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The Ox Warble Flies

Hypoderma bovis de Geer *Hypoderma lineatum* de Villers

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OHIO
AGRICULTURAL EXPERIMENT STATION
Wooster, Ohio

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Hypoderma bovis de Geer

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Order, *Diptera* Family, *Oestridae*

DON C. MOTE

INTRODUCTION

Domestic cattle in Ohio are subject to attack by two species of warble flies—*Hypoderma bovis* de Geer and *Hypoderma lineatum* de Villers. Every cattleman is familiar with grubs that produce the tumors or warbles on the backs of cattle in the spring and nearly everyone is familiar with "gadding" among cattle. Very few, however, connect either the grubs or "gadding" with the adult flies, commonly known as "heel" flies, or warble flies, and much misinformation and even superstition are spread around concerning "gadding" and cattle grubs.

The damaging effects of the warble flies' activities upon Ohio's cattle and dairy industry were given publicity by the Ohio Experiment Station in 1914 (46)†. Preliminary observations indicated that the pest was causing serious loss of meat by what is known as "licked" beef, which is useless for human food; loss of condition among beef and dairy animals; and loss of milk, with consequent reduction in profits. The substantial losses, moreover, in damaged hides for which the warble flies are responsible made it apparent that studies on the life, habits, and control of these flies should constitute one of the Station's projects in the study of the parasites of domestic animals of Ohio.

The studies, of which this paper is a report, were begun in a preliminary way in 1913 and continued until 1918. The inquiry did not yield as much original information as the writer desired, due largely to the limited time for study because of other projects and duties and to the nature of the flies' life history, for the larvae live internally in the cattle for a period of eight or nine months, beginning at various times from late May or early June onward thru the summer, so that study and treatment are rendered exceedingly difficult.

*The writer is indebted to Doctor Herbert Osborn and Professor Jas. S Hine, both of the Ohio State University, for their valuable help and assistance in this work.

†Numbers in parentheses refer to Literature cited, page 43.

The writer planned to continue the studies and accordingly delayed publication of the information already obtained until further inquiry should yield more complete data. The opportunity, however, has never presented itself and now it seems that the information obtained should be published, fragmentary as it is.

In recent years much valuable information has been obtained on the life, habits, and control of the pest by investigators in the United States, Canada, England, Ireland, Germany, France, Denmark, and other countries. The writer will try to incorporate the salient features of these investigations in this publication. Because of inaccessibility, he has not been able to consult as many publications as would be desirable, and any omissions, it is hoped, will be charitably considered.

HOSTS

The normal host of these two flies is cattle, *Bos taurus*. The American bison, *Bos bison*, however, is known to be infested at times with *H. lineatum*, but bison do not appear to be so heavily infested as are cattle raised under similar conditions in the same regions.

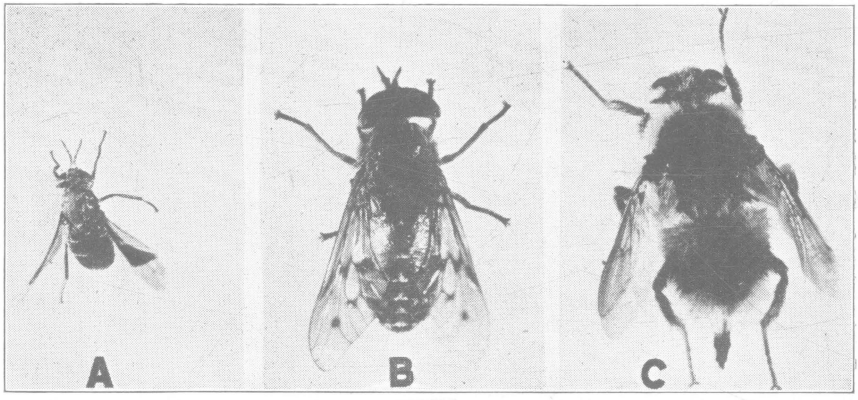

Fig. 1.—Blood sucking flies (A, B) often erroneously thought to be the cause of cattle grubs (enlarged 2.2 times). Compare with the ox warble fly, *Hypoderma bovis* de Geer (C), the cause of the cattle grubs

The horse occasionally is infested with Hypoderma larvae. A number of reports of cattle grubs in the backs of horses were received: one from J. Allyn, of Hiram, Ohio; another from Frank Noble, St. Mary's, Ohio; and still another from Mr. Franks, near Wooster, Ohio. Mr. Franks reports that his horse was purchased

in the region of Roscoe Young, who had a horse with several grubs in its back. Mr. Noble made a survey of the township in which he lived and found horses on three farms infested. He writes as follows: "There were three farms that had infested animals. These farms are separated from two to five miles. There was one horse on each farm that was infested and only one that had more than one grub. On one farm there were twelve horses; on one, four; and on the other, only two. On all these farms the cattle were badly infested, and had been in the same pasture with the horses. The grubs are very similar in appearance to the ones in the cattle. I have made a pretty thoro canvass of our township and fail to find any grubs, but should I find any will send them to you at once."

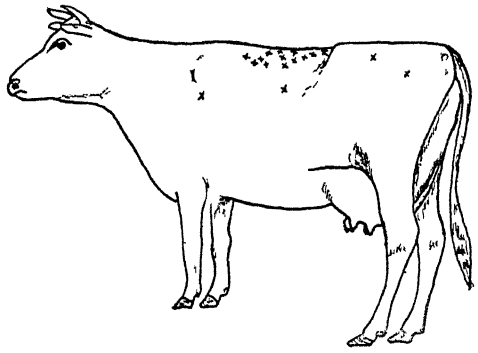

Fig. 2.—Larvae were taken from the backs of different cattle at the positions marked x

The part of the animal in which the grubs are found during their last stages is the back. Here they may be found distributed for the most part from the loin to just back of the shoulder. Less frequently they may be found on the rump, or some distance down on the side or on the shoulder. The choice of the back region to go through the last stages has some advantages. Here they are less likely to be injured; there is less play of the muscles, and the animal itself is less likely to receive serious injury.

Infestations of humans, especially children, by cattle grubs are not uncommon. The clinical histories of many cases of dermal, or "creeping myiasis", appear in medical literature; but only in a few of these has the specific determination of cattle grubs been made.

EFFECTS OF THE WARBLE FLIES ON MAN AND ANIMALS

For purposes of discussion the injuries caused by warble flies may be classified as follows: 1, fright produced by the adult flies during the egg laying period; 2, lesions produced by the migrating larvae; and 3, anaphylaxis or anaphylactic shock.

The degree of injury caused by fright varies with the abundance of the insects and with the species present. *H. bovis* apparently causes the most excitement to stock and when present produces the greatest damage in this respect. Losses caused by this annoyance include marked reduction in milk flow, failure to fatten or put on flesh normally, and mechanical injury due to wild efforts of the animals to escape attacks.

The damage from lesions may be divided into five divisions: 1, injury produced by the penetration of the young larvae thru the skin; 2, possible inoculation of disease, like anthrax and blackleg by the larvae in their passage thru the skin; 3, the inflammation produced in the gullet and in other internal organs by the migrating larvae; 4, the irritation produced along the spinal cord and on the main branches of the nervous system by the burrowing of the larvae; and 5, lesions produced by the later larval stages in the subdermal tissues of the back, with the accompanying pus formation.

The presence of exudate and pimples on cattle immediately under the eggs of *Hypoderma* from which the larvae had emerged was first recorded by Carpenter, Hewitt, and Reddin in 1914 (7). Hadwen (21) has rather fully described the skin lesions of *lineatum*. He proposes the name "hypodermal rash" for the condition resulting from larval penetration and reports that this condition may be mistaken for mange or cowpox (27). Bishopp (2) has observed repeatedly that violent stamping, kicking, and licking of the affected parts by the host occur soon after the hatching of the eggs begins, and a few days later soreness and the formation of scabs caused by exudation and hardening of serum are apparent. When these scabs are removed, a cluster of hatched eggs is usually found attached to the hair in their midst. No experiments have been reported, proving that the larvae may inoculate disease, but Hadwen (27) has shown that in case of reindeer Bot infestations with *B. pyocyaneous* are common.

Little is known concerning the irritation produced by the wanderings of the larvae after they have penetrated the skin. When the larvae reach the gullet, however, they may produce marked inflammation. Des Gayets and Vaney (17) and Jensen (31), who made a special study of the lesions caused by the larvae in the oesophageal wall, met with cases of stenosis of the gullet caused by them. The submucous tissues are edematous, usually yellowish and sometimes bloody in the region of the larvae. Cases are on record in which heavy infestations of the esophagus produced edematous conditions with large swellings (27).

Lesions in the spinal canal are not as easily verified. No signs of inflammation in the chord were noticeable in the neighborhood of the larvae found by the writer. Other investigators, on the other hand, have observed inflammation (22) and instances are recorded in which the larvae, burrowing in the spinal canal, have caused paralysis of the posterior parts.

When the young larvae first reach the subcutaneous tissues along the back, they frequently cause irritation, inflammation, and marked swelling. In addition to this injury to the flesh, the skin is damaged by holes cut in it by the grubs. Later the animal changes its form of resistance from an active leucocytosis to a segregation of the grubs by the formation of encystment sacs. Altho much of the pain and annoyance now apparently subsides, the injurious effects of the grubs are still in evidence. Great numbers of large pus abcesses, usually caused by the closing of the orifice of the grub cyst before the grub reaches maturity, have been encountered. In most cases these result in the death of the grub. Such abscesses are always greatly relieved by discharging them (2).

The fourth type of injury was first noted by Jensen in 1903 (30, 31) and later by Hadwen and Bruce (23). They have shown that the injection of the juice of a few grubs into a bovine may cause death by anaphylactic shock in a few minutes, and that the crushing of a number of grubs in the back of an animal may cause marked anaphylactic symptoms. Their explanation of this fact is that when an animal has been infested with larvae of *Hypoderma* it becomes sensitized, and if the contents of grubs are introduced either by absorption thru crushing of the larvae in the back or by injection into the animal, anaphylactic symptoms may be produced. That these symptoms are not always produced is pointed out by Bishopp (2) who states that in nature cases of anaphylactic shock are rather rare, tho they may follow the crushing of a considerable number of larvae in the back of an animal. He and his colleagues treated more than 200 head of cattle by puncturing the grubs and squeezing out their contents before removing the grub skin. No ill effects were observed, but healing of the holes in the skin was retarded by the hardening in them of the skins of the grubs. Presumably the absorption was not rapid enough to produce severe shock.

In this connection it is of interest to note that there is an acute but usually transient and not fatal cattle disease, known as rose fever, prevalent in the spring in some localities. There is extensive edema, especially on the eyelids, muzzle, and lower jaw, and often

on the udder and in the region of the anus and vulva. The disease usually has been attributed to mistakes in feeding, but Brodersen (6) finds that it frequently follows immediately on the operation of the expression of *Hypoderma* larvae, and he attributes it to the toxic effect of the grubs crushed beneath the hide.

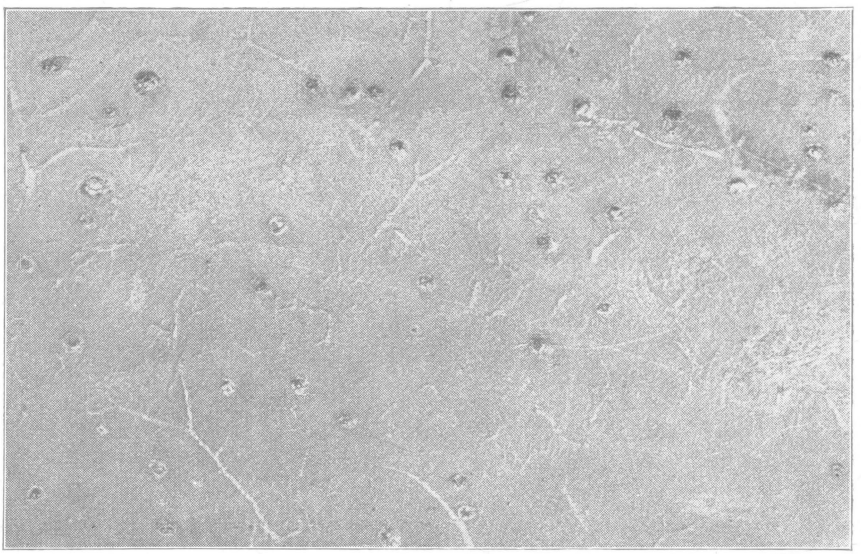

Fig. 3.—Portion of tanned hide showing injury caused by grubs

The effect of infestation by *Hypoderma* larvae on man has been recorded by several writers. Glaser (19), while experimenting with the fly, accidentally infested himself. A female fly deposited an egg on the left leg of his trousers. The larva hatched and penetrated the skin of his thigh. Sometime later its presence in the gastric and esophageal regions was detected by an uncomfortable feeling. The larva apparently passed up the esophagus and was later extracted at the base of one of the lower molar teeth. This incident suggests the source of infestations in man. Most of them occur in children and usually the affected individuals have been rather closely associated with cattle.

ECONOMIC IMPORTANCE

The most obvious economic loss caused by warble flies is the damage done to hides. The valuable part of the hide near the middle of the back is ruined by the warble holes of the current year and the weakened scar tissues of previous infestations. A hide

containing more than 4 grubs is classed as a Number 2 by most buyers, and the difference in price ranges from 1 to 2 cents per pound. The hides taken off during December begin to show grubs, but the packers make no selection for grubby hides on December take-off, according to information received from a leather dealer of Cleveland, Ohio. January hides usually average 20 to 30 percent grubby. February, March, and April show 30 to 45 and sometimes 50 percent grubby, especially the February and March hides. May hides show a small percentage of grubs.

To estimate accurately the annual loss to Ohio cattlemen from this one source alone would require the collection of statistics from every dealer who handles hides from Ohio cattle, an exceedingly difficult task. The monetary loss in Ohio must be great; various writers estimate the loss in hides and leather in the United States due to grub damage at from $5,000,000 to $10,000,000.

Meat packers and butchers often call attention to the inflammation along the back caused by the grubs known as "licked beef" and they point out that the affected parts have to be trimmed out as unfit for human food, frequently resulting in a loss of a considerable amount of meat and leaving the carcass in an unattractive and less saleable condition. The aggregate amount of these losses may or may not be high. There is little quantitative information available covering this phase of grub damage.

Other ill effects of warble fly attack, which have long been recognized by dairymen and stock feeders, are the loss of milk and flesh by "gadding" and heavy infestation with grubs. Exact information upon this phase of grub damage is likewise meager. In March, 1913, the writer found 91 warble cells on the back of a 15 months old Hereford heifer on a farm near Creston, Ohio. At that time the heifer weighed 325 pounds; its weight before grubs made their appearance in the back was 400 pounds. In December, 1913, this animal, altho not in good condition, weighed 475 pounds. In reporting this weight the owner wrote, "She has seemed to be in bad health ever since the heavy grub infestation." In 1917 the writer had an opportunity to compare the gains in weight of four young dairy bulls, two of which were heavily infested with grubs.

The gain in weight from Aug. 1916 to Feb. 1917 was 243 pounds for the infested and 245.5 pounds for the non infested animals, a difference of 2.5 pounds in favor of the non infested bulls. No definite conclusion, however, can be drawn from these observations since the bulls in the two lots varied from 5 to 7 months in their ages.

DISTRIBUTION

The following discussion is based on a study of the numbers, dates of occurrence, and distribution in Ohio of the Ox Warble flies, as determined from an examination of 628 grubs and 15 adult flies collected for the most part during the years 1914 and 1916.

Collections were obtained from 10 counties in northeastern, 10 in northwestern, 10 in southwestern, and 2 in southeastern Ohio.

TABLE 1.—Counties in Which Collections or Reports Were Made Numbers of Each

Northeastern counties			Northwestern counties			Southwestern counties			Southeastern counties		
Counties	Col.	Rpts.	Counties	Col.	Rpts.	Counties	Col.	Rpts.	Counties	Col.	Rpts.
Ashtabula	2		Wood	1		Miami	1		Fairfield		1
Lake		2	Williams		1	Franklin	2		Perry		1
Cuyahoga		2	Seneca		1	Clarke	1		Muskingum	1	
Lorain	1	7	Hancock	2	2	Greene	2	3	Guernsey		1
Huron		4	Van Wert		1	Montgom'y	2	3	Noble		1
Medina		2	Mercer	1		Preble	1		Belmont		2
Summit		3	Allen		3	Clinton		2	Hocking		1
Portage	1	2	Auglaize	1	1	Highland	3	5	Washington		2
Trumbull	2	2	Hardin	1	2	Brown	1		Athens		2
Columbiana	2	2	Marion	1		Clermont	1	3	Meigs	1	
Stark	1	2	Delaware	1	2	Hamilton	1		Jackson		1
Wayne	6	7	Union	1	1						
Richland	1	2	Logan	1							
Knox	3	1	Shelby	1	1						
Holmes		1	Darke		1						
Coshocton		3									
Tuscarawas	1	1									
Harrison		1									
Totals	20	44		11	16					2	12

Hypoderma bovis.—Early in the investigations the two species of warble flies (H. bovis and H. lineata) were recognized. Contrary to expectation, H. bovis was much more abundant, the number taken being 404, or 83.5 percent of the total collection.

In the northeastern section, 257 specimens, or nearly 53 percent of all the specimens were obtained. This should not be taken to indicate that the northeastern section is more heavily infested than any other. When the collections made in the vicinity of the Ohio Station are excluded, the northeastern and northwestern collections of H. bovis specimens are about equal, that of the latter comprising 106 grubs. It may be pointed out, however, that the fly seems to be more generally distributed in the northeastern section. A study of the map shows a much larger number of herds free from infection in the northwestern section than in any other section of the State.

The earliest collections containing fourth stage grubs were received early in March from northeastern Ohio. The earliest specimen (one fourth-stage grub) came from Ashtabula County. At this date it was the only grub to be found in the cattle's backs. Later (May 3) most of these cattle were reported to be infested. The latest collections were received on June 6 and 10, from southwestern Ohio. In the Ohio Station herd one warble was observed on July 14. On July 20, the grub had emerged. As only H. bovis grubs had been taken from the Station herd for more than three years, it is assumed that this specimen was a representative of H. bovis. Thus H. bovis grubs may be emerging from the first of March until the middle of July. The greatest number of fourth stage grubs were received during April and the next largest number during May. The length of the season in which the grubs make their appearance is of very great importance in deciding what time of year is best to undertake their eradication.

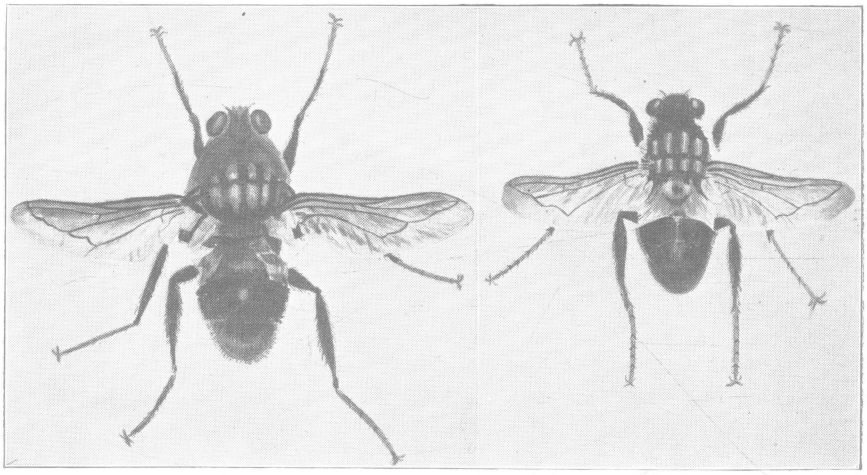

Fig. 4.—Ox warble flies. Left, *Hypoderma bovis* de Geer, right, *Hypoderma lineatum* de Villers

Hypoderma lineata.—Only 80 specimens of lineata are represented in the collections, or 16.5 percent of the total number obtained. This species is most abundantly represented in northeastern and southwestern Ohio, only two collections of 1 and 8 individuals coming from the other sections. Eight localities, just as many as is represented by bovis, are represented in the collection from southwestern Ohio, the total number of specimens received being 27. Seven localities are represented in northeastern Ohio, the total number of specimens being 44.

The earliest lineata collection came from Highland County, on March 25. The latest collection, consisting of two specimens, came from Brown County on May 11. The largest number of collections and specimens were received during April, only one collection, the one from Brown County, being received after April 20.

Seasonal succession of the species.—That H. bovis is generally later in emerging from the backs of cattle in the spring than H. lineatum, is a fact noted by several investigators. This order of their succession is borne out by a study of the data collected in Ohio. It should be stated that, in view of the fact that the grubs were squeezed out, many of them were removed at an earlier date than they would have come out naturally. The figures, then, in Table 2 do not represent the total number of grubs received or removed from cattle, as many of the grubs were not in the fourth stage and hence could not be classified. However, H. lineatum is apparently the earlier fly, as only two fourth-stage grubs were received after April 20. An adult fly was taken as early as May 16. In the H. bovis life history experiments at Wooster, when the grubs were allowed to come out naturally, 17 out of 21 came out in May.

TABLE 2.—Emergence of *H. lineatum* and *H. bovis*

Species of warble grubs	March	April	May	June	July
H. lineatum	8	70	2		
H. bovis	42	231	115	16	1

BIOLOGY AND HABITS

The flies appear during warm sunny weather and seldom attack animals in the shade, as is shown by the following note, taken July 15, 1918:

> While making observations in the pasture field upon the efficiency of several fly repellents, I observed a warble fly suddenly appear among the animals and attempt to alight on the thigh of one of them. Before I could make further observations, this cow galloped across the field and the others scattered. Most of the animals sought the shade of a clump of trees. Continuing my observations on the animals in the shade, I was surprised by a warble fly which flew swiftly by me and alighted upon the left foreleg of a Holstein cow. The fly had no more than hit the cow when she made an attempt to drive it away with her head, stamped her feet, and then started on a gallop across the field. Some of the animals remained in the shade and others later returned. None of these animals was again disturbed, while those in the sun were disturbed several times.

The date of appearance of the adult flies and their period of activity varies with the species and with seasonal and local climatic conditions. The earliest date upon which cows were observed to "gad" at the Ohio Experiment Station was May 28, 1918, but no warble flies were actually observed on that date. On June 11, 1918, at 11:45 a. m. I observed several heifers chasing wildly around the pasture field; again at 12:30 p. m., and from this time until 3:00 p. m., the heifers in the dairy barn pasture were being attacked. Two of the flies causing the trouble were captured and proved to be *H. bovis.*

The latest date that *H. bovis* was observed "gadding" cattle was July 15. Undoubtedly there were a few flies present after that date, since a few grubs have been observed in the backs of cattle as late as July 20. In 1917 the flies were on the wing in June; on the 18th a specimen was taken resting on the screen of the Animal Parasite Laboratory.

Adult flies of *H. bovis* reared in the laboratory from larvae squeezed from the backs of cattle at Columbus, O., emerged from the pupal cases about April 26 and May 12, 1916. At Wooster, adults reared from larvae appeared between June 14 and June 19, 1915. In New York, *H. lineatum* has been taken from the middle of April to the end of June; and *H. bovis,* from the latter part of May to the middle of September, the maximum annoyance to cattle occurring from June 1 to July 15 (2).

H. lineatum, it is observed, is the earlier fly to appear and where both species occur, as they do in Ohio, the fly season may be longer than where there is only one species.

The season of egg laying of each species is about coincident with that of adult activity. Flies of *H. bovis* reared at Wooster, began laying eggs as early as 18 to 48 hours after emerging from the pupal case. *H. lineatum* has been observed to lay eggs 65 minutes after leaving the pupal case (2).

The eggs are laid on the hairs of cattle. On June 29, I placed a female fly on a calf confined in an outdoor screen cage. The fly remained quiet for a brief spell, then extended its ovipositor. An egg was observed emerging, and when nearly free, was held almost at right angles to the ovipositor. Several times the ovipositor was extended down among the hairs, apparently in an attempt to attach the egg to a hair. After several unsuccessful attempts, the egg still being held by the claspers, I rubbed my index finger over the free grooved end of the egg and it stuck to my finger. A female fly, when two days old, deposited 11 eggs, all in about 45 min-

utes—3 loosely among the hairs and 8 attached singly at the base of the hairs in 10 minutes. The egg is attached singly to the base of a hair, rendering it invisible unless the hairs are spread apart. The attachment is effected by means of a groove in the clasper which is closely appressed to the hair and held in place by means of a sticky substance which exudes around the hair and clasper. Glaser (19) affirms to have observed a female deposit 538 eggs in 45 minutes, each on a single hair. He reports, moreover, that the heifer became restless, kicked, and became furious at the contact of this insect, from which he concludes that the panic of cattle may be attributed to these flies. This was not my experience. The three calves in the Station experimental cage never became restless nor paid the slightest heed to the buzzing or contact of the flies. Cattle on pasture, however, became frantic when attacked by the fly, as is pointed out later.

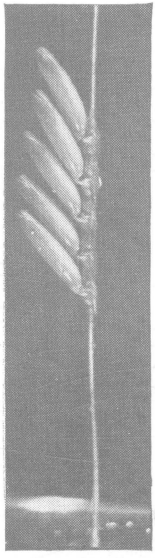

Fig. 5.—Eggs of *H. lineatum* attached to hair (enlarged about 10 times). (Courtesy F. C. Bishopp, entomologist, U. S. Dept. Agr.)

H. lineatum attaches 5 to 12 eggs in series, and occasionally as many as 20, to a single hair. Bishopp (2) reports observing *H. lineatum* lay 446 eggs.

The eggs are seldom, if ever, laid in the region of the back where the warbles later appear. The writer has observed H. bovis strike animals in the following locations: side of abdomen, region of rear heel, fore leg, rear leg, region of rump, under side of abdomen, outer thigh, and left foreleg just above knee. Since this species frightens cattle and continues to follow them, depositing eggs while pursuing the running cattle, the egg are distributed generally over the animal, altho the majority are laid on or near the hind quarters.

Hadwen, Bishopp and others report that *H. lineatum* is more stealthy in its attacks upon cattle than is *H. bovis* and chooses the heels by preference. It approaches the animal on the wing, usually alighting on the ground close to the animal and approaching the hind legs by a series of short flights that resemble jumps. Sometimes it lights directly on the heel, below the dew claw. In many instances it has been observed to oviposit on cattle while they are lying down. The fly, when the animal becomes aware of its presence, lays its eggs higher up on the legs, even on the flanks and in the region of the shoulder.

As has been mentioned, the act of oviposition by *H. bovis* excites uneasiness and even terror among cattle and "gadding" results. The fly no sooner gets near a cow than she begins to stamp and kick, switch vigorously with her tail, and attempt to drive the fly away with her head. Failing in this, the animal starts out across the field with head down and tail in the air.

It is difficult to explain the cause of this terrorism and several theories have from time to time been advanced. The act of oviposition itself cannot be responsible, for, as previously mentioned, animals have been confined with flies in the experimental cage without alarm. When standing a few feet away from animals being attacked in the field, the writer could not detect a buzz, altho in the experimental cage, the movement of the flies did give rise to a buzzing noise. There is reason to believe that this noise may be responsible in part for the terror. Frequently Anton Russ, superintendent of livestock at the Ohio Station, caused the cattle to "gad" by making a buzzing sound similar to that of a fly or bee.

Among entomologists it is generally accepted that the ovipositor is in no way fitted for pricking or piercing the skin and that this organ, therefore, is not directly responsible for the irritation and fright. Hadwen (25) thinks that this fear is caused mainly by the persistent attack of the fly. Bishopp and co-workers (2) agree with Hadwen and add that the fear of this insect is to some extent instinctive and, further, that the animals are more easily aroused and terrorized as the areas of attack become sore and tender from the penetration of the larvae.

Undoubtedly the annoying and persistent attack of *H. bovis* would drive the most amiable animal into a state of frenzy and anger. Approaching the animal on the wing, and with the speed of a bullet, the fly must strike hard in its attempt to lay its egg. The cow kicks and stamps her feet and attempts to drive the fly away with her head, but the fly returns; the animal starts to run and the fly pursues, and finally the animal in terror gallops madly across the pasture to escape the pest, seeking refuge in the nearest pool of water or shade of trees or building.

The writer in his work with reared flies obtained a number of eggs, but none of these hatched. The usual incubation period on the host, as reported by various authorities, is three to six days for each species. The eggs give rise to tiny larvae, about 0.8 mm. (1/30 in.) in length, adequately equipped with apparatus for boring into the skin. The head is furnished with a median

piercing tooth, flanked by a pair of sickle-shaped mouth hooks and each segment is armed with small spines. The larva crawls down the hair and bores into the skin.

Five different theories have been proposed by various investigators in regard to the way in which *Hypoderma* larvae enter the host. The early view was that the back of the cow is pierced by the ovipositor and the egg laid under the skin, with the infliction of great pain—hence the gadding. As early as 1738, however, this theory was questioned by de Reamur (16). He could find nothing of a piercing nature in the ovipositor except the minute chitinized points at its extremity. He even was somewhat skeptical of the extreme suffering of animals so tolerant of the goad and would not adopt Vallisnieri's view that a poison was inserted with the egg.

Furthermore, in 1739, Linnaeus (35) published information on the related reindeer bot *Oedamagena tarandi* L., and expressed his opinion that the eggs are attached to the skin or hairs and are not pushed thru the skin.

In 1888 Hinrichsen (28) suggested that the cattle obtain the eggs or newly hatched larvae from the grass and that the larvae bore into the oesophageal wall and thence by way of the spinal canal to their final situation in the back.

Regardless of the statements of these eminent authorities, most writers, up to the time of Miss Omerod 1884-1894, believed that the flies place their eggs under the skin of the host. The popular essay on bots by Bracy Clark (11) helped to establish this theory so firmly in popular belief that even now one occasionally hears this view expressed by laymen. In his later papers Clark (12) admitted that the piercing theory must be abandoned, and held that the flies probably deposit their eggs on the skin of the back.

It remained for G. Schaupp, a Federal field assistant from Texas, to give a correct view of the matter of egg laying. In 1892 he sent Riley a very complete account of the oviposition of *H. lineatum* in Texas. There the fly was known as the heel-fly from its habit of attacking the lower part of the legs of standing cattle. The actual process of egg-laying was studied in the case of an old and feeble animal, incapable of gadding to take refuge in the water. Lying helpless on the ground, it was entirely at the mercy of the warble flies, and during the first few days of March it was seen to be attacked by about 50 flies. The flies were observed to approach very swiftly and deposit their eggs anywhere on the sides, belly, or tail near the anus, and on the front legs. The flies were left

unmolested. After remaining on or about the animal, in many cases from five to ten minutes, they flew off. The eggs, which were found without difficulty, usually were placed four or six together and fastened to the hair.

Prior to this significant discovery, Curtice (15) published his hypothesis, that eggs or young larvae are licked by the cattle from the back, based on the finding of immature larvae in the submucous membranes of the gullet and in other tissues of the body, often months before the larvae appear on the back and cut holes thru the skin.

Riley (42) accepted Curtice's theory of the entrance by way of the mouth and concluded that an additional link in the chain of circumstantial evidence pointing toward this method of ingress is supplied by the fact that the eggs are laid largely on the legs and that cattle lick themselves in that region.

Following the publication by Curtice and the subsequent one by Riley, practically all scientists, except Koorevaar, accepted Curtice's theory. Koorevaar (33) concluded as a result of his observations and tests that in bovines the larvae reach the gullet or spinal canal after extensive wanderings from the place where they bored thru the skin, and that they do not reach the gullet by way of the mouth.

Carpenter and his colleagues in Ireland (7) endeavored to test the licking theory by muzzling calves in an effort to prevent them from licking themselves. The earlier results were conflicting and the authors changed their viewpoint from year to year. Improved methods, however, gave a distinct indication that muzzling did nothing to decrease the number of warbles, the inference being that such eggs or larvae as were licked off came to naught.

Glaser (19) had failed in attempts to get the young larvae to penetrate thru the shaven skin, but in one case the larvae penetrated thru the skin of his own leg.

In 1914 Carpenter, Hewitt, and Reddin (7) were more fortunate. "Instead of shaving we clipped closely a small patch on the shoulder of a black calf, thus keeping conditions more nearly normal, and put seven newly hatched *H. bovis* maggots on it—immediately they were put on the hairs they crawled down them to the skin and directed their bodies perpendicular to its surface. We soon found that they were disappearing slowly into the skin; four were lost sight of, but the other three were watched cutting the epidermis with their mouth hooks and occasionally bending the

hinder regions of their bodies until they disappeared completely. It took them about six hours to get into the skin; possibly hair folicles may have facilitated their entrance."

In 1916 Hadwen (21) published a number of observations on the action of *H. lineatum* larvae on living hosts and on pieces of skin freshly cut from cattle. He failed to observe the penetration of larvae on living animals, but in a number of tests on pieces of hide removed from a bovine he observed the larvae to burrow partially, and in a few cases, completely out of sight. On May 7 (1915) a piece of skin underlying three hairs to which twelve eggs were attached was removed from the cow. At the foot of one of the hairs a small droplet of clear serum was exuding, which kept increasing in size. By doubling the skin and squeezing, Hadwen expressed two larvae, one of which made determined efforts to reenter the hair folicle. Carpenter, Hewitt, and Reddin (7) had a similar experience. They first noticed soreness and scabs in the regions near where eggs of *H. lineatum* were attached. Beneath these they found holes indicating penetration and from one of these they squeezed along with serum a first-stage larva, which had evidently penetrated thru the skin at that point.

As to the actual procedure of the newly hatched larva, Bishopp (2) writes: "The larva of *H. lineatum* after hatching usually crawls down the hair which bears the egg and after feeling about with the mouth parts, begins to burrow directly into the skin at the base of the hair. The body is usually more or less extended along the hair, and during the initial efforts there is considerable twisting, expansion, and contraction. After the first few segments have been worked into the skin the larva becomes more quiet. The burrowing is slow but usually rather steady in case of vigorous specimens. Progress is retarded as the middle body segments reach the surface of the skin, and usually it is slightly accelerated when the larva has become almost completely imbedded. The time occupied for a larva to disappear after it has begun burrowing has been observed to be about one and one-half hours, and sometimes considerably longer."

In a series of tests designed to demonstrate that the normal method of ingress for the parasite is directly thru the skin and not by means of eggs or larvae taken in by the mouth, Carpenter and his colleagues (8) found that no grubs were recovered in calves to which numerous larvae were fed, but heavy infestations developed in carefully muzzled calves exposed to the oviposition of flies.

In a series of tests carried out at Dallas, Texas, Bishopp and his associates (2) report similar results. Flies were allowed to oviposit on the legs and bodies of 28 animals, which were prevented from reaching any part of their bodies with tongue or mouth. Of these 28 animals, 22 were found later to be infested with cattle grubs. In 2 the grubs were found in the gullet and in 20 in the region of the back during the normal grub season. On the other hand, in not a single instance did infestation appear among the 8 animals to which larvae and eggs had been given by mouth.

LARVAE IN THE GULLET AND SPINAL CANAL

Little information is available on the route followed by the first-stage larvae after penetration of the skin.

In a post-mortem, Stub (43) observed a yellowish jelly infiltrated area in the superficial connective tissue on the inside of the right fore limb, and succeeded in following the track over the shoulder, around the muscles of the neck to the tissue on the oesophagus, where it enters the thoracic cavity. Here he found a number of larvae. They measured 1 to 2 mm. in length. Hadwen and Fulton (27) observed the tracks of the larvae up the tendons to the knees or hocks, in the elbow and patellar regions, and in some cases farther up the legs; no larvae, however, were recovered in these regions.

In 1888 Hinrichsen published the results of his observations in which he found larvae, which he doubtfully ascribed to *H. bovis*, lying between the periosteum and the dura mater in the spinal canal. Two years later Curtice (14) noted the appearance of Hypoderma larvae, which he termed first stage larvae of *H. bovis*, in the oesophageal walls. These were really not the first stage larvae, for later C. V. Riley (42) in 1892 first described the first stage larva which he obtained from an egg just before hatching. Since that date many investigators have verified these observations and all agree that larvae identical with the earliest stage found in the back occur with regularity in the oesophageal wall soon after the fly season and in other parts of the body and spinal canal before their appearance in the back.

In Ohio larvae have been found in the gullet from August to February, rarely after that date. The largest average number of larvae per gullet appeared during the month of December. On November 16, 1915, the writer in company with Dr. Redhead visited two Cleveland abatoirs, and examined 35 gullets, 20 of

which, or 57.1 percent, contained larvae. In the 20, 124 larvae were found, or an average of 6.2 larvae per gullet. The greatest number of larvae found in one gullet was 51.

It was thought that an examination of the position and direction of travel might give some clue relative to the entrance into and exit from the gullet. The majority of the larvae were toward the middle of the gullet or toward the stomach end, some being very near the entrance of the paunch. The direction of the head end of the larvae varied, as many pointing toward the stomach as away. A few (not more than 5) were lying crosswise in the submucous layer. As a general rule the location of the grub was indicated by a small area of gelatinous material in the loose connective tissue of the gullet after the muscle was stripped off. There was no inflammation on the lumen side or mucosa of the infested gullet. All the larvae were found in the abundant submucosa, some nearer the muscular coat, some nearer the mucosa. There was no evidence indicating that the larvae had entered by way of mouth and had bored their way into and thru the mucosa of the oesophagus.

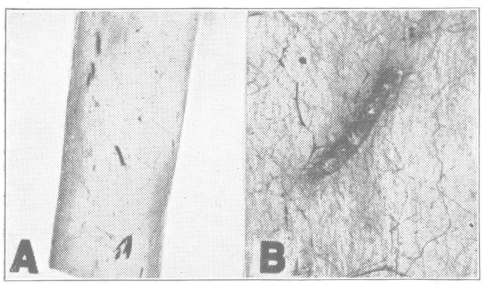

Fig. 6.—A. Hypoderma grub in the submucosa of the gullet near the paunch end (about ⅓ natural size). B. Portion of lining of oesophagus containing grub (from a photograph of a dried specimen, enlarged about 3 times).

Thru the kindness of Dr. R. J. Carver, chief food inspector, City Board of Health, Columbus, O., information was obtained on the occurrence of Hypoderma larvae in the gullets of cattle killed at Columbus. Table 3 is based on information gathered by three or four inspectors at the Blumer-Sarten Packing Co., and covers practically all cattle killed within the dates specified. The cattle slaughtered by this company were gathered up indiscriminately from all sections of the country, according to Dr. Carver, some of them coming from territory surrounding Columbus, and the remainder shipped into the city, mostly from the Chicago stockyards. On the other hand, the information in Table 4 is based on examination of cattle slaughtered by Denton Bros. packing house, an establishment which slaughtered mostly native cattle.

The greater number of the larvae were pointed toward the paunch, each and every month; altho the orientation was quite irregular, some being pointed anteriorly, some crosswise. On the other hand, there is no clear evidence in Table 3 to support the statement frequently made that the larvae are at first chiefly congregated towards the pharyngeal end of the oesophagus and later near the entrance to the stomach. In September, 16 out of 25 (64%) were found in the end nearest the paunch; in October, 66 out of 103 (64%); in November, 232 out of 277 (93%); in December, 301 out of 464 (65%); in January, 11 out of 92 (12%); in February 4 were taken in the anterior end, 3 in the middle, and none in the paunch end of the oesophagus. In Table 4, however, the information more clearly indicates a definite tendency on the part of the larvae to congregate in the paunch end of the oesophagus in the later months of the larval occupation.

TABLE 3.—Data on the Appearance of Ox Warble Fly Larvae in and Adjacent to the Gullet, 1915-1916

Section, direction larvae headed	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	Total
	No.	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*
Anterior end—orientation not reported	....	3	18	34	28	2	85
Toward pharynx	1	.....	....	... .	... ..	1	2
Toward paunch	4	2	12	25	9	1	53
Crosswise	.....	4	.....	.....	.....	.....	4
Total	5	9	30	59	37	4	144
Middle Section—orientation not reported	. ...	6	.....	45	37	3	91
Toward pharynx	1	9	.....	.. .	.....	.....	10
Toward paunch	3	12	11	59	7	.....	92
Crosswise	.....	1	4	..... .	.....	... ..	5
Total	4	28	15	104	44	3	198
Posterior end—orientation not reported	.....	16	118	231	8	.....	373
Toward pharynx	3	6	....	.....	.....	.....	9
Toward paunch	13	36	112	70	3	.....	234
Crosswise	.....	8	2	.....	.....	....	10
Total	16	66	232	301	11	.....	626
Total larvae headed toward pharynx	5	15	.....	.....	.. ....	1	21
Total larvae headed toward paunch	20	50	135	154	19	1	379
Total larvae headed crosswise	.....	13	6	.....	.....	.....	19
Larvae not definitely located	.....	.....	170	356	.....	.....	526
Total larvae in gullets	25	103	447	820	92	7	1494
Total gullets examined	74	142	176	122	113	60	687
Average larvae per gullet	0.337	0.725	2 54	6.72	0.81	0.116	2.17
Larvae in pillars of diaphragm	.....	.....	.....	8	.....	.....	.....
Larvae in subcutaneous tissues of back	.. ....	.....	1 animal	4 animal	numerous animals		

*Columbus, O.—Cattle gathered indiscriminately from various sections of the United States.

TABLE 4.—Data on the Appearance of Ox Warble Fly Larvae in the Gullet, 1916-1917*

Section, direction larvae headed	June	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	June	July	Total
Anterior end													
Toward pharynx			2										2
Toward paunch		5	1	8	19	1							34
Total		5	3	8	19	1							36
Middle													
Orientatjon not reported			2										2
Toward pharynx		2	1										3
Toward paunch		2	1	6	32	2			2				45
Crosswise			1										1
Total		4	5	6	32	2			2				51
Posterior end													
Toward pharynx													
Toward paunch				22	115								137
Crosswise			1										1
Total			1	22	115								138
Total larvae													
Toward pharynx		2	3										5
Toward paunch		7	2	36	166	3			2				216
Crosswise			2										2
Grand total larvae	0	9	9	36	166	3	0	0	2	0	0		225
Gullets examined	93	134	119	164	215	95	104	170	137	143	9		1383
Average larvae per gullet		.066	.075	.219	.77	.031			.014				.169

*Cattle from vicinity of Columbus, Ohio.

The largest average number of larvae per gullet was found in December, when as many as 100 larvae were found in a single gullet. In passing, it is interesting to note that in that month 8 larvae were observed in the pillars of the diaphragm, indicating their probable route after leaving the oesophagus.

The utilization of the oesophagus for a prolonged stopover on the way to the back is of considerable interest. There are two points of supreme importance to the parasite, as pointed out by Hadwen (20) : it must avoid organs where the reaction to its presence would be so great as to endanger its life or that of its host, and it must provide against the possibility of encystment. Encystment is avoided by constant motion, and the oesophageal wall is admirably suited for this purpose, as the reaction is slight unless the larvae are numerous.

The larvae found in the oesophagus are the Hypoderma larvae. This has been definitely established by Hadwen (25) and Bishopp (2) by introducing the larvae under the skin of other cattle and later recovering them in the subdermal tissues of the back.

The writer met with failure in an attempt to transfer larvae from the gullet to other cattle. Three calves born in May or June, 1915, were used in the test. During the summer they were kept in the barn and were not exposed to hypoderma infection. On November 16, 1915, the writer returned from Cleveland with a goodly supply of hypoderma larvae freshly collected from the gullet. With the aid of a large syringe about one dozen were injected orally into each of the black calves. In the third, a heifer calf, three incisions were made in the hide, two on the side just back of the shoulder, and one on the neck in front of the shoulder. Two grubs were placed in each of these incisions.

The remaining larvae were placed in normal salt solution in a small petri dish in order to determine if they were still alive. Several of them were observed to move and some even migrated slowly over the bottom of the dish.

These calves were wintered in the dairy barn and in the spring of 1916 frequent examinations revealed no warble grubs. The test gave negative results.

Peculiarly enough the specific identity of the larvae in the gullet was unknown until Laake (34) discovered a means of identifying the immature larval stages. Bishopp, Laake and colleagues (2) found only one larva of *H. bovis* in the gullet in a series of observations involving 1140 larvae removed from the

gullets of 563 cattle in regions where *H. bovis* occurs. They conclude that the larvae of *H. bovis* do not have the habit of going to the gullet and spending some time there as do those of *H. lineatum*. The route from the oesophagus to the back is not completely known, tho the probable routes have been indicated in a few instances. The finding of larvae along the ribs (Curtice) on the diaphragm (Table 3) and in the neural canal indicates that they pass from the gullet across the diaphragm to the ribs, or directly up the diaphragm from the gullet to the back.

In this connection it is of interest to note that the writer found six larvae in the neural canal of an experimental animal that had been exposed to Hypoderma infestation during the previous summer. There were two animals in this test. On December 18, 1917, they were killed and carefully dissected. The gullet was stripped of its muscular coat, but no grubs or indications were found either in the submucosa or muscular coat. An examination of the diaphragm revealed no grubs. On December 29 the spinal chord was removal from the hind quarter and in the areolar tissue which surrounds the dura mater grubs were found. Three were found in the region of the second lumbar vertebra and two in the areolar tissue of the chord from the same region. In the neural canal of the front quarter of this animal one grub was found. It also was located in the areolar tissue in the region of the eleventh thoracic vertebra. All of the grubs were lying in a horizontal position. They measured 10.5 mm., 11 mm., 10 mm., 11.5 mm., and 10 mm. An examination of these larvae by E. W. Laake indicated that they were third stage larvae of *H. bovis*.

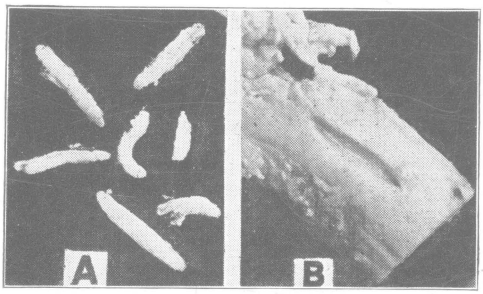

Fig. 7.—A. Third stage *H. bovis* larvae taken from areolar tissue of the spinal cord. B. Location of larvae in tissue of spinal canal.

These observations support that made by Bishopp and associates (2) that the larvae of *H. bovis* enter the neural canals of cattle more frequently than do those of *lineatum*. Bishopp and his associates report finding the larvae of *bovis* in the neural canal from October to March, in New York. Possibly they had utilized the neural canal for a prolonged stay on their way to the back

rather than the gullet. Certainly the canal where the larvae are found between the periosteum and the dura mater affords an easy passage backward and forward and gives easy access to the part of the back in which the warbles occur. See Figure 2.

The grubs make their appearance underneath the hide of the back in late winter and early spring. The earliest recorded observation is December 15, 1912. On this date several large swellings were observed on the loins of a young bull just imported to the Ohio station from Pennsylvania. Later, about January 1, the swellings had receded and a minute hole thru the hide covering each swollen area was observed. The larvae, when first observed under the hide were the same stage as those found in the oesophagus and spinal canal. They soon underwent a molt and changed from the third to the fourth stage, later changing to the fifth or last stage. Migration having ceased the host animal began to wall off the intruder by the formation of an encystment sac or pouch. In this pouch the larvae continued development, feeding on the products obtained by irritation of the walls of the cyst by their spines and breathing in fresh air by means of their spiracles closely appressed to the exit hole.

When the fifth-stage larva completes its growth it emerges thru the hole which has been formed and maintained by the grub during its stay on the back. The grub works its way out thru the hole by the inflation and constriction of its body segments. The caudal end is first forced thru, then this part is inflated and the next adjacent part constricted and forced thru and so on until the larva extricates itself. Generally there is considerable activity before the larva starts actual operations resulting in cleaning the sides of the opening of any obstruction that might be present. The actual process of emergence takes only a few minutes. In my work one grub came out while I was fixing the sieve over it. It could not have taken more than two or three minutes for the operation.

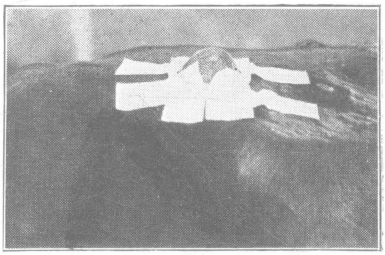

Fig. 8.—Sieve attached to catch grub as it leaves the warble cell

The writer's observations confirm those of other investigators that the great majority of the grubs emerge in the early morning hours. Glaser (19) working in Germany records the greater

percentage, 49.4% to 68.2%, as emerging between the hours of 5 and 7 a. m. Bishopp (2) working at Dallas, Texas, records the greatest number emerging between 8 and 10 a. m. Since the majority of the examinations reported by Bishopp were made after 8 a. m., the number of larvae dropping in the earlier morning hours is undoubtedly too small.

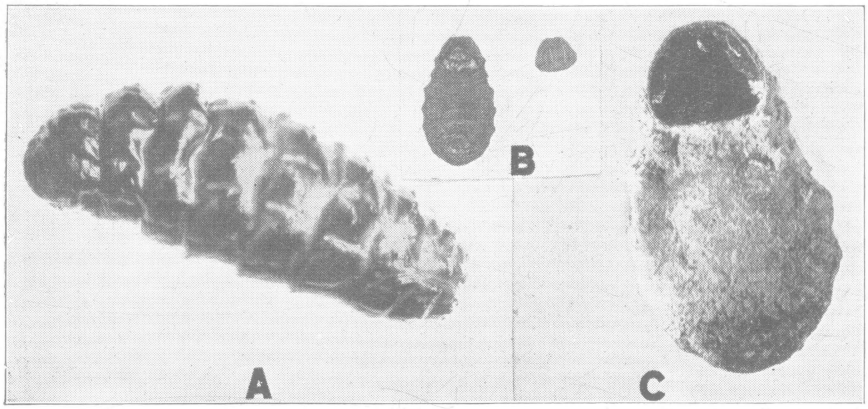

Fig. 9.—A. Warble fly larva or cattle grub. x 2.4 times
B. Puparium with cap removed, showing fly about ready to emerge. Slightly reduced
C. Puparium from which *H. bovis* fly has emerged. x 2.6 times

There appears to be a correlation between the egress of the grubs from the backs of cattle and their activities. The animals become active about feeding time, which at the Ohio Station was between 5 and 6 a. m. In the instances cited by Glaser, it appears that feeding took place very early and hence his observations appear to substantiate the correlation. Bishopp also believes that the activity of the host has much to do with the dropping of the larvae. The feeding of the animals, he observed, usually took place between 8 and 9 a. m. and 4 and 5 p. m. At the other times the animals were quiet, usually lying down. Just how the activity of the host should influence the dropping of the larvae is not easy to explain. Possibly the muscular movements stimulate the grubs. Bishopp suggests the possibility that the warming up of the back in the early morning by the sun, following the cool night, may tend to stimulate emergence. This hypothesis, however, does not explain the early morning emergence (5 a. m. and earlier as observed by the writer) from the backs of cattle kept in a barn.

The grub on dropping to the ground worms its way under the nearest loose objects to prepare for pupation. It crawls slowly and

generally does not move far from the place where it dropped. Within a few hours it becomes quiet and within 24 hours, sometimes longer, the skin hardens and forms a pupal case within which the adult fly is formed.

The duration of the pupal stage varies depending, apparently, upon the temperature and moisture. The writer's records on *H. bovis* at Wooster are 42 to 60 days and at Columbus 29 and 40 days. Glaser (19) records the period as being 37 to 56 days in Germany. Lucet (36) records a range from 29 to 40 days in the vicinity of Paris, France. For *H. lineatum*, Hadwen (20) observed a period of 13 to 19 days when the specimens were kept in an incubator at 32° C. (90° F.). Glaser (19) records a pupal period in Germany for this species of 23 to 38 days. Bishopp (2) reports a range of 18 to 77 days for this species at Dallas, Texas, and 26 to 41 days at Middletown, New York.

EMERGENCE OF THE ADULTS

The flies emerge from the puparium usually in the morning. On several occasions the writer found fully dried adult flies in the rearing cages at 8 a. m. In four instances flies emerged between 9 and 11 a. m. These observations were all made upon *H. bovis*. Apparently *H. lineatum* adults have the same habit. Bishopp (2) states that the majority of the adults were found to escape from the puparia during the early morning hours.

TABLE 5.—Life History Data of Ox Warble *H. bovis* (Ohio Experiment Station, 1915)

Grub left back of steer*	Fly emerged from puparium	Sex	Length of pupal period	Eggs laid		Length of life of fly
Date	*Date*		*Days*	*Date*	*Number*	*Days*
April 15	June 14	Female	60	....	. ...	3
26	16	Male	51	.....	.....	Dead in cage
28	16	Male	49	... .	.....	Dead in cage
May 5	21	Male	47	....	.. ..	2
9	21	....	43	....	.....	3 (escaped)
12	23	Female	42	....	... .	6
12	25	Male	44	.. ..	. ...	3
12	28	Male	47	. ...	....	5
12	29	Female	48	July 1	11 eggs	5
13	23	Male	41	.....	....	7
14	27	Female	44	June 27	2 eggs	3
				June 29	1 egg	
14†	.....	.....	.....	....	....	.....
19	June 25	Male	37	.....	.....	2
23‡						

*All grubs pupated within 24 hours after leaving steer's back.
†Dead in cell. ‡Lost in litter of stable floor.

The cause for the early morning emergence is not known. The pupa apparently is fully mature sometime before it emerges, and with the aid of a relatively large tumor-like swelling on its

head forces the cap off the puparium. It then crawls out and immediately begins to unfold its wings and preen itself with its fore legs, and soon is able to fly about its business of egg laying.

In rearing *H. bovis* the sexes were noted. Out of 10 individuals 7 were males and 3 were females. The number of observations, however, is too small to draw conclusions and the proportion in nature probably is more nearly equal. Bishopp and his associates observed 51.4% males of *H. lineatum* and 47.1% males of *H. bovis*. They report that the males usually, tho not always, emerge slightly before the females. The writer's observations (Table 3) indicate that the emergence of the females is adequately intermingled among that of the males.

Apparently the supply of food carried over to the adult stage from the larva is sufficient to meet the needs of the adult insect thruout its life, for no one so far as the writer is aware, has ever observed the adult feeding. The mouth parts are not developed and apparently are not capable of functioning. In spite of this fact the length of life of the adults in nature undoubtedly extends over several days. When kept in captivity, the flies are very active and restless, and soon destroy themselves so that life in captivity is probably much shorter than in nature. The flies reared by the writer lived from 2 to 6 days. Bishopp reports *H. bovis* adults as living from 4 to 10 days and *H. lineatum* from 1 to 25 days.

COMBATING THE WARBLE FLIES

EXTRACTING AND DESTROYING GRUBS

The possibility of combatting the warble flies by squeezing the grubs out of the backs of cattle or applying smears was recognized many years ago. In 1894 Omerod in England recommended the application of smears to the backs of cattle. The object in view, however, was the prevention of infestation by repelling the flies, and not the destruction of larvae in the subcutaneous tissue. Later writers have recommended the application of smears for the destruction of the grubs. In 1896 Osborn (38) presented a plan for completely eliminating this pest from given areas. He says:

> While it is certain that this insect could be practically exterminated in the U. S. in a single year, we realize fully the great difficulty in getting every person owning cattle to know or appreciate the need of using the necessary means.....We cannot close this sketch of remedies without presenting a plan which, tho it may be styled fanciful or ideal, must if carried out result in the extermination of the pest and the saving, we believe, of not less and probably more than $50,000,000 per year to the farmers of the U. S.

Professor Osborn then outlines a plan of having all the cattle examined and the grubs extracted or destroyed by chemical means. Subsequent authors have presented somewhat similar suggestions and, peculiarly enough, it has remained for cattlemen in countries other than the United States to demonstrate the feasibility of such an undertaking. Boas (3) reports a systematic grub extraction campaign undertaken by a dairy association in Denmark. On a farm in the center of the area the following number of grubs were found present and destroyed on seven succeeding years beginning 1889: 832, 215, 65, 229, 64, 0, 0. Complete eradication was not accomplished toward the edges of the areas covered by the campaign, but the number of grubs was greatly reduced.

To date no such extensive control campaign has been undertaken in the United States. The writer had under consideration for several years while at the Ohio Experiment Station a plan for combatting the grubs in a given area by means of systematic extraction, but funds were not available for putting it into effect. That such a plan would require cooperative community action over a considerable area is clearly indicated by a test in which the grubs in the Ohio Station herd were destroyed systematically for a period of four years.

From about 80 to 135 head of cattle were carried on the Station farm. During the grub season of 1913 the cattle were examined and the grubs extracted and destroyed at intervals thruout the season. The number of cattle infested that year was 32; the maximum number of grubs on one animal was 20; the total number extracted was 123.

In 1914 the cattle were similarly examined and all the grubs extracted. The number of cattle infested that year was 46; the largest number on any one animal 23; the total number extracted 187; the average per infested animal for the year 4.06; the average number of grubs per animal in the entire herd 2.1.

During 1915 the cattle were gone over eight times and the grubs extracted and destroyed. The number of cattle infested that year was 44; the maximum number on one animal 19; total grubs extracted 145; average per infested animal 3.3; average number of grubs per animal in the entire herd 1.6.

In 1916 the cattle were gone over ten to twelve times. The number of cattle infested that year was 22; the largest number on one animal was 16; total grubs extracted 76; the average per infested animal 3.45; the average number grubs per animal in the entire herd 0.56.

The results of this test indicate that a systematic campaign of extracting the grubs and destroying them will greatly reduce the average number of grubs per animal in the herd. On the other hand, enough flies come in from adjoining farms to keep up the infestation.

TABLE 6.—Ox Warble Grubs Extracted From Station Herds During Control Test, 1913-1916

	1913	1914	1915	1916
Angus herd				
Cattle in herd	39	31	28	64
Grubs extracted	102	130	96	65
Average grubs per head	2.6	4.2	3.4	0.98
Dairy herd				
Cattle in herd	38	59	62	70
Grubs extracted	21	57	49	11
Average grubs per head	0.55	1	0.78	0.15
Total				
Cattle in herds	77	90	90	134
Cattle infested	32	46	44	22
Grubs extracted	123	187	145	76
Average grubs per head	1.6	2.1	1.6	0.56
Average grubs per infested animal	3.8	4.1	3.3	3.4

Bishopp, Laake, and colleagues (2) reported a similar experience on a farm in Texas. The average number increased rather than decreased after four years of systematic destruction of the grubs. Duncan, Hewitt, and Jardine (18) reported a like experience on a farm in Ireland. The average number of grubs was materially reduced after the first year's destruction, but for several succeeding years it remained rather constant, tho relatively low, because no similar action was being taken on the adjacent farms.

On the other hand, the writer has reports from dairymen to the effect that they have practically exterminated the warble flies on their farms by a systematic extraction and destruction of the grubs. Undoubtedly this is possible on isolated farms. For example, the Superintendent of the Mansfield Reformatory reports complete eradication in three years. In 1912, the report states, many grubs were extracted from the cattle. In 1913 only a few grubs were found and extracted. In 1914 none were found save in 9 cows purchased in northern Ohio in January. Continuance of freedom from grubs, therefore, is insured even on isolated farms only on condition that no infested animals are imported. Isolation of treated animals or similar treatment pursued thruout wide areas must be maintained if the "squeezing out" method is to be successful.

This fact is clearly demonstrated by Carpenter and Hewitt (8) in control tests on Clare Island. This island afforded suitable environment for the work, the isolation necessary to ensure success being easily maintained. During a period of five years (a longer time than was anticipated), 1915-1920, the workers succeeded in eliminating the warble fly from the island cattle, numbering about 400, with an infestation of 6,000 grubs in 1915. The continuance of freedom would be ensured provided no infested animals were imported.

In this connection it is of value to call attention to the Danish experience in which squeezing out of the grubs was followed by rose fever. Jensen (31) says that hitherto the extraction of Hypoderma larvae had been considered rather safe. From different sources, however, it was learned that urticaria might occur. Schottler saw urticaria following in cases where the larvae had been punctured and then squeezed out. He also said that by this method of treatment serious suppuration may follow. These experiences are reported, not to discourage cattlemen from adopting this method of combatting the fly, but to urge care in the extraction of the grubs. Hadwen (26) cautions against the lacerating of the hide or walls of the warble cell. In fact, he believes that before laymen are advised to undertake this method in a wholesale manner further properly controlled tests should be made.

LARVACIDES

It is claimed by many stockmen, not without some foundation, that squeezing out the ripe maggots is a bit troublesome and expensive for use on a large stock farm. With a view to eliminating this difficulty attempts were made to find some effective larvacide which, when injected into the warble cell or applied as a wash to the back, will kill the grub without injuring the host animal.

In 1913 preliminary tests were initiated to determine the effectiveness of kerosene, crude carbolic acid, grams solution, and arsenous acid. Pure kerosene was injected into 17 warble cells on 9 dairy cows. A week or so later when the cells were examined only one of the grubs treated appeared to have been killed by the kerosene. The grub was dead when squeezed out and there was a strong odor of kerosene present. In the test of crude carbolic acid, 36 warble cells on 13 animals were treated by injecting the material into the cell. This treatment was too effective. It not only killed the grubs but also severely injured the hide and hair in the region of the warble opening.

Grams solution was injected into several warble cells (A. Lucet 36) but in no instance did it affect the development of the grub. In the test made by the writer, arsenous acid was injected into 48 warble cells on nine animals. Two weeks later the warble cells had increased in size and the grubs that were squeezed out were alive and did not appear to have been affected by the substance.

On the other hand, arsenic may have some value in combating the pest as is brought out in the following letter from the late Dr. B. H. Ransom, written March 13, 1913.

> Referring to your inquiry of March 29, my observations on the effect of arsenical dips on the ox warble have been that one or two dippings do not insure the death of all warbles that may be present in the backs of cattle, but some appear to be destroyed. Reports received from the field where dipping has been carried on systematically for the eradication of ticks indicate that the following season the number of warbles is very much reduced. In some cases these parasites become so few in number that they can be found only with difficulty if at all. Whether this result is accomplished because of the direct action of the dip on the warbles in the backs of the cattle, or whether it is brought about by the destruction of the eggs of the fly, or from a combination of both causes has not been determined.

Other investigators have tried numerous materials some of which have given promise of success by killing a high percentage of the grubs treated. An enumeration of the more promising materials together with the method of application will be of value to those who may wish to try them.

1. (a) Derris—formula used:

A

Derris (Kurmange) ..... 1 ounce
Water ..... 1 quart

B

Derris (Kurmange) ..... 1 ounce
Water ..... 1 pint

Method of application—Injection of the solution into the warble cell by means of a stout syringe.

Results—Out of 440 warbles treated 378 grubs were killed, or 86 percent, with formula A, and 581 grubs killed out of 614 treated, or 96 percent, with formula B (Dept. Agriculture and Fisheries, London (45)).

(b) Derris powder dry, dusted into hole of warble cell, killed 95 percent of the grubs treated (2).

(c) Derris powder 1 part, petrolatum 2 to 20 parts, pressed into hole killed 96 to 100 percent (2).

(d) Derris powder 16 ounces, soap 4 ounces, water 1 gallon, thoroly applied to the back with a stiff brush, one and two applications being made, killed 98 to 100 percent (2).

2. Nicotine sulfate (40 percent nicotine) and lime (Dept. Agriculture and Fisheries, London (45).

Formula: Nicotine sulfate .....2 fl. oz.
Fresh hydrated lime .....1 lb.
Water ....1 gal.

First place the lime in a vessel, then add the water gradually, stirring thoroly to prevent the formation of lumps, and finally add the nicotine sulfate. This material will not retain its strength and should be prepared only as used.

Dr. Macdougal (Scotland) reports excellent results, 83 to 100 percent kill, with this material when applied by means of a syringe, and no damage to the hide or health of the animal. A slight irritation, however, was felt when it splashed upon the face.

Nicotine dust (2 percent) dusted into hole gave 100 percent kill (2).

3. Iodoform ointment. Successful use of an ointment consisting of 1 part iodoform to 5 parts vaseline has been reported by Bishopp and co-workers (2) and by Walton in N. Wales (44). Four treatments are recommended by these authorities.

4. Pyrethrum ointment, consisting of pyrethrum powder (open flowers) 1 part to 2 parts petrolatum pressed into the warble holes, gave 100 percent kill (2).

5. Benzole or carbon tetrachloride injected into the warble cells by means of an oilcan gave good results in the experimental tests conducted by Bishopp and his colleagues (2).

Too few large scale control experiments using these dressings have been made to warrant the unqualified recommendation of any one of them. An experiment covering a large area or on an isolated farm would be valuable in establishing the time, number, and method of applications; the efficiency of the material; and cost of eradicating the grubs by dressings.

FLY REPELLENTS, OVICIDES

Many have reported on the effectiveness of fly repellents in controlling the grubs. The writer's experiments and experience would indicate that repellents are of little value.

Thru the cooperation of J. H. Lichty, Creston, Ohio, the effectiveness of Cow-Ease, a commercial fly repellent, was tested. The cows were sprayed lightly every day thruout the fly season. The first year's results were very encouraging but the second year's results were not so encouraging. The only other remedy used, according to Mr. Lichty, was to remove and destroy all warbles in infested cattle before pasture time in the spring. By this method and not by spraying it is believed that the average infestation was reduced. The average for the season of 1912-13 is not definitely known, but it exceeded a round dozen. That season Mr. Lichty began a systematic campaign of extraction and destruction of the grubs with the result that the next year, 1914, he found only 31 grubs in eight head, or an average of 3.87 per head. In 1915 he reported an average of only 1¾ grubs per head for his herd of 12 milk cows and 30 yearlings and 2-year-olds.

Investigations by the zoological division of the Bureau of Animal Industry indicate that the applications, by spraying and wading the cattle thru vats, of the following materials—used automobile oil, sodium silicate, and coal tar creosote dip, are of material benefit in reducing the infestation the following season. (Imes and Schneider (29)). The Bureau of Animal Industry (37) subsequently reported that a satisfactory degree of control may be brought about in range cattle thru the use of wading vats. On the other hand, the Bureau of Entomology reports little or no protection to cattle passed thru wading vats containing various arsenical solutions or a 2 percent coal tar creosote solution. The viability of the eggs themselves is not affected even when dipped in a 2 percent creosote solution. Bishopp and his colleagues (2) report several tests in which eggs in different stages of development were submerged for a period of one minute, with the result that as many larvae hatched from the treated eggs as from the untreated eggs.

Altho there appears to be small hope of discovering a satisfactory fly repellent or ovicide, an investigation of this phase of control should, it is believed, be continued. Possibly a systematic study of the chemotropic responses of the adult flies may lead to some important control measures.

MEDICINAL TREATMENT

Very little experimental work with a view to killing the maggot within the animal during its early migratory stages (first, second, and third stages in the fly's life history) thru drugs given to the animal has been undertaken. One experiment is reported by the Warble Fly Committee of the Ministry of Agriculture and Fisheries, London (45). In this test the killing of the early-stage maggots by injecting subcutaneously five cattle with Arrhenal (a preparation of organic arsenic) was attempted. The method, however, produced negative results. Since this method of attack would appear to offer no inherent impossibilities, additional tests should, it is believed, be undertaken.

NATURAL IMMUNITY

During the progress of the grub control campaign, the writer noted that certain animals are invariably infested while others pastured in the same field are consistently free from grubs. This great difference in the number of grubs found in different cattle in the same herd has been noted by various investigators. The factors responsible for this difference in degree of infestation are not as yet clearly understood. It may be that some animals are quicker in detecting the presence of the flies than others and thus prevent infestation. On the other hand, certain animals with eggs attached to their hairs do not become infested with the grubs. A very definite reaction is set up by the host animal against the larva from the time it penetrates the skin until after it reaches the subcutaneous tissues of the back, which is highly destructive to the invading parasite. Hadwen (24, 27) advances the theory that the invasion of the larva stimulates the production of both antisubstances and eosinophiles, to neutralize the cast-off products of the grubs, and in addition, that there must be a third substance which is antagonistic to the parasite itself. He believes this substance is secreted by the eosinophiles and that it paralyses or kills the grubs which are surrounded by the eosinophiles in the tissues.

Further studies in this field, it is believed, will be of value and may lead to preventive measures in which a high degree of resistance or even immunity may be conferred upon the entire herd.

That the host animal can be immunized against an animal parasite has been demonstrated by Johnson in his work with the protozoan parasite, *Eimeria avium,* which causes white diarrhea in chickens. (Or. Sta. Bul. 230).

PROTECTION OF CATTLE BY HOUSING

There is no record of the warble flies ever entering the barn in pursuit of cattle to lay their eggs. This fact apparently accounts for the numerous examples of the great reduction of infestations affected by keeping the herd in the barn during periods of fly activity. Some cattlemen leave their barns open or provide sheds which the cattle can enter when attacked by flies. This method, altho of value, does not offer complete protection as was demonstrated in certain dairy animals at the Ohio Station. These animals with others were turned out in the barnyard for exercise and water twice a day. They had free range of the barnyard and shed open at one end. Still, three of the animals became infested.

H. bovis AND *H. lineatum* DIFFERENTIATED

The difficulties encountered by the early investigators in breeding out adults or capturing the flies creates a sympathetic bond of interest among the students in this field. Only those who have undertaken studies of the ox warble flies can appreciate the many discouraging obstacles that arise. It was some years before Vallisnieri, an Italian physician of Padua, and the pupil of the celebrated Malpighi, succeeded in breeding out the single imperfect specimen which he described in 1710. Reamur was more fortunate and succeeded in rearing several excellent specimens of the fly. In 1776 De Geer named a fly, which was captured "in the country;" *Oestrus bovis.* This fly he considered identical with Reamur's specimens. In 1825 Latreille established the genus *Hypoderma.*

It is interesting to note that Linaeus had confused the ox warble fly with the horse bot fly and that his *Oestrus bovis* is the same as *Gastrophilus intestinalis* (equi). This mistake on the part of Linaeus led Bracy Clark astray and it was not until his researches were completed that he became aware of the discoveries of de Geer, Reamur and Vallisnieri (11). Jolly in 1846 made anatomical studies of the fly using only 3 specimens and Brauer 1863 published his valuable monograph with but few specimens available.

The history of the recognition of *lineatum* is also exceedingly interesting. Altho described by de Villers in 1789 as *Oestrus*

lineatus, this fly was not definitely associated as a cattle parasite until 1890. For this reason the insect concerned in many European and American writings on the ox warble fly previous to 1890 was in reality *H. lineatum*. In 1875 Brauer received from Dr. Hagen a larva taken from a bison in Colorado which he recognized as different from *H. bovis* and which he named *H. bonassi*. In 1888 Handlirsch captured some Hypoderma flies which were not bovis, in a field where cattle were pastured, and the following year he, in company with Brauer, found a pupa corresponding exactly with his *bonassi* larva, from which he bred a similar fly, of which the normal host was as yet uncertain. The matter was definitely settled by Brauer in 1890 when the fly was proved to be a cattle parasite and was found to be the same as the one described by de Villers in 1789 as *Oestrus lineatus* (5).

The specific name now ends in "m" instead of "s" or "a" to conform with the rules in zoological nomenclature. Clark (11, 13) evidently worked with *lineatum* but had serious doubts as to its identity for at different dates he named it *Oestrus haemorrhoidalis* var. B. (1797), *Oestrus bovis* ♂ *var. B. vernalis* (1815) and later, following Leach (1817), *Oestrus ericetorum* (1843). Walker in 1853 described the insect from Nova Scotia as *Oestrus supplens*.

The characters by which the two species can be distinguished at the various stages of their life history have been worked out by various investigators. It may be of value to describe briefly and illustrate these characters.

THE ADULT

The most obvious differences between the adult flies (Fig. 9) may be tabulated as follows:

(Pinned specimens)	*H. bovis*	*H. lineatum*
Average length	Larger, more robust 14 mm.	12.7 mm.
Thorax	Forepart densely covered with yellow hairs hiding longitudinal markings and contrasting strongly with the black mesothracic region.	Forepart thinly covered with black and yellowish hairs leaving 4 distinct longitudinal marks visible, hence lineatum.
Wings	Vein reddish to dark brown; alulae reddish-brown border.	Expanse 23 to 25 mm. Slightly fuscous, veins dark brown to black; alulae uniformly white.

Legs	Femora and tibia black and well covered with yellow hairs; tarsi brown and much less hairy than *lineatum.*	Well covered with black and orange colored hairs Femora black; tibiae and tarsi brown.
Abdomen	Hairs on terminal segments lemon-yellow, distinctly paler than in *lineatum.*	Hairs on terminal segments orange-yellow.

THE EGG

The egg of *H. bovis* was first described and figured by de Reameur (1738) from specimens obtained from the ovipositor of a captured fly. Riley was the first to figure and describe the egg of *H. lineatum* obtained in the same manner.

	H. bovis	*H. lineatum*
Size	Slightly larger, 0.81 mm. long, 0.29 mm. wide. Foot shorter and broader; attachment more nearly to middle of base of egg; petiole more elbowed. Normally attached to hair singly.	0.76 mm. long, 0.21 mm. wide. Sides more nearly parallel. Attachment of foot on side of base of egg away from the hair. Normally attached to hair in rows.

THE LARVAE

The growth of the larva is marked by a number of instars, or stages, separated by the act of ecdysis, or shedding of its skin. The number of instars is not as yet definitely known. Because of this fact there is considerable confusion in the names and numbers applied to the different stages. We now know the first stage larva and also the three final stages in the case of both flies. Carpenter and Hadwen 1912 (27) and more recently Laake (34) in the case of *lineatum* have shown that the larvae in the walls of the oesophagus hitherto considered as all of the same instar, present two different forms; the younger spiny, the older smooth. In the case of *bovis,* Phibbs (39) has described a second stage larva similar to that of *lineatum.* Laake and others report that second stage larvae of *H. bovis,* with a single exception from the oesophagus, were all collected from the neural canal. The larvae found by the writer in the spinal canal were third stage larvae of *H. bovis.*

First-stage larvae.—The first stage larva of *H lineatum* was first described by Riley (40) and later by Laake (34). The first stage larva of *H bovis* outside the egg was first described by Carpenter, Hewitt and Reddin (7), and Glazer (19). The larva of *H bovis* (0.8 mm. long) is slightly larger than *H lineatum*

(0.55—0.65 mm. long). The color is creamy or dull white and all the segments are densely covered with spines. The spines on the terminal segments and the mouth hooks serve to distinguish the two species in this stage. The flattened spines on the border of the anal spiracles of *H bovis* appear smaller in comparison with the large surrounding spines, and are actually smaller than those in *H. lineatum.* In the mouth hooks of *H. bovis* (Fig. 11, H. l.) note the forked anterior and blunt rear end of the cresent which is not closely applied to the median spear. In *lineatum* (Fig. 11, H. b.) the mouth hooks are more cresent-shape, closely applied to the median spear; the anterior end sharply pointed with a well-formed tooth some distance below and rear end slightly pointed.

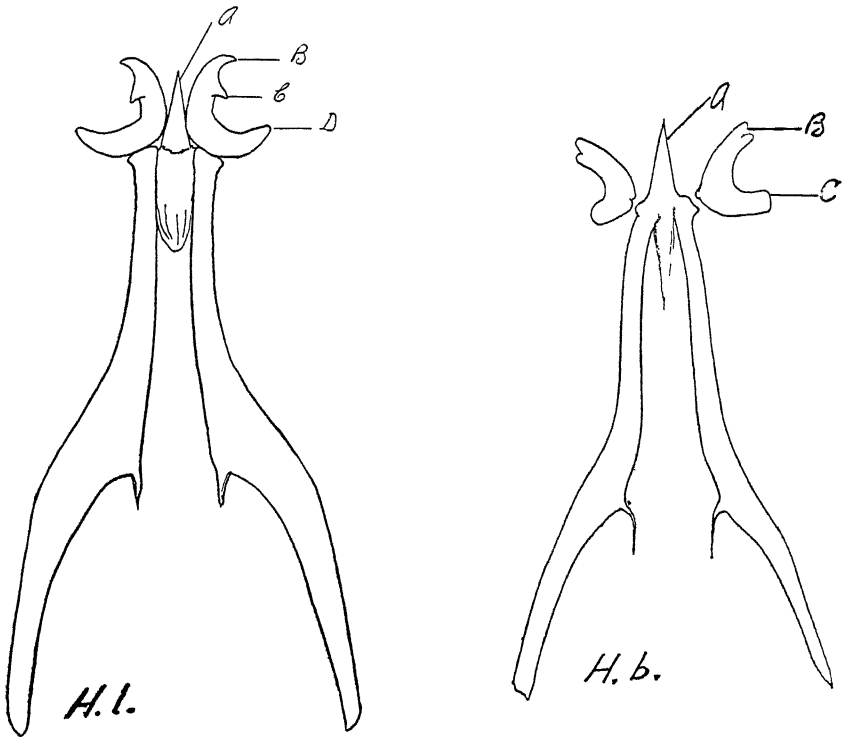

Fig. 10.—*Hypoderma lineatum*: **Cephalopharyngeal skeleton and mouth hooks of third-stage larva. *A*, spine; *B*, anterior end; *C*, tooth; *D*, posterior end of mouth hooks.**

Hypoderma bovis: **Cephalopharyngeal skeleton and mouth hooks of third-stage larva. *A*, spine; *B*, anterior end; *C*, posterior end of mouth hooks. Greatly enlarged (Laake). Courtesy F. C. Bishopp, entomologist U. S. Dept. Agriculture**

Second-stage larvae.—The second stage larvae of *H. lineatum*, altho first dscribed by Laake in 1921 (34), was noted by Carpenter and Hadwen 1912 (27), and is found in the oesophagus. The 2d stage larva of *H. bovis* was first described by Phibbs in 1922 (39) and found in the neural canal. The two species are remarkably similar in this stage, ranging in size from 3 to 14 mm. and still possessing a spiny armature on all segments. The same differences exhibited in the mouth hooks of the first stage serve to distinguish the species in this stage. (Fig. 10).

Third-stage larvae.—The third stage larva of *H. lineatum*, or first stage found in the back and heretofore known as the second stage, was first collected by Curtice in 1890 (14) in the oesophageal walls and in the subcutaneous tissue of the back. That of *H. bovis* was first noted by Hinrichsen in 1888 (28), a veterinarian in South Jutland, in the spinal cavity of cattle. This stage is known as the smooth stage for there are rarely any spines on the body segments. Length, H. bovis, 10 to 18 mm., H. lineatum, 12 to 16 mm.

Here again an outstanding difference which serves to distinguish the species is that in the mouth hooks, as noted for the first and second stage.

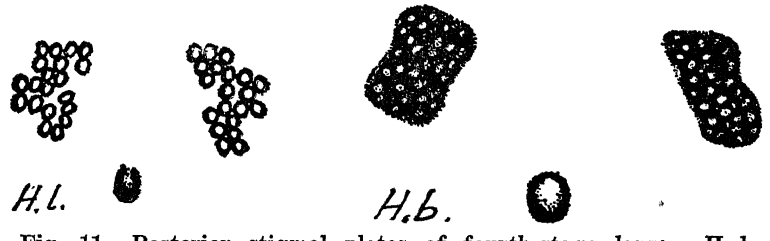

Fig. 11.—Posterior stigmal plates of fourth-stage larva. H. l., *Hypoderma lineatum*; H. b., *Hypoderma bovis*. Greatly enlarged (Laake). Courtesy of F. C. Bishopp, entomologist, U. S. Dept. Agriculture.

Fourth-stage larvae.—As pointed out by Laake (34) the only character that can be depended upon to separate the fourth stage larvae of the two species is the posterior stigmal plates. Under a low or medium power (binocular) microscope each plate is observed to be composed of a varying number of discs or rings. In *H. lineatum* there are from 12 to 30 orange or yellowish-brown, loosely connected discs in each group. (Fig. 11, H. l.). In *H. bovis* there are from 29 to 40 dark-brown to black, compactly bound discs in each group. (Fig. 11, H. b.).

Fifth-stage larvae.—By means of an ingenuous form of a diagram, Brauer as early as 1890 (5) represented the complicated

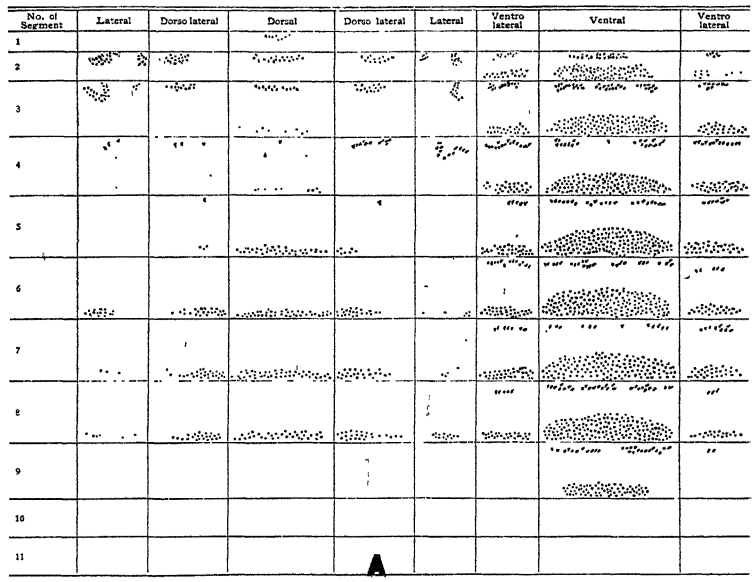

Fig. 12.—Showing location of spines on posterior segments: A—*H. bovis*, B—*H. lineatum*

spiny armature of the fifth stage (called 3d stage by Brauer) larvae of the two species. He found a constant difference between the two species relative to the presence or absence of spines on the posterior segments. In *H. bovis* the last two segments are entirely free of spines on the ventral side, while in *H. lineatum* the last segment only is naked (Fig. 12). Laake (34) points out that the species may also be distinguished by the spiracles and may be recognized while the grub is still in the warble cell. In a study of several hundred specimens of both species, the writer found that these characters hold true. In *H. bovis* the reniform stigmal plate exhibits a cup-shaped or funnel-form surface, the central boss being depressed while in *H. lineatum* the whole surface is level.

H. bovis, length 23 to 25 mm., width 10 to 13 mm.
H. lineatum, length 12 to 20 mm., width 7 to 11 mm.

General color ranging from brown to black, rugged and heavily clothed with spines on most every segment.

THE PUPARIA

The species may be distinguished in the puparia also by the stigmal plates, the plates of *H. lineatum* exhibiting the flat surface and those of *H. bovis* the funnel shaped surface so characteristic of the last stage.

The puparium, dark brown to black in color, retains the larval armature, but the spines are not as easily seen. The shape is best indicated by Figure 9.

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