bark.

¹⁰ The larvae of *Eupsalis minuta* Drury cause wormy oak; the eggs are laid under bark.

rejected for barrel staves and heads of tight cooperage, unless the holes are few and can be plugged. Such stock can be used where the holes can be plugged, puttied, and painted over, or as a base for veneer.

Pinholes or wormholes one one-hundredth to three-sixteenths of an inch in diameter in green saw logs with the bark on, of basswood, buckeye, chestnut, black walnut, cottonwood, yellow poplar, and birch (fig. 17), are caused by the sapwood timber worm,¹¹ which may cause a 5 to 10 per cent loss of a log. This defect is described as "wormholes, no living worms or decay," and can be prevented.

The insect lays its eggs in dying trees and green saw logs which are allowed to lie in the woods with the bark on from April to July, in the States north of the Gulf. The eggs are deposited in crevices in the bark. The beetle will not lay its eggs in barked logs or logs which are floating in log ponds.

In the sapwood or heartwood of oak, maple, tupelo gum, and beech, grouped holes from one-eighth to three-sixteenths of an inch in diameter and

all more or less connected by irregular blackened streaks are caused by tenebrionid timber worms.¹²

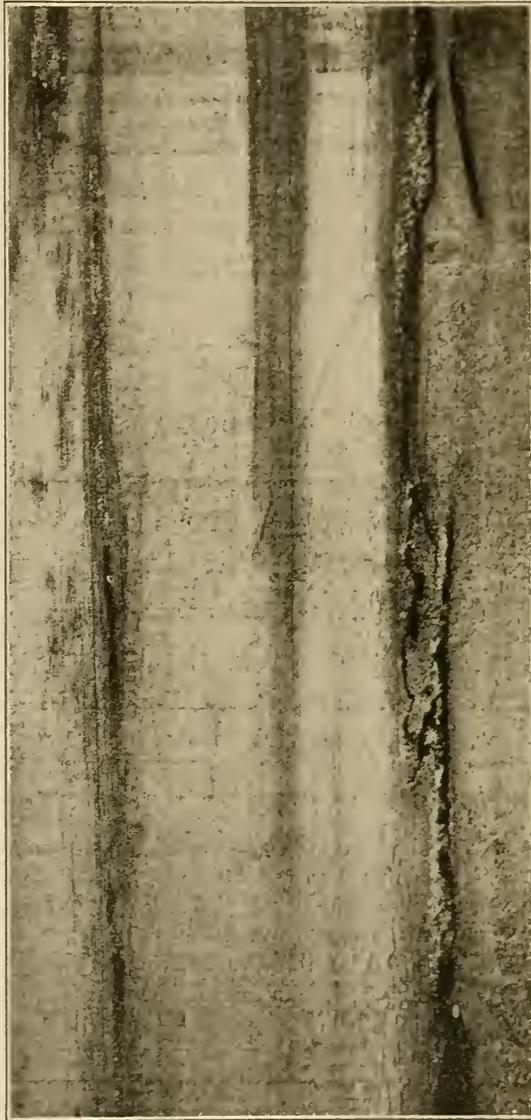


FIG. 18.—Holes caused by termites (*Coptotermes niger*) in log imported from Honduras; damage to the living tree caused this defect in the board

¹¹ *Hylecoetus lugubris* Say.

¹² The larvae of *Strongylius* spp. cause wormholes in hardwoods.

Pinholes of these and all other kinds made in timber after felling are preventable by prompt handling and rapid utilization of felled timber. Green logs or bolts, either with or without the bark on, should be placed in the mill pond as soon as possible after being cut, especially during the warm months of spring, summer, or fall, or in damp weather. In the mill pond the logs should be floated in loose booms, so that they can be rolled over and turned to make sure that they are periodically submerged on all sides. The damage can also

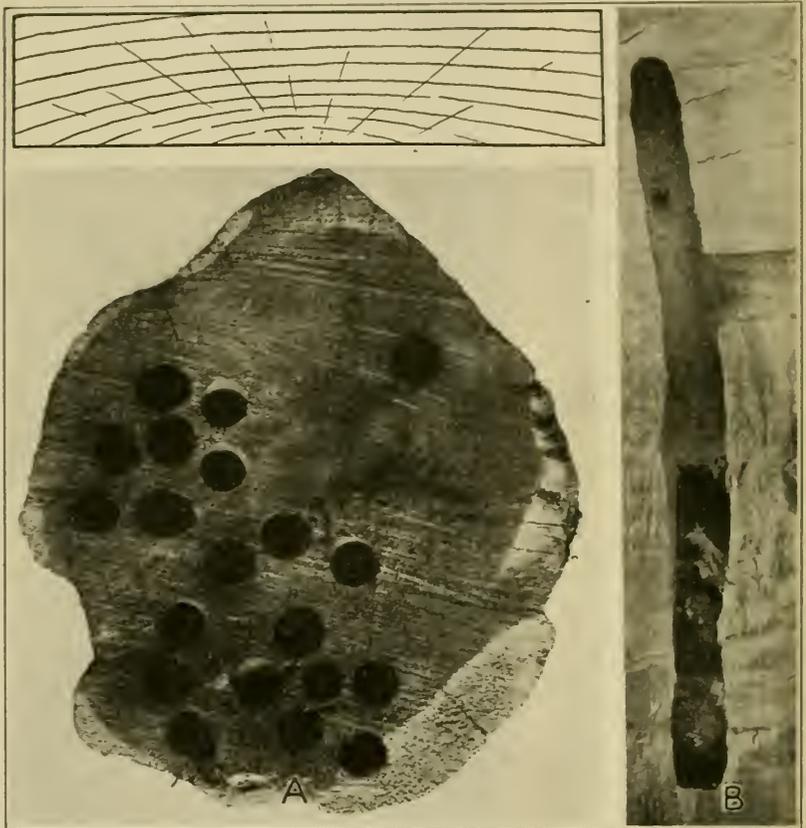


FIG. 19.—Grub holes and burrow caused by carpenter bee (*Xylocopa* sp.) in juniper from Arizona

be prevented by sawing the logs into timber and lumber as soon as possible.

If it is not possible to get the logs into the mill pond, they can be sun cured or dried rapidly (10, 11, 15, 16, 17, 18, 19, 20) to bring about conditions unfavorable to insect attack, which is accomplished by peeling them and placing them on "browse" (limbs) on knolls in open places in the sun. Other preventive measures consist of girdling before cutting, peeling, cutting, and leaving the tops on for a time before logging or after cutting. Barking the logs will prevent

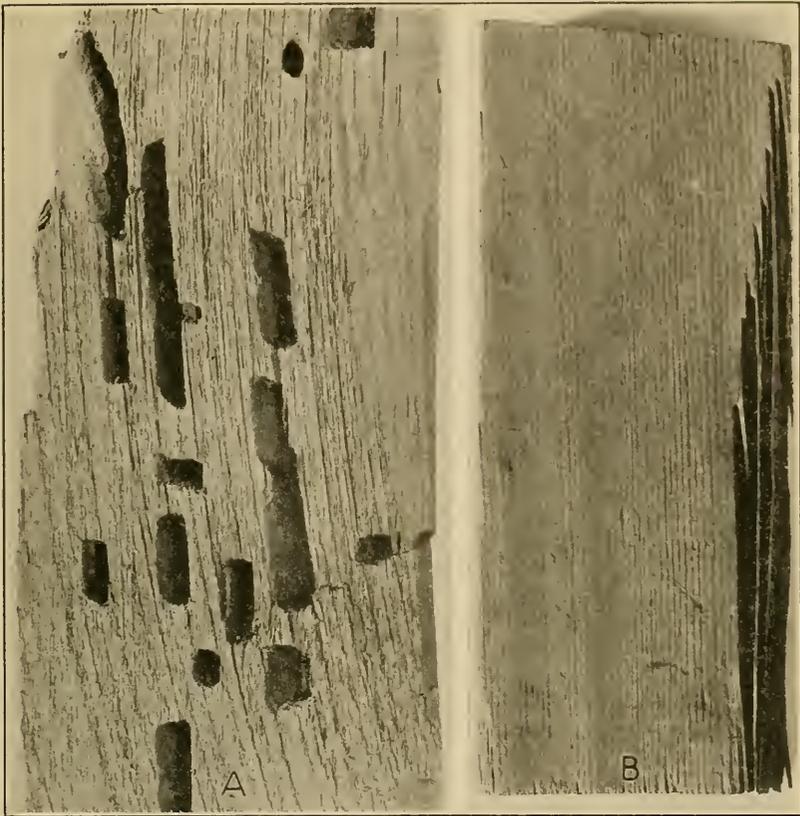


FIG. 20.—A, enlarged holes made by carpenter ants (*Camponotus* sp.) in red cedar in Washington; B, redwood damaged by carpenter ants in California

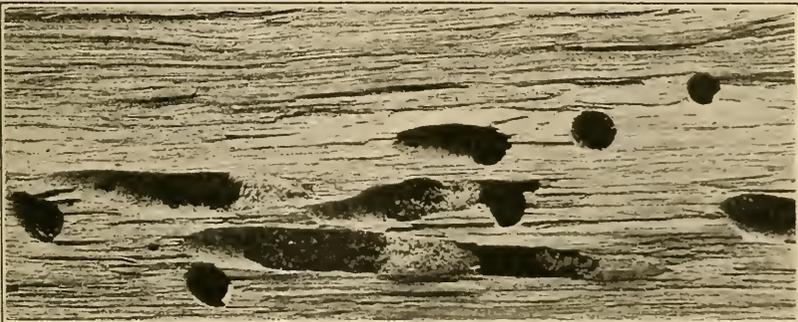


FIG. 21.—Work of a horntail (*Urocerus albicornis*) in a decaying softwood log

damage by timber worms, as will also coating or spraying with preservatives.

Repellent, poisonous, or sticky chemical sprays, to prevent attack by ambrosia beetles on more valuable species and products, can be used where the bark is on the logs and the wood will not be discolored (12). The preservative coating known as hardened gloss oil has the advantage of preventing checking.

Green lumber should be kiln-dried (49); or, where this is not practicable, piled on stickers (1), to insure rapid air seasoning. Air

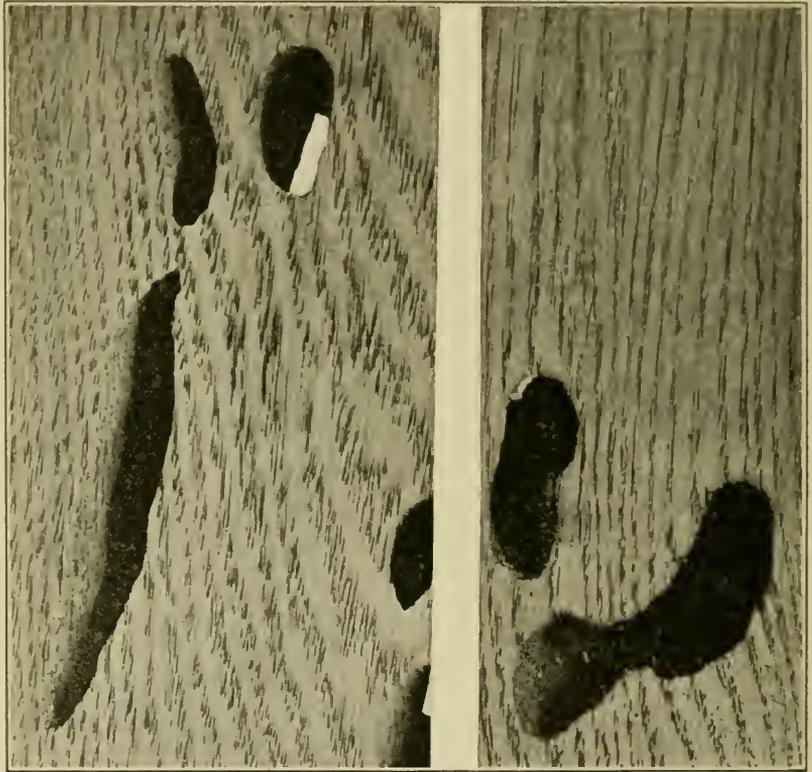


FIG. 22.—Grub holes made by the oak carpenter worm (*Prionoxystus robiniae*)

seasoning of green freshly sawn timber or lumber by open or loose piling is a preventive. In cribbing or proper piling of green sawn stock to facilitate rapid drying, care should be taken to insure against severe checking from too-rapid drying. Heavy dimension timber should be stacked in loose piles. If it were possible to kiln-dry the material, insect damage, of course, would be prevented.

In the case of damage to stave stock, by special methods of sawing the waste can be reduced to a minimum and a very considerable saving of material effected. Where the holes are not too numerous, they can be plugged with wooden pins and the wood used for casks.

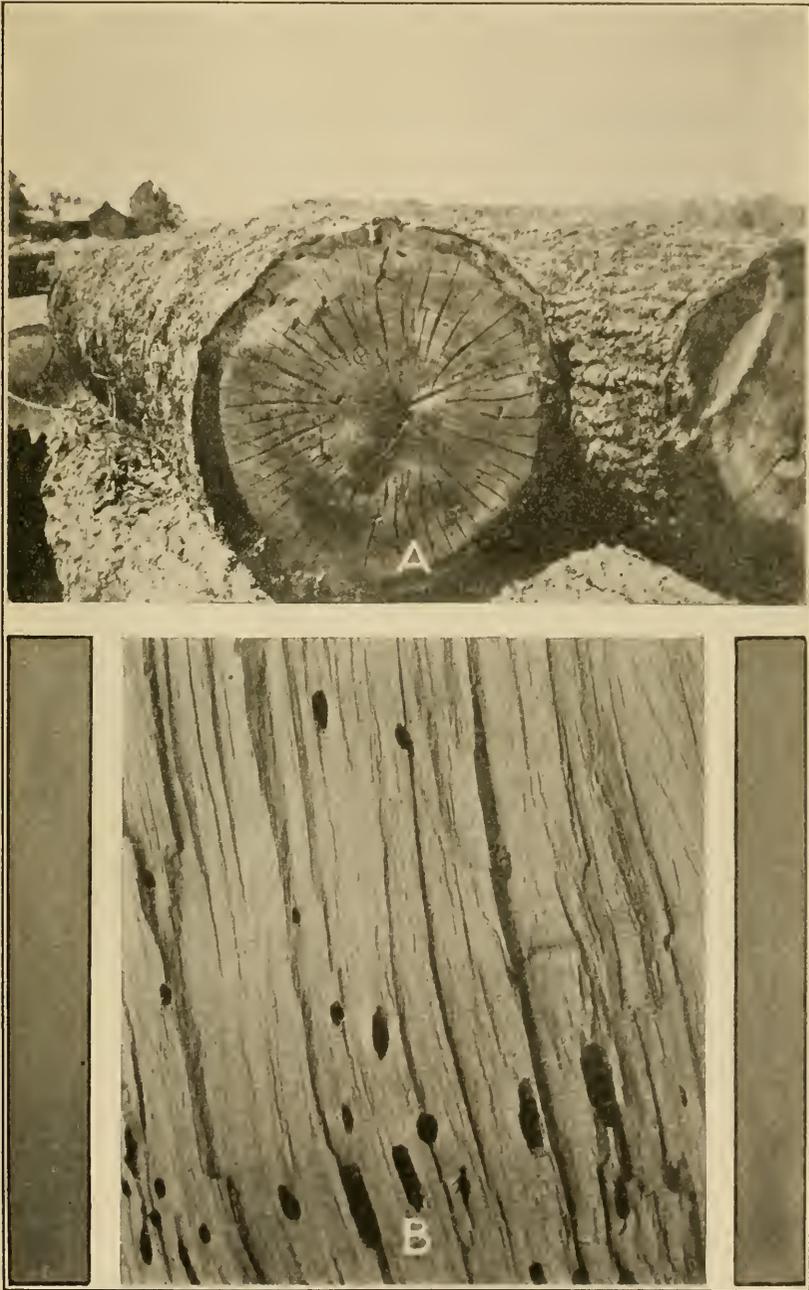


FIG. 23.—A, grub holes in overcup oak, made by the Parandra borer (*Parandra brunnea*) near Vicksburg, Miss.; B, grub holes in soft maple made by the Parandra borer in Maryland

The defect does not deteriorate furniture and inside-finish stock. This defect is considered under "wormholes, no living worms or decay," and in the interest of conservation and closer utilization, timber with these defects should be used.

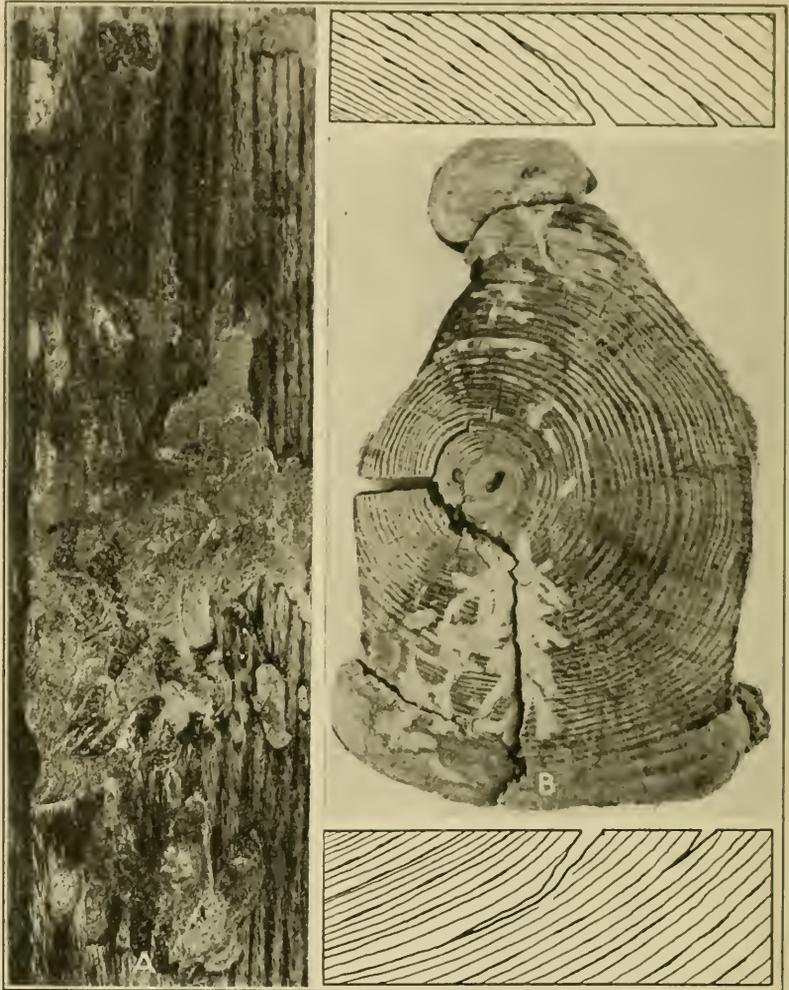


FIG. 24.—A, grub holes made by a flat-headed borer (*Buprestis apricans*) in the pitchy "fatwood" of the basal log of long-leaf pine; B, the same in a turpented tree

PINHOLE INJURY TO IMPORTED LOGS

Large quantities of tropical woods in the rough, round, or squared log are yearly shipped into the United States from Central and South America, the West Indies, Africa, and the Philippines. (Figs. 12, 13, and 14.) Almost invariably such timber, if received within a year after it is cut, contains many species of pinhole-boring beetles, but these never live over the winter, except perhaps in the Gulf States.

Under present methods of lumbering, such imported logs usually are infested by pinhole-boring beetles of many species, which attack the logs after they are cut, and continue to live in them for several months and in some cases a year or more. If such logs are shipped into another country with a similar climate, the insects may survive and attack logs of native timber; if, on the other hand, logs are exported to a much colder or hotter country, the insects will rarely, if ever, become established in the country of import.

There is, therefore, some danger of introducing destructive species through the commercial interchange of timber in the form of logs.



FIG. 25.—Wormholes caused by "sawyers" (*Monochamus* spp.) in pine. A and B, wormholes in southern yellow pine; C, wormholes in white pine

For example, many insect species are widely distributed over tropical America that do not occur in tropical Africa, Asia, Australasia, and the Pacific islands. Tropical Australia, the Philippine Islands, and tropical Japan doubtless have a considerable number of the same species of pinhole borers. One country may have a few that do not occur in the others.

DEFECTS CLASSED AS GRUB HOLES OR WORMHOLES

Grub holes are medium to large, circular, oval, or irregular holes from three-eighths to 1 inch in diameter, in both sapwood and heart-

wood of all kinds of timber. They may either be stained black inside or be of the same color as the surrounding wood, and they may be free and open or filled with tightly-lodged boring dust, depending on the kind of insect making them. This boring dust does not fall out when the wood is jarred. Grub holes are made in the living tree, in the saw log, or in piled green lumber. In nearly all cases the injury is caused by the young borers, sawyers, or grubs, but occasionally also by adult termites or white ants (fig. 18), adult

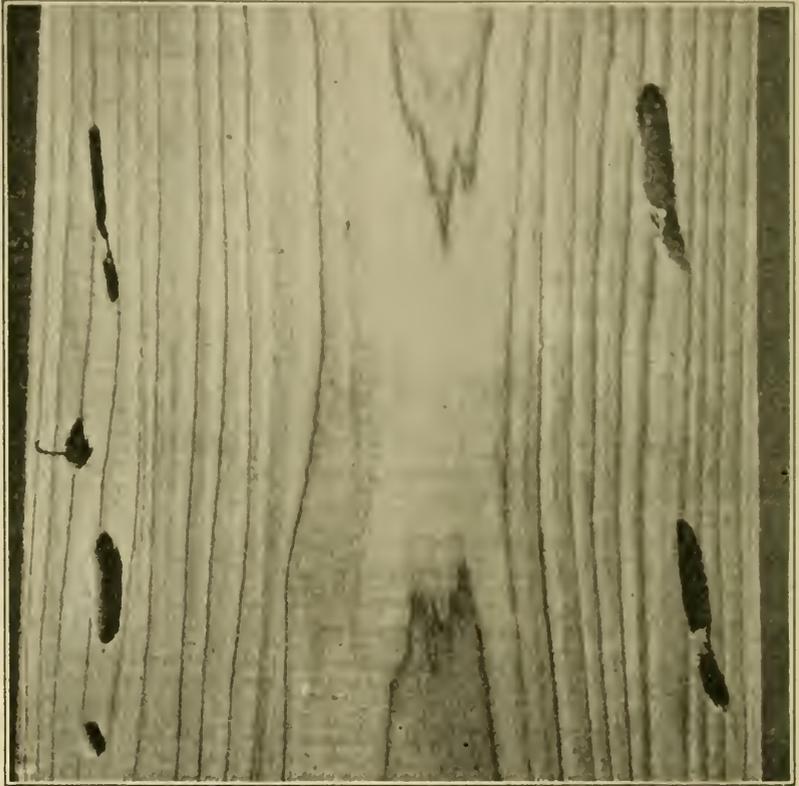


FIG. 26.—Wormhole defects in cedar, caused by the round-headed borer *Callidium antennatum*

carpenter bees¹³ (fig. 19), or carpenter ants¹⁴ (fig. 20), or by the larvae of horntails¹⁵ (fig. 21). Usually this type of injury is considered as "wormholes, no living worms or decay," especially if the holes are stained black, and no further damage will result, except in rare cases.

Grub holes constitute a standard defect and are also included under "equivalent defects." They are often of considerable size

¹³ *Xylocopa* spp.

¹⁴ *Camponotus* spp.

¹⁵ *Tremex columba* L., or *Sirex* spp.; they usually damage only dead wood or trees or logs that have been left in the woods too long.

and consequently reduce the structural strength of the wood, especially when cut into smaller dimensions; therefore timber having such borer holes should be used in as large dimensions as possible.

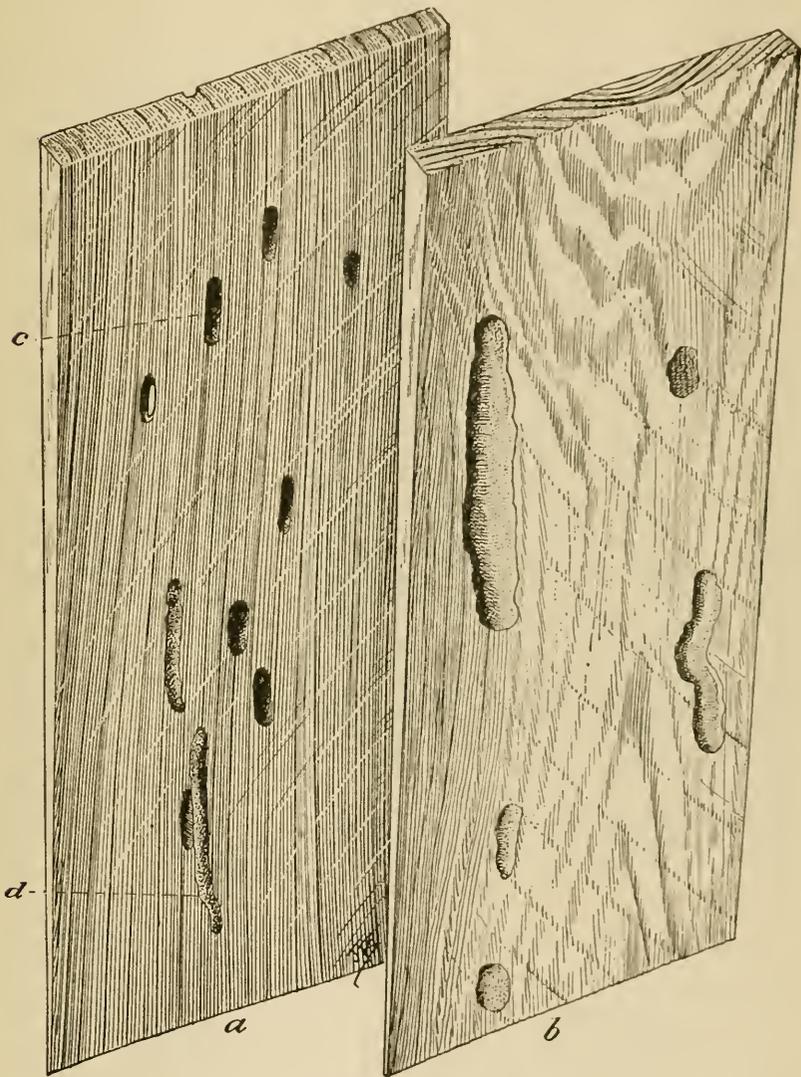


FIG. 27.—Western red cedar shingles badly damaged by grub holes and burrows of flat-headed borers (*Trachytele blondeli*). (7). *a*, Quarter-sawn shingle showing both cross and longitudinal sections, *c*, *d*, of the larval mines; *b*, bastard-sawn shingle showing larval mines

GRUB-HOLE INJURY TO LIVING TREES; A NONPREVENTABLE LOSS

Grub-hole defects in living trees can not be prevented by lumbermen, since often these defects occurred many years before the tree was cut. Sometimes the insect holes are partially healed over by

new growth of the tree, or they may have been enlarged by carpenter ants. This type of injury can be recognized as follows:

(1) In the sapwood and heartwood of hardwoods very large circular holes, one-half to 1 inch in diameter, are open and but slightly stained and are usually lined with a silky yellowish-brown web.¹⁶ (Fig. 22.)

(2) In sapwood or heartwood of hardwood trees the holes are darkly stained and are open, containing little or no sawdust or frass.¹⁷

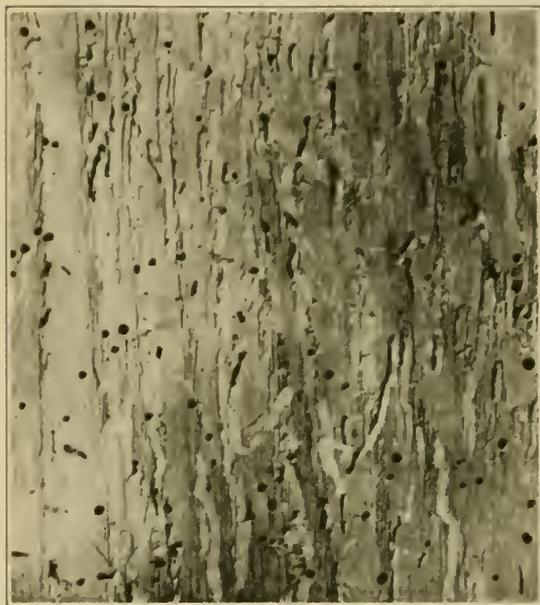


FIG. 28.—Powder-posted white ash shipbuilding lumber showing larval burrows and exit holes of adults of *Lyctus planicollis*; board from a closely piled stack of lumber throughout which larvae had burrowed

(3) In the heartwood of butt logs of gum and a few other hardwoods, unstained holes contain mined granular and fibrous frass¹⁸ (fig. 23).

(4) In the heartwood of butt logs of softwoods, chiefly pine, very irregular holes are narrowly oval, without stain, but surrounded by much pitchy "lightwood," or "fatwood," and are very tightly packed with fine granular frass¹⁹ (fig. 24) (7).

(5) Pinholes or worm holes in softwood logs and lumber in the Northern States are caused by a melandryid timber worm.²⁰ These larvae

gain entrance to the living sapwood through scars or blazes and also attack recently felled timber. The holes are filled with fine sawdust.

GRUB-HOLE INJURY TO GREEN SAW LOGS AND LUMBER; A PREVENTABLE LOSS

All types of borer holes other than those mentioned above are made after the trees have been felled, and are preventable by proper methods of handling the logs. These borer holes occur in the sap-

¹⁶ This injury is found principally in oak, chestnut, locust, and cherry and is caused by the carpenter worm, *Prionoxystus robiniae* Peck.

¹⁷ These holes are found principally in oaks and are caused by the round-headed borers (Cerambycidae) *Goes* spp. and *Romuleum* sp.; in hickory, they are caused by *Goes* sp.; in hickory in the South, small darkly stained holes are caused by a wood-boring enterpillar, *Cossula magnifica* Bailey; and in hard maple they are caused by the maple-tree borer, *Glycobius speciosus* Say.

¹⁸ This injury is caused by *Parandra brunnea* Fab.

¹⁹ This injury is caused by *Buprestis apricans* Hbst. and occurs especially in fire-scarred long-leaf pines and trees boxed for turpentine. This borer causes an excess of pitchy wood near the injury. The injury often amounts to the reduction of 5 to 10 per cent of the lumber to lower grades and the wind-throw of much second growth on turpentine operations.

²⁰ *Sceropulus barbatus* Schall.

wood of hardwoods or softwoods as unstained irregular holes from one-fourth to 1 inch in diameter, which may be open, loosely or tightly filled with powder, with granular or fibrous frass, or with pellets.²¹

These and similar types of borer injury can be prevented by prompt handling of the logs after they are felled. Logs, bolts, and sawn or squared timbers should never be allowed to lie where cut in the woods, after the 1st of February in the Gulf States, or after the 1st of April farther north. Other preventive measures include: Rapid utilization; submergence of logs in water, where they will not be attacked, and working them up as soon as removed from the water; sun-curing, with or without the bark on (care should be taken to provide against excessive checking); and removal of bark strips from freshly sawn material. The damage can often be prevented by peeling the bark (both outer and inner) from the logs or bolts, timbers, or edges of lumber, as the bark offers a favorable place under which the insects can lay eggs. Both the outer and inner bark of sawn timber should always be carefully removed and the timbers placed where they will season rapidly (1).

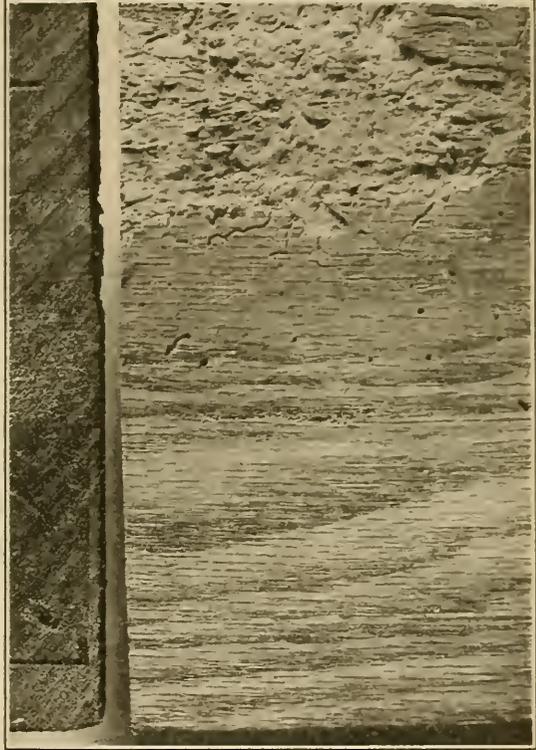


FIG. 29.—Powder-posted sapwood oak veneer laid on a core of chestnut (door stock); work of *Lyctus planicollis*. Note that the heartwood oak and the chestnut have not been attacked

DEFECTS CLASSED AS POWDER POST

Powder post is indicated by holes from one-sixteenth to one-fourth of an inch in diameter, in the surface of the wood, in the sapwood and

²¹ The principal injury of this character found in pines, spruces, and firs is caused by the pine sawyers, *Monochamus* spp. (fig. 25) (50); the loss due to pine sawyers in green logs and storm-felled timber is often as high as 35 per cent. In ash the defects are caused by the banded and red-headed ash borers, *Neolytus cuprea* Say and *erythrocephalus* Fabricius; in hickory by the banded hickory borer, *Cyrtene pictus* Trury, and the red-headed ash borer; in locust by the locust borer, *Cyrtene robiniae* Forster; in cedar by the round-headed borer *Cullidium antennatum* Newm. (fig. 26); in cypress, western redwoods, and cedars by flat-headed borers, *Trachykele* spp. Barrows made by *Trachykele* are tightly packed with pellets of excrement, and shingle stock is full of holes (fig. 27) (7).

heartwood of both hardwoods and softwoods, from which the powder will fall when moved or jarred.²² The interior is honeycombed by irregular burrows made by the larvae and when badly damaged is converted into a mass of closely packed material, which readily crumbles into fine flourlike powder or coarser pellets of excreted wood. This is held together by an outer thin shell and intervening



FIG. 30.—Powder-post defect in pine made by *Xyletinus peltatus*

fibers of sound wood. These defects will be discussed in the order of the size of the holes caused by the various types of insects. All powder-post damage can be prevented.

POWDER POST CAUSED BY
LYCTUS BEETLES

The injury caused by *Lyctus* beetles is confined to the white-wood or sapwood of hardwoods (34). It consists of small holes one-sixteenth to one-twelfth of an inch in diameter, with irregular burrows filled with flourlike powder. Air-dry or kiln-dry sapwood material, and sapwood which has been stored or piled in one place for two, three, or more years, especially second-growth ash, hickory, and oak, are princi-

pally affected; but other hardwoods, such as walnut, maple, persimmon, cherry, elm, poplar, and sycamore, are also damaged.

Seasoned shipbuilding and airplane lumber and gunstock blanks, stored in large quantities, and finished stores, such as wheelbarrows, tent poles, oars, airplane parts, shovel and pick handles, and many other hardwood articles used in the military services are subject to serious damage by powder-post beetles. (Fig. 28.)

Hickory, ash, and oak furniture, interior woodwork of buildings (fig. 29), and the woodwork of farming machinery and implement handles; ladder stock, such as rungs; vehicle stock, such as hubs, spokes, felloes, rims, singletrees, poles, and shafts; and cooperage stock (barrel-stave bolts) are also injured.

²² Insects which have this peculiar habit of reducing wood fiber to a powderlike condition belong chiefly to the families Lyctidae, Ptinidae, Anobiidae, Bostrichidae, and Cerambycidae. By far the larger part of the injury is caused by species of the genera *Lyctus* and *Neolyctus*.

The loss to seasoned hardwood products ranges from 10 to 50 per cent, sometimes representing a loss of thousands of dollars to a single manufacturer or dealer who neglects to adopt the proper preventive measures. The affected articles are not only reduced in value, but

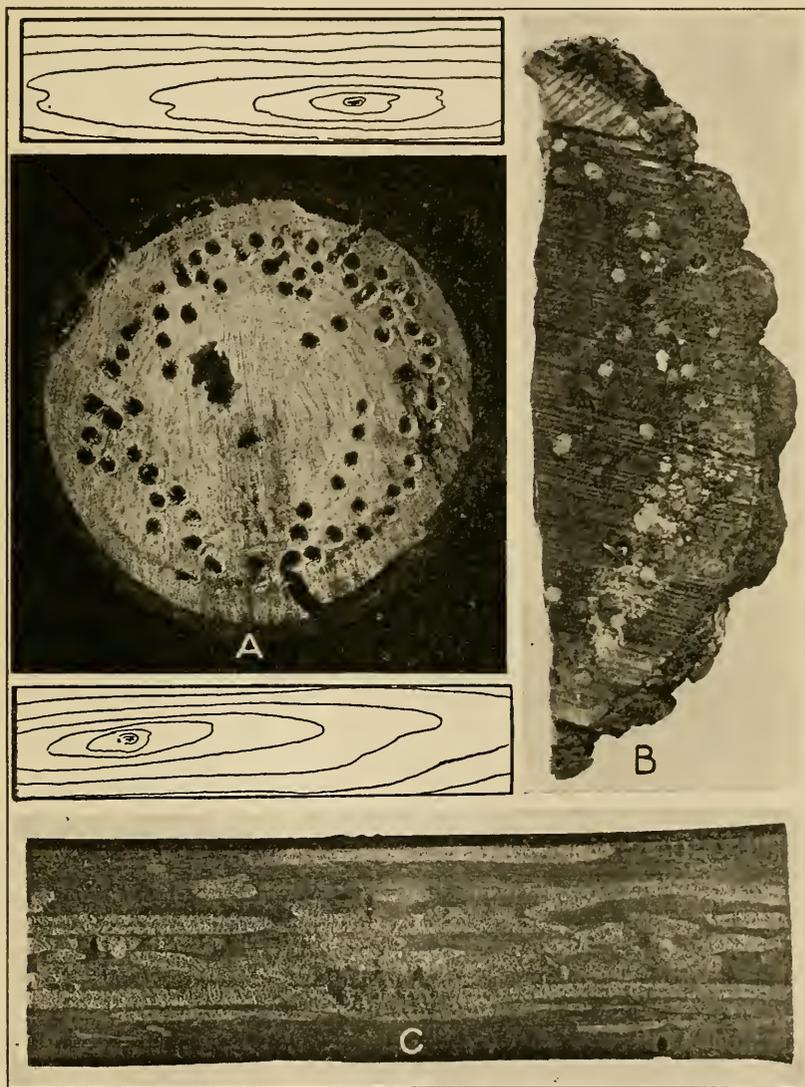


FIG. 31.—Powder-posted seasoned hickory stock in the rough damaged by *Xylobiops basilaris*. A, end of bolt; B, end of section of bolt; C, planed section of damaged bolt

frequently are rendered worthless for the purposes for which they are intended. In the aggregate the direct financial loss that has been caused by these beetles in this country has amounted to hundreds of thousands of dollars. The loss increases with the length of time the infested stock is held in storage; the wood may be reinfested by many

generations over a period of 20 years or more. In certain cases powder-post injury may be a menace to human life, as in the weakened woodwork of buildings, vehicle stock, or ladders.

Losses due to Lyctus beetles can be prevented by proper methods of classification and piling of stock by kinds; by keeping heartwood

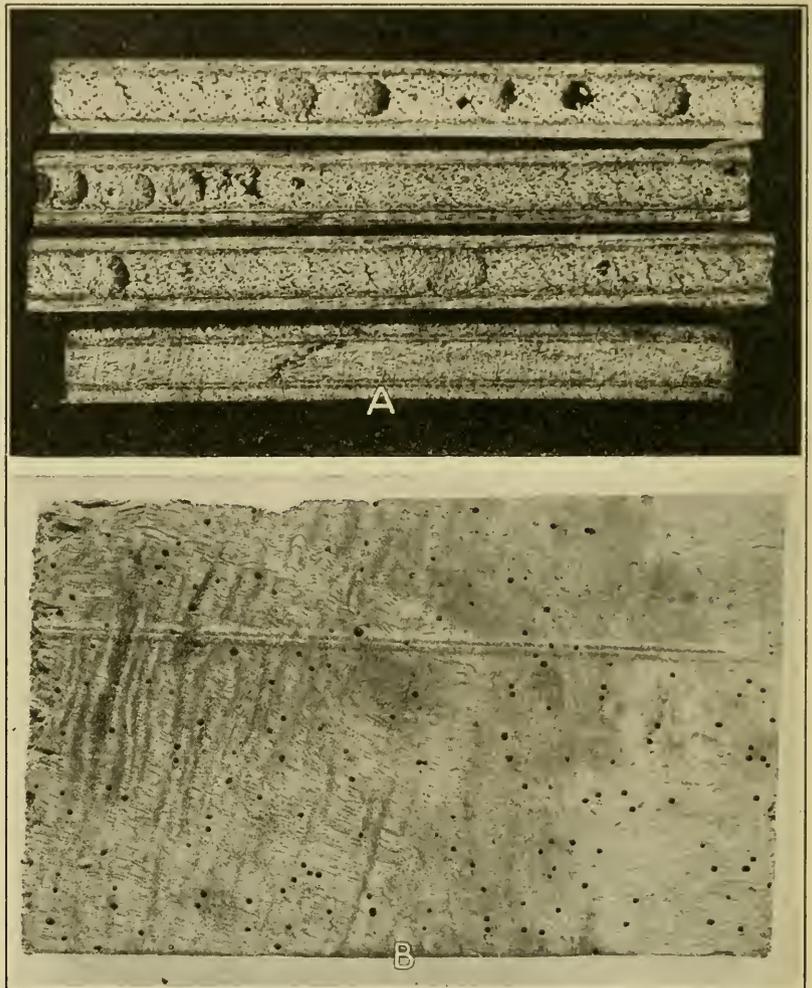


FIG. 32.—A, Duali plywood, imported from the Philippine Islands, powder-posted by *Bostrychopsis parallelus*; B, bostrichid powder-post injury to myrtle in Oregon

and sapwood stock separate; by periodical inspection, utilizing the older stock first (34); and by using only heartwood piling sticks; or by submergence in water for four months, which renders the wood immune from attack, even after removal from the water.

In the case of finished wood products, it may often be practicable to treat the wood with substances to prevent attack. Creosotes are

effective preventives, but they stain the wood: hence, where they can not be used, in the light of the discovery of the place and manner of the laying of the eggs in the pores of the wood, any substances that will close the pores will prevent oviposition in wood not previously infested. In wood from which beetles have emerged, however, eggs might be laid within the exit holes. Paraffin wax, varnish, linseed oil, or other fillers effectively close the pores of wood. A certain varnish known as hardened gloss oil is commonly used. Wood that has been seasoned less than 8 to 10 months will not be attacked by *Lyctus* beetles; therefore, in applying chemical preventives, only sapwood that has been seasoned for 8 to 10 months and longer need be treated. The seasonal history of these beetles indicates that preventives should be applied before March 1.

The great and recurring expense of treating infested wood can be avoided by prevention of attack by proper methods of management. Since only the sapwood or whitewood is attacked by *Lyctus* powder-post beetles, it is recom-

mended that more heartwood be used to replace sapwood. Although the demand of the trade is for whitewood handles, etc., the prejudice against heartwood is not warranted

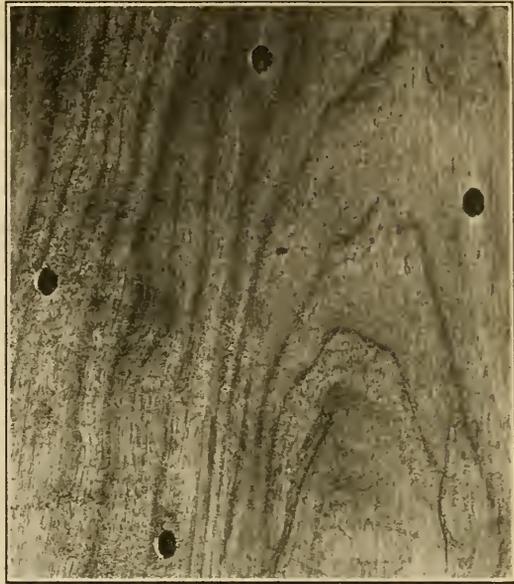


FIG. 33.—Holes made by the banded ash borer (*Neoclytus caprea*), one of the powder-post beetles

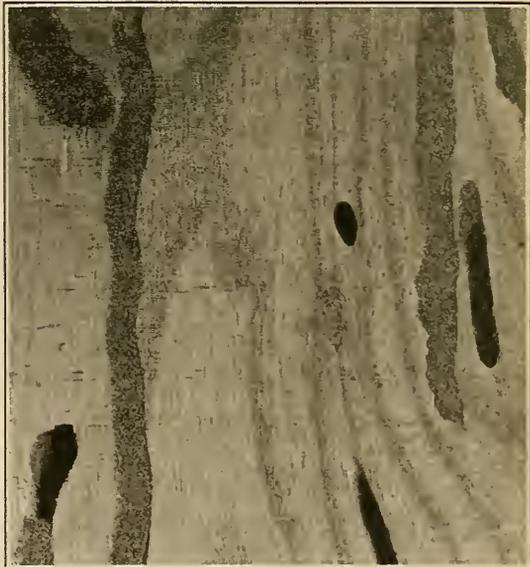


FIG. 34.—Powder-posted ash shipbuilding lumber, showing coarse powdery frass in the burrows made by *Neoclytus caprea*

and should be overcome by educational propaganda. Weight for weight, red or heartwood hickory is as strong as white or sapwood. Closer utilization can be effected by larger use of heartwood. Some manufacturers paint their stock, to overcome this trade prejudice.

Effective remedies include kiln-drying at high temperatures (180° F. and over); steaming at 130° F. (this will not insure against future attack) (46, 47); and treatment with orthodichlorobenzene or a mixture of kerosene and coal-tar creosote, after which the material should be kept in quarantine a sufficient length of time to deter-

mine whether a second treatment is required.

Partially damaged material which is too valuable to be destroyed should be salvaged, when practicable, by trimming off and burning the sap edges and other damaged and infested parts.

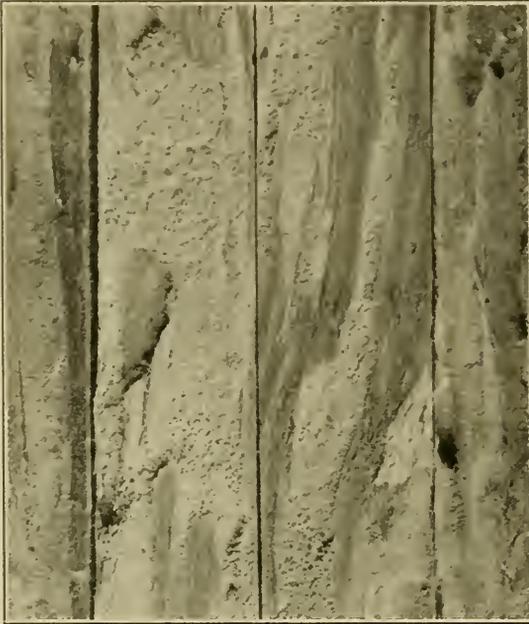


FIG. 35.—Powder-posted southern yellow pine boards damaged by *Hylotrupes bajulus*

POWDER POST CAUSED BY PTINIDAE AND ANOBIIDAE

This damage consists of small holes one-sixteenth to one-eighth of an inch in diameter and irregular burrows in the wood of both softwoods and hardwoods (fig. 30). The damage is similar to that caused by *Lyctus* bee-

tles, except that softwoods are also attacked and the defect occurs²³ in the heartwood. Most injury by Ptinidae is caused to seasoned wood, or logs that have been left lying in the woods too long.

POWDER POST CAUSED BY BOSTRICHIDAE

This damage consists of circular holes one-eighth to three-eighths of an inch in diameter and irregular longitudinal burrows filled with frass, or with coarser dust in the sapwood and heartwood of hardwoods, which does not fall out so readily. (Figs. 31 and 32.)

These insects²⁴ attack freshly felled logs with the bark on. The eggs are laid within the log near holes made by the adult beetles.

Submerging the logs in the mill pond and prompt utilization will prevent much loss. In the case of vehicle, handle, and similar

²³ This defect is caused by *Xyletinus peltatus* Harris, which attacks both hardwoods and softwoods.

²⁴ Bostrichidae: *Scobicia*, *Xylobiops*, etc.

stock, all the bark and edgings should be removed; treatment with shellac or wax will also prevent the adult beetles from boring into the wood to lay eggs.

POWDER POST CAUSED BY ROUND-HEADED BORERS (CERAMBYCIDAE)

Holes about one-eighth of an inch in diameter, tightly packed with finer frass, in the sapwood or heartwood of oak and hickory, are made by the flat powder-post beetle.²⁵ It attacks both freshly cut and seasoned timbers and continues to work for a number of years. Damage can be prevented by prompt handling of the logs, removal of the bark, and disposal of infested stock.

Oval holes about one-fourth of an inch in diameter or irregular burrows tightly packed with coarse, powdery frass, in the heartwood and sapwood of ash, are caused by a round-headed borer.²⁶ (Figs. 33 and 34.) This insect attacks only freshly cut timbers, but when infested logs are stored the borers continue to work for several years (51).

Prompt utilization, submerging the logs in the mill pond, rapid seasoning, or removal of the bark will prevent this defect. Timber should be felled in the late fall or winter, so that the bark may dry somewhat and be less attractive to the

beetles when they are flying and depositing their eggs early in the spring. In the Gulf States logs should not be allowed to lie in the woods at any time for more than two to three weeks, or after the 1st of April farther north, nor should they be

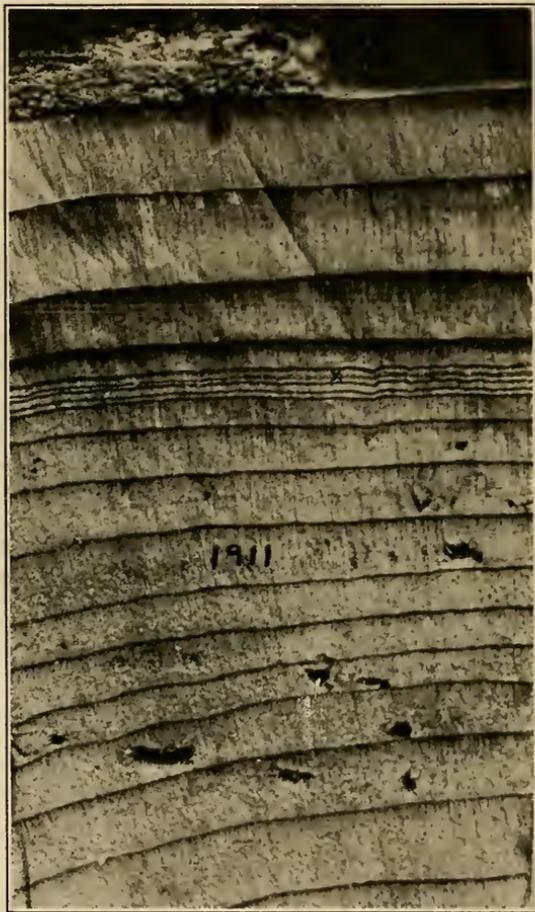


FIG. 36.—Ring distortions in balsam caused by the spruce bud worm. Base of tree attacked in 1911 showed accelerated growth for two years, followed by retardation and incomplete ring in 1918 (X), and rapid recovery later. (18)

²⁵ *Smodicum cucujiforme* Say.

²⁶ *Necolytus capraea* Say.

stored in closely packed piles for long periods. After the 1st of February logs should be cut up into sizes as small as commercially practicable and seasoned as promptly as possible; or sun-cured; or placed in the mill pond. Narrow strips of bark left on the edges of boards and planks or timber cut from green logs in February and March serve to attract the insects to such places to lay their eggs; therefore the logs should be trimmed off and the trimmings burned.

Irregular oval holes from one-fourth to one-half inch in diameter, filled with a mixture of coarse granular and fine powdery frass, found in softwoods, are caused by the "old house borer."²⁷ (Fig. 35.)

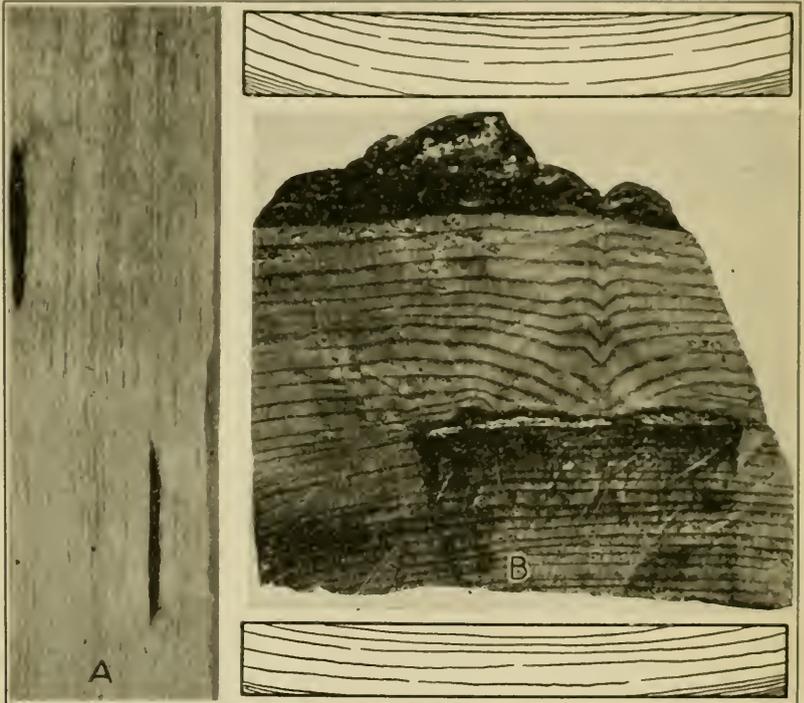


FIG. 37.—Pitch pockets in western yellow pine, caused by unsuccessful attack, years ago, by the Black Hills beetle (*Dendroctonus ponderosae*). A, pitch pockets in sawn board; B, end of log showing pitch pockets

It attacks only well-seasoned wood which has been stored for more than a year. This borer continues to work for years, until the wood is thoroughly perforated.

All bark edges should be removed from lumber and timber; the stock should be inspected frequently for evidences of falling dust, which indicates the presence of these borers, and all such wood should be promptly burned; or the stock may be dipped in orthodichlorobenzene, if only slightly injured.

POWDER POST CAUSED BY FLAT-HEADED BORERS (BUPRESTIDAE)

In bald cypress in the Eastern States and in western redwoods and cedars, powder-post injury is caused by flat-headed borers.²⁸

²⁷ *Hylotrups bajulus* L.

²⁸ *Trachyketo* spp.

The burrows are tightly packed with pellets of excrement, and shingle stock is full of holes. (Fig. 27.)

The injury occurs in living, dying, or dead trees, and consists of a flattened, oval, gradually enlarging, more or less tortuously winding mine or wormhole, which, when completed, widens out into an elongate-oval pupal cell. This cell connects with the outer surface by a short, oval exit hole. The mine has its surface marked by fine transverse, crescentic lines, and is usually tightly packed with sawdustlike borings and pellets of woody excrement.

To prevent such injury, the forest should be kept clear of dead and dying trees and of felled trees which afford ideal breeding spots. Such trees might be used for fuel, or they could be piled with the limbs and tops and burned. If trees must be deadened in the lumbering operations, the "deadening" should be done at a time of the year when the sap is not actively flowing. October, November, and December would probably be the best months for this. If the timber must be felled and left in the woods for a time, the felling should be done during the same months, and the logs should be barked and left so that they will dry quickly and thus become distasteful to these borers.

If the timber is found to be newly infested while standing, or on felling, the most

practical remedy is to cut it into logs at once and place the logs in a pond or stream so that the larvae will be destroyed and further damage prevented. If the damage has been done before the lumberman has noticed the injury, which is usually the case, much loss can often be prevented by utilizing the damaged stock to the best advantage. It may be used for poles, posts, planking, sills, small construction timbers, or where the wormholes are not particularly detrimental; it should not be used for cooperage, shipbuilding, shingles, doors, finishing, cabinetmaking, or furniture, in which clear stock is desired; otherwise the loss is apt to be severe, both because of the poor quality of the product and because of the extra labor necessary to produce it (7).



FIG. 38.—Longitudinal section of yellow pine sapling, showing damage to wood from attack of *Pinipestis zimmermanni*. (5)

OTHER TYPES OF DEFECTS

Other common defects—ring distortions, pitch pockets, gum spots, black check, staining, and pith flecks—are often caused by insects or associated with insect attack. Such defects, however, are not always necessarily caused by insects.

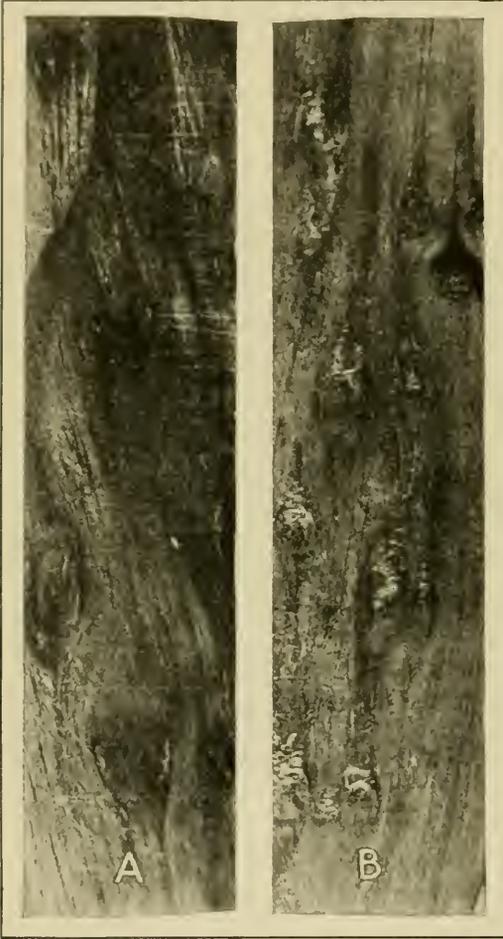


FIG. 29.—A and B, two views showing small "pitch pocket" or "bird's eye," caused by larva of a fly in western yellow pine

DEFECTS CLASSED AS RING DISTORTIONS

Characteristic distortions and abnormalities in the annual rings of trees result from defoliation by leaf-feeding insects, as well as from other causes, as pointed out by Hartig, Harper, and Craighead (48). Destruction of the leaves at certain periods causes a reduction in the normal amount of food manufactured by the tree, with consequent loss in the amount of wood laid on and the formation of incomplete annual layers or double rings (false rings). Many species of trees are subject to defoliation, though little is known of the resulting effects except in a few cases.

Larch, fir, spruce, jack pine, lodgepole pine, western yellow and white pines, hemlock, oak, hickory, catalpa, birch, and cherry are some of the trees subject to frequent or periodic defoliation.

RING DISTORTIONS CAUSED BY DEFOLIATION BY THE BUD WORM

Defoliation by the bud worm²⁹ on spruce and fir produces the first year a decided decrease in wood on the upper stem, while an abnormally larger ring is laid on at the base. In subsequent years a gradual reduction occurs, the narrowest ring being laid on some four or five years later throughout the tree. Gradual increase then

²⁹ *Cacoecia (Harmologa) fumiferana* Clemens.

follows in recovering trees. In fir trees one, two, or three rings may fail to form completely around the stem, particularly at the base, and are represented only by partial arcs (fig. 36) (48).

Rings of traumatic resin ducts are frequently deposited in the terminal portions of defoliated fir trees during the first to third years of feeding.

Complete defoliation of certain hardwoods in the early spring produces a double ring the same year. These defects result in a great loss of increment, increasing the rotation from 3 to 10 years, and cause confusion in growth studies based on the annual rings.

Similar distortions of rings are found in Douglas fir, due to defoliation by the spruce bud worm, and in western fir, spruce, yellow pine, and particularly lodgepole pine, due to defoliation by the needle miner.³⁰

Such losses and defects can be prevented only by the prevention of defoliation, a problem of forest management.

DEFECTS CLASSED AS PITCH POCKETS AND PITCHY TIMBER

Pitch pockets are openings between the grain of the wood which contain more or less pitch or bark. They are graded as small, standard, and large pitch pockets. These pockets range from one-eighth inch to 2 inches in width and from 3 to 12 inches in length. Sometimes, instead of pockets, there are merely pitch streaks. These defects may be caused by insects as well as other agents.

The pockets are small, usually about one-half to 1 inch in length, and about one-half inch in width, full of pitch; in pine, they are parallel to the grain. Sometimes they are as large as 2 inches in diameter and contain a large quantity of pitch. This injury may be caused by unsuccessful attacks of bark beetles³¹ which have failed to kill the tree and have been drowned out by the flow of pitch. (Fig. 37.) It is a sound defect which can be prevented only by controlling the bark beetles that attack the living trees.

Excessive pitchy streaks in yellow and other pine lumber are sometimes caused by the larvae of a moth³² working in the cambium (fig. 38), especially in mature trees.

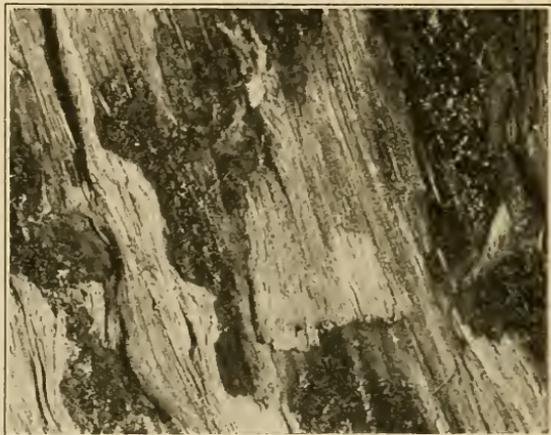


FIG. 40.—Gum spot in Douglas fir, caused by a flat-headed borer (*Melanophila drummondii*)

³⁰ *Recurvaria milleri* Busck.

³¹ *Dendroctonus* spp. The term "pitch pocket" is here used to define what is apparently the tree's further means of defense from attack by bark beetles, after the pitch running out of the entrance hole, forming a pitch tube, has failed to drown out the beetles.

³² *Pinipestis zimmermanni* Grote, the Zimmerman pine moth.

The wood of trees that have been infested by larvae of the moth is invariably so permeated with pitch that the lumber cut from such logs is either materially reduced in value or is rendered wholly unfit for commercial use. This moth is especially abundant; in southeastern Montana a large percentage of the trees are pitch-soaked. For this reason the lumber is utilized only as rough lumber for sheds and similar structures where shrinkage can be discounted (5).

Serious damage by this moth can be lessened by clean forest management.

"Pitch seams," "gun check," or whatever these defects may be termed locally, have always been recognized as a serious depreciating factor in the utilization of Douglas fir (4).



FIG. 41.—Black check in western hemlock, radial section. (6)

The loss is occasioned by the work of the Douglas fir "pitch moth,"³³ which causes the difference in price between absolutely clear lumber and the lower grades or dimension stuff. These insects work in the portions of the trunks of living trees which later clear themselves of branches; hence only those logs are affected which, were it not for previous infestation by the moths, would yield the better grades of lumber.

Sawyers of Douglas fir estimate a general loss in the entire Douglas fir product of between 7.5 and 15 per cent due to this defect of pitch seams in the logs used (4). The depreciation is lowest in the Rocky Mountain region and heaviest toward the Pacific coast. Such pitch pockets are not always caused by insects.

Another pitch moth, the Sequoia pitch moth,³⁴ greatly retards the growth of lodgepole pine in western Montana (3).

Under present forestry conditions in this country it is impracticable to control these insects over large areas.

Similar defects due to the working of the larvae of moths and flies³⁵ (fig. 39) in pitch near insect wounds or other wounds, occur in all sections of the country.

DEFECTS CLASSED AS GUM SPOTS OR STREAKS

"Gum spots" in western hemlock³⁶ and Douglas fir³⁷ are caused by insect attack.

Gum spots entail practically no loss to mills, nevertheless they cause losses to the builder and consumer. Gum-spot defects are also due to causes other than insects.

³³ *Sesia norarocensis* Hy. Edw.

³⁴ *Vespa minima sequoia* Hy. Edw.

³⁵ *Chetoxia* spp.

³⁶ *Alcinoiphila drummondii* Kirby causes this defect in both hemlock and Douglas fir (fig. 40).

³⁷ The pitch moth (*Pinipestis zimmermanni* Grote) is responsible for not more than 10 per cent, *Dendroctonus pseudotsugae* Hopkins for not less than 70 per cent, and all other causes for about 20 per cent of the damage.

DEFECTS CLASSED AS BLACK CHECK

“Black check” is the lumberman’s name for a common defect consisting of a dark stain in the heartwood and sapwood, surrounded by thickened, curled, or abnormal layers of wood (fig. 41) (6). It should not be confused with stains associated in the wood with other boring insects (as ambrosia beetles), where the wood is rarely distorted. Although also caused by other agents, it particularly applies to the defect in western softwoods (hemlock, fir, spruce, and yellow pine) produced by the maggots of several small flies³⁸ or moths,³⁹ but the term is also used for a somewhat similar defect in oaks produced by the larvae of large beetles.⁴⁰ (Figs. 42 and 43.)



FIG. 42.—Pile of logs with grub holes made by round-headed borer (*Romalcum rufulum*). This defect is considered as “wormholes, no living worms or decay”

These defects are caused by the insects injuring the growing tissue of the tree and killing a small area of the outer layers of wood. The subsequent growth of the tree finally heals over this injury, but many annual layers are stained and distorted. The original small pocket or cavity where the insect was working remains, and in coniferous trees it fills up with pitch.

Western hemlock contains more of this injury than any other softwood. In quarter-sawn (vertical-grain) wood the checks appear as small seams one-half to 1 inch long, with one side curly, while in bastard-sawn (flat-grain) boards they appear as oval or rounded spots from one-half to 1 inch in diameter. The defects in other conifers are similar but not so numerous.

³⁸ *Cheilosia* spp.

³⁹ *Parlarmonia*.

⁴⁰ *Romalcum* sp. and *Goes* sp.

In oak the black checks are larger, often 6 inches long over an area of several square inches. In quarter-sawn boards they appear as dark distorted or curly wood and run through many layers of wood, while in bastard-sawn boards they form black scars several inches long by 1 or 2 wide. In the Ozark Mountains of Arkansas this is a very common defect.

Timber from softwoods or hardwoods is not seriously reduced in strength by such defects, but the wood is lowered in grade and rendered useless for finishing, turning, staves, and woodenware. It can, however, be used for structural material or for purposes for which the marred appearance will not be detrimental. Since black

check is always the result of injury to the living tree, it is not preventable, from the lumberman's standpoint.



FIG. 43.—Black check in oak, caused by round-headed borer (*Goes* sp.) in the living tree. The wound has healed over

DEFECTS CLASSED AS BLUING OR STAINING

Bluish-black streaks or stains in the sapwood of pine, especially in southern yellow, western yellow, and sugar pines, as well as in certain hardwoods, such as red gum or sap gum, are classed as bluing. This defect occurs either in the standing tree or in recently cut green logs or green lumber and is caused by fungi developing from spores which are no doubt carried by insects. In pines the bluing directly follows in-

festation by tree-killing bark beetles⁴¹ in the standing trees (fig. 44) (29). This defect can be prevented only by the control of tree-killing bark beetles. Similar staining defects are caused by many ambrosia beetles⁴² in both the living trees and green saw logs and green, freshly sawn lumber. (Figs. 4, 9, and 13.) This staining can be prevented in green saw logs by prompt utilization of the green logs; by placing them in the mill pond soon after cutting; or by sun-curing. When the lumber is sawn it should be either kiln-dried or air-seasoned rapidly. Bluing is not always dependent on bark beetles (42).

⁴¹ *Dendroctonus* spp.

⁴² *Gnathotrichus*, *Xyleborus*, *Platypus*, etc.

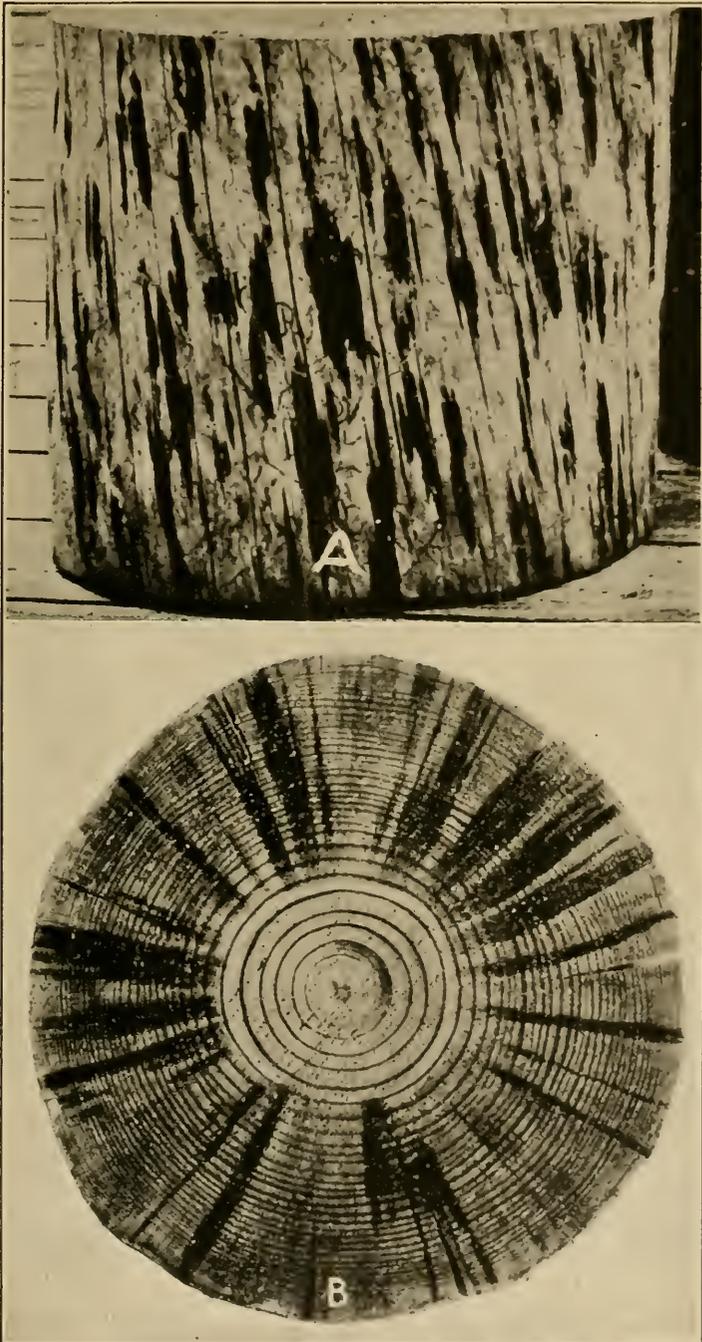


FIG. 44.—Section of short-leaf pine, showing "blue stain" of sapwood after attack by the southern pine beetle (*Dendroctonus frontalis*). A, side view; B, cross section showing stain extending to the heartwood. Serious bluing in the log sometimes appears to take place without the aid of insects

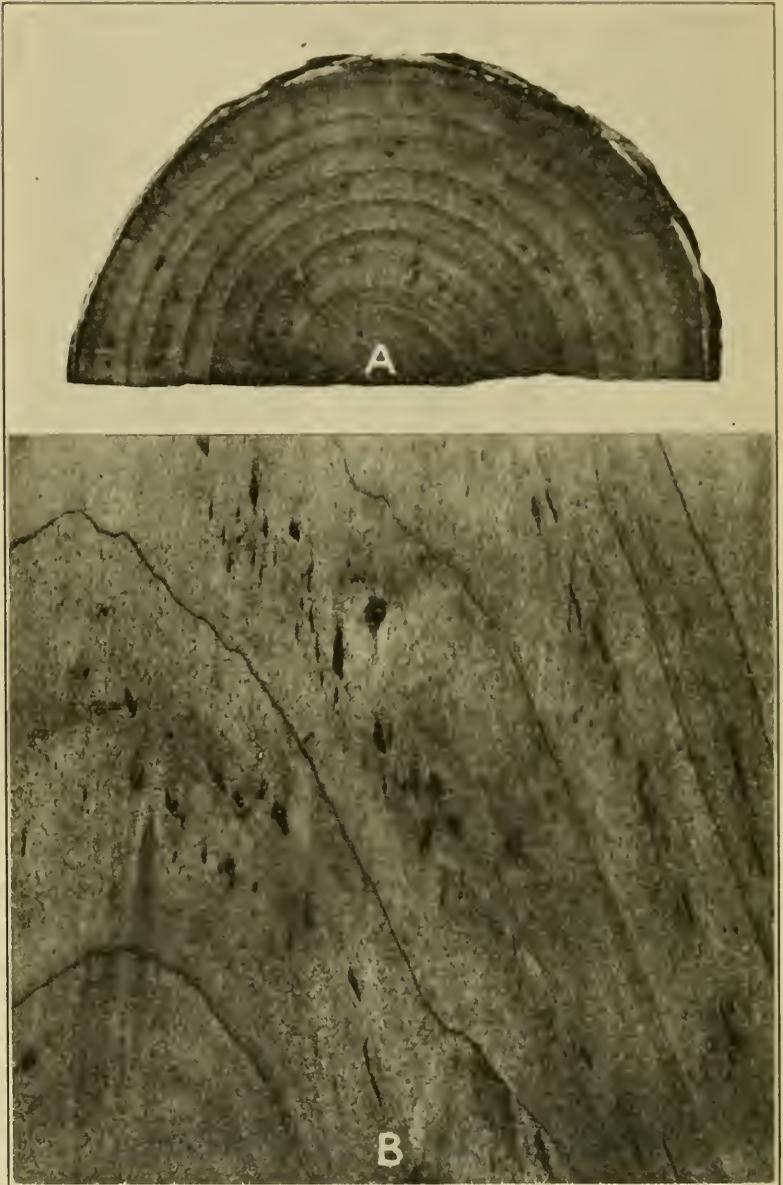


FIG. 45.—A, Pith flecks in river birch, transverse section, caused by *Agromyza pruinosa* (?); B, pith flecks in silver maple, tangential section, caused by *Agromyza aceris*. Natural size

More general and excessive bluing by stain fungi in green lumber after it has been sawn causes a sound defect and is also called "sap stain." Rapid handling of the logs, kiln-drying the lumber, steaming it in a kiln, and air-seasoning are preventive measures. Dipping the lumber in chemical solutions is effective under certain conditions, but this method of prevention has not been entirely satisfactory (37, 38, 40).

DEFECTS CLASSED AS PITH FLECKS

PITH-FLECK INJURY CAUSED BY THE LARVAE OF FLIES

Birch, cherry, maple, oak, poplar, and many other less commonly used hardwood trees have small "pith flecks," i. e., yellow-brown spots or narrow streaks in the sapwood and heartwood, due to the burrows made by larvae of flies⁴³ in the cambium of living trees (fig. 45) (2, 21, 22). This is a very common and widespread defect, more common in soft than in hard maples, and more common in river birch (*Betula nigra*) than in the other birches. Where clear birch is used, as for spool stock, it throws out considerable material. However, this is merely a trade prejudice and should be overcome by educational propaganda, in accordance with the move for closer utilization. This is a sound defect caused in the living tree, the flies laying their eggs in young branches and burrowing down the trunk through the cambium long distances to the roots, where they emerge and pupate. There is no known remedy to prevent the insect injury to the living tree, and hence there is greater need for closer utilization of the product.

PITH-FLECK INJURY CAUSED BY THE FEEDING OF ADULT WEEVILS

Another pith-fleck defect is that caused by the feeding of adult weevils.⁴⁴ This defect has been described (48) as occurring in fir. The adults puncture the bark to feed on the inner phloem, removing a small circular or oval disk one-fourth inch in diameter to one-fourth by 1 inch. This cavity fills with scar tissue and some gum and later heals over. It is very common in fir, but is not of much commercial importance. No doubt this defect occurs in other trees, as pine and spruce, which are attacked by species of this genus of weevils.

SUMMARY

Defects in timber caused by wood-boring beetles and grubs cause serious losses either by rendering the affected material unfit for use or by reducing it to lower grades.

Much of this loss can be prevented through proper methods of lumbering and management, usually involving but slight changes or modifications in present handling of the timber.

Some of the damage can not be avoided, but in such cases considerable loss can be prevented by periodical inspection and proper classification, piling, and handling of stock. More rapid and closer utilization of the material can often be attained.

⁴³ *Agromyza* spp.

⁴⁴ *Pissodes dubius* Rand.

This bulletin presents facts which will aid in determining the nature and cause of defects caused by insects, gives recommendations for avoiding preventable injury, and discusses the types of defects which are not preventable. Of course it is not intended to supersede previous classifications of timber and lumber, based on defects other than those due to insects.

The principal damage comes under two types of defects, designated as wormholes, with no living worms or decay, and powder post.

Sound wood can be utilized where the lower price offsets the lower grade and the defect is not objectionable. There will be no extension of the damage after the wood is dry or seasoned. Sound, wormy chestnut even can be exported with no fear of further damage from the insects which caused this defect to the wood of the tree when living.

Powder-posted stock can not be safely utilized because the damage is continuous in the seasoned and finished product and will not only cause further damage but will be a menace to other hardwood stock stored near by.

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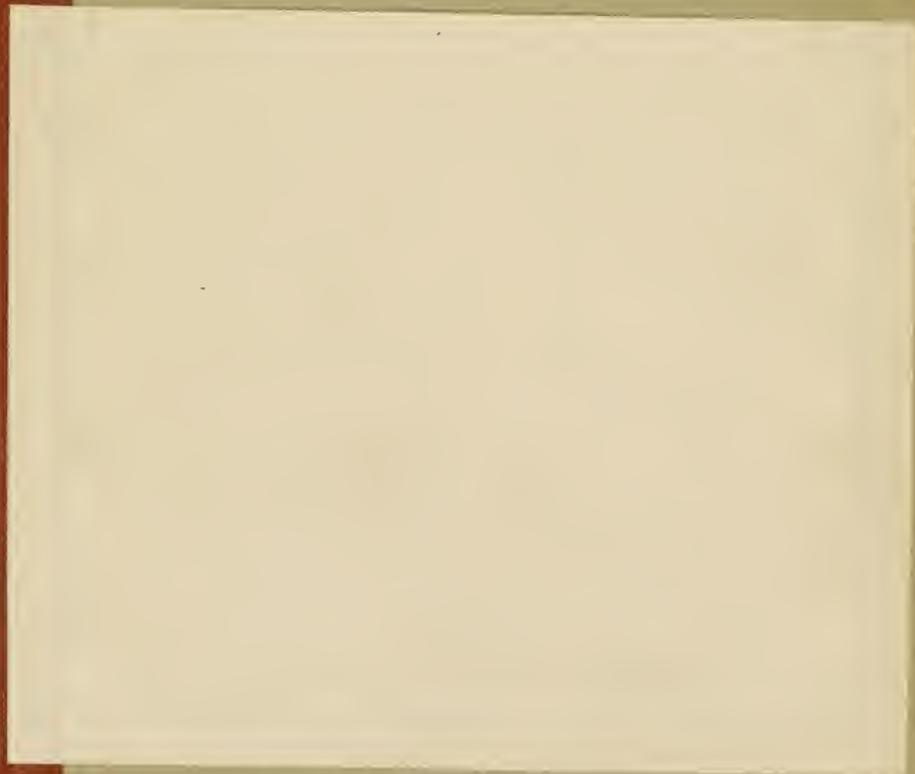
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