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ON THE LIFE HISTORY OF "WIREWORMS"
OF THE GENUS *AGRIOTES*, ESCH., WITH
SOME NOTES ON THAT OF *ATHOUS HAEMORRHOIDALIS*, F.

PART I.

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(With 5 Text-figures and Plate IV.)

INTRODUCTION.

At the beginning of 1916 the necessity for increased crop production caused by war conditions, with which we had then been faced for some eighteen months, brought forward the constantly recurring "wireworm" problem more acutely than ever. Farmers were being urged to plough up more grass-land for the production of cereals and potatoes; but the reply constantly met with was that if the grass-land were ploughed up, the farmer had no security of harvesting a crop, owing to the probability that the wireworms, which were supposed to exist in great numbers in all old grass-land, would at once concentrate their attention on the crop as soon as it began to grow. The force of this reply was manifest to those who had had experience with the pests. Our knowledge of the life history, or even of its duration, was incomplete, while it was felt that none of the methods of control usually recommended could be relied upon to form a complete rejoinder to the objection of the farmer to altering his system of cultivation.

In these circumstances it was decided by the authorities at Rothamsted to make an attempt to supply some of the missing facts and work was accordingly begun in the same year.

The present paper represents the results obtained in the biology and life history of *Agriotes*, while it is hoped in the future to publish those obtained in the internal anatomy of the larva and on the research made to secure an adequate insecticide for control purposes.

Many details are still incompletely known, but as certain points of

the life history have in some measure been cleared up, it has been felt that these should be put on record without further delay.

To Dr E. J. Russell, the director of the Station, for the opportunity to carry on the work, also to Mr J. C. F. Fryer and Dr A. D. Imms, in addition to Dr Russell, for suggestions and information at many different points, my hearty thanks must be here expressed.

METHODS.

In order to obtain eggs from the parent beetles, grass plants were potted up in small (4 inch) pots and the surface of the pots enclosed by glass cylinders, the tops of which were covered by a piece of butter muslin. The beetles, when available, could be placed in the cage so formed either by removing the muslin covering the top of the glass cylinder, or by removing the whole cylinder, afterwards pressing it down a little into the soil of the pot, when replaced in position. In this manner the beetles were safely enclosed and by keeping the pots in a shady place and watering sufficiently for the needs of the plants, eggs have been obtained from *Agriotes obscurus* and *A. sputator* in 1916 and from the same two species, with the addition of *Agriotes sibiricus* and *Athous haemorrhoidalis*, in 1918. The pots, after having received their full complement of beetles, were left alone for three or four weeks to allow the beetles time to deposit their eggs without disturbance.

When it was judged that sufficient time had elapsed, the soil was carefully turned over with the point of a penknife and the eggs (if found) were laid bare. Discovery is facilitated if the soil is of a dark colour, is friable and does not contain many grains of sand, which may be mistaken for solitary eggs.

When eggs were obtained, they were taken into the laboratory and placed on damp soil in watch glasses or similar vessels for further observation. The soil being kept moist, no difficulty was experienced in hatching out the larvae. In some cases it was found necessary to pack the eggs for travel and this was done by transferring them to corked tubes containing fresh, moist, moss. Even when kept in these tubes with a bung of moss to replace the cork, for a fortnight or so, the results were satisfactory in the numbers hatched, though the ova appeared to run some risk from moulds which were inclined to spread their hyphae over the moss.

Beside the eggs which were taken from the pots for examination and observation in the laboratory, others remained and hatched in the soil of the pots. During the autumn of 1916 in view of the approaching

winter conditions and in order to give the larvae more scope for movement, the soil and grass plants from the small pots which contained larvae were bodily transferred to larger glazed earthenware pots containing more soil. These pots are the usual long pots used at Rothamsted for botanical and other pot work. They measure some 15 inches in length, 5 inches in diameter, and have a lateral bung-hole about one inch from the bottom. It was intended to sink these pots in the soil, bringing the soil-level in the pot to that of the surrounding ground. After experiment, however, great difficulty was experienced in draining the water from the pots without risk of the larvae escaping, so the pots were dug up and transferred to a lean-to shed facing North. Here they remained during the winter and the larvae, at least those of *Agriotes obscurus*, have successfully withstood the rigour of three winters under these conditions. In the summer the pots were transferred to the open and watered sufficiently to keep alive the plants of grass growing on the surface. For the first eighteen months no further supply of food was introduced, but in the spring and summer of 1918, a few slices of potato were given and have been eaten by the larvae.

In addition to the larvae bred from the egg, wild-caught larvae have been kept, in the laboratory chiefly, for observation. Owing to their predilection for a diet of their own kind, especially at times of moulting, it has been found necessary to keep each individual larva separate. Round tin "pill-boxes" or "salve boxes" have been used for this purpose, each larva being placed in a piece of turf or soil and supplied with food from time to time. It is necessary however to exercise care in giving sufficient water, for, as is well known, wire worms are excessively prone to desiccation and the soil must not therefore be allowed to become dry.

It is not pretended that these laboratory-reared larvae are reared under anything approaching natural conditions, but certain points have been elucidated by this method and wherever there is reason to doubt that observations made under such conditions would be different in the field, they can usually be checked.

I have obtained larvae from several different sources, the principal ones, beside the local ones of Harpenden, being Cambridge and Windermere.

From the latter place an almost unlimited supply has been obtained from heaps of stacked sods, originally taken from a meadow on its conversion into garden. Many pupae and newly emerged adults, principally of *Agriotes obscurus*, have also been taken from the same place.

DEFINITION OF THE WORD "WIREWORM."

Many farmers and gardeners, even yet, use the word "Wireworm" in a loose way to include millipedes and centipedes as well as the larvae of *Elatерidae*. The two former must obviously be excluded, and the only question that arises in regard to the name is as to how many of the latter should be included.

In many papers on applied entomology, both in America and in this country, the term has been used to denote the larva of any Elaterid which is known to be destructive to crops. Curtis⁽⁷⁾ himself uses it in this way; in one place (p. 153) speaking of eleven species of wireworms, though eventually (p. 189) he refers to the "true wireworms" as *Agriotes lineatus*, *A. obscurus*, *A. sputator* and *Athous haemorrhoidalis*. Westwood⁽²⁵⁾ in his *Classification* (p. 237) refers to *Agriotes lineatus* and *A. obscurus* as "the wireworm," being in some doubt whether the latter is specifically distinct from the former. He says they (i.e. the wireworms) are so called from "their cylindrical form and hard texture." This definition was meant of course to apply to the two species named only, but it is equally applicable to the other species of the genus. It does not apply to an equal extent to species of other Elaterid genera which may be classed as "pests." Following Westwood therefore, the name should belong exclusively to the genus *Agriotes*.

Since, however, the word has been so generally used in recent years to denote the larva of any injurious Elaterid, it seems undesirable to define it any more closely than did Curtis, but to use it as applying primarily to the larva of the genus *Agriotes* and to that of *Athous haemorrhoidalis*, F. The larvae of other species of Elaterids may eventually also have to be included, such as those of *Athous hirtus*, Hbst. (*niger* of Brit. Cat.) and *Corymbites cupreus*, F.

The principal distinguishing characters of *Agriotes* larvae are as follow:

- (i) The presence of a tooth, situated dorsally, on the inner edge of the mandible, near its apex, and
- (ii) the two eye-like pits situated near the base of the 9th abdominal segment. These pits, originally supposed to be spiracles, are now usually referred to as "muscular impressions," e.g. by Ford⁽¹¹⁾ and Henriksen⁽¹⁵⁾, but are believed to be sensory organs and are here referred to as "sensory pits."

Athous haemorrhoidalis, F. may be distinguished readily from all the species of *Agriotes* in the larval stage by the absence of the characters

just mentioned, by its broader and somewhat flattened appearance and by the presence on the dorsal surface of the ninth abdominal segment of a kind of impressed shield, bearing at its posterior end two pairs of prongs or cerci, which give it the appearance of possessing a bifurcated tail.

This shield is present in many other Elaterid larvae; but the orange-yellow colour of *A. haemorrhoidalis* together with the presence on the ninth abdominal segment of a single median sulcus, from which three or four transverse tributary sulci branch on either side, will serve to distinguish it from any larva with which it is likely to be confused, with the exception of *A. vittatus*—a somewhat uncommon species—and *A. longicollis*, which is rather obviously rugose above.

RELATIVE ABUNDANCE OF SPECIES.

In Cheshire, North Staffordshire and South Lancashire, Ford found that the common "wireworm" is the larva of *Agriotes obscurus*, L. For England certainly and probably also for Wales and Scotland, the same general statement holds good. There appear to be limited districts where *A. lineatus*, L. or *A. sputator*, L. exceed it in numbers, but the predominance of either of these two latter species seems to be quite local.

Athous haemorrhoidalis, F. is a common and generally distributed beetle and to collectors frequently appears to be more common than the common species of *Agriotes*. This is however a mistake, due to the habits of the beetle itself, which flies more readily than the latter and, being found on flowers and the leaves of trees, is more readily taken with a sweeping-net. *Agriotes obscurus*, *A. lineatus* and *A. sputator* are more frequently found upon the ground or in hiding, so that their abundance as compared with *Athous haemorrhoidalis* is somewhat masked.

In order to gain some idea of the relative abundance of the species of *Agriotes* a number of well known coleopterists and economic entomologists were asked for data of adult beetles of the genus in their particular localities.

The following gentlemen have most kindly given me the benefit of their experience: Commander J. J. Walker (Oxford), Prof. G. H. Carpenter (Dublin), Prof. J. W. Carr (Nottingham), Dr W. Evans Hoyle (Cardiff), Dr R. Stewart MacDougall (Edinburgh) and Messrs G. C. Champion (Woking), F. H. Day (Carlisle), J. Davy Dean (Cardiff), J. C. F. Fryer (N. Cambs.), C. T. Gimingham (Bristol), J. N. Halbert (Dublin), B. S. Harwood (Sudbury), J. H. Keys (Plymouth), W. Mans-

bridge (Liverpool), A. V. Mitchell (Plymouth), W. E. Sharp (Crowthorne, Berks.), H. J. Thouless (Norwich), J. B. Walsh (Jarrow-on-Tyne).

The data obtained serve to confirm that of Fowler⁽¹²⁾, from whose book the following extracts within inverted commas are taken, the remaining notes being deduced from information supplied by my correspondents:

Agriotes sputator, L. "Common and generally distributed throughout the south and midland districts of England; not so common further north." The line, north of which the species is comparatively scarce, appears to run through Norfolk, Nottingham and Cheshire.

A. obscurus, L. "Generally distributed and common throughout the kingdom."

A. lineatus, L. "Common and generally distributed throughout the greater part of England, but more local further north." Usually less common than *A. obscurus* or *A. sputator* even in the Midlands and south of England, but locally it is the dominant species, usually in low-lying positions. Such localities are the water-meadows along the Cherwell and Isis at Oxford (Walker), the banks of the river Trent in the Nottingham district (Carr); the salt marshes of the Solway (Day). In the northern Fen District, Mr J. C. F. Fryer tells me it is equally common with *A. obscurus*.

A. sordidus, Ill. "Very local and usually rare."

A. sobrinus, Kies. "Rather local; . . . not recorded from Scotland." This species also appears to be a southern and midland species. It is "by no means common" in Durham (Walsh) and "scarce" in Cumberland (Day), while it is not recorded in Sharp's *Coleoptera of Lancashire and Cheshire*.

A. pallidulus, Ill. "Generally distributed and common throughout the greater part of the kingdom."

Athous haemorrhoidalis, F. "Very common and generally distributed throughout the kingdom." As already mentioned this refers to the adult; the larva is less common than those of the commonest species of *Agriotes*.

So far as Scotland is concerned, Dr MacDougall reports that *Agriotes obscurus* is the commonest species; he has no record of *A. pallidulus*. In Ireland *A. obscurus* and *A. lineatus* are the only species of *Agriotes* known to occur, but both are widely distributed. Prof. Carpenter and Mr Halbert believe that *A. obscurus* is rather the commoner of the two.

GENERAL LIFE HISTORY AND HABITS.

THE IMAGO.

When newly hatched from the pupa, the adult beetles are of a pale straw colour. From this colour they pass through a stage in which they appear of a reddish-brown colour (similar to the var. *cinnamomeus*, Buys.) and finally, as the chitin becomes hardened, assume the normal coloration of the species. The process of hardening takes some three or four days, during which the beetles remain within the earthen cell.

Most of the soil-dwelling Elaterids appear to remain in the soil during the winter, but as is pointed out in the leaflet of the Board of Agriculture(4), both *Agriotes lineatus* and *A. sputator* have been found during the winter "in tufts of grass, hedge-bottoms or refuse of dykes." In his *Coleoptera of Lancashire and Cheshire*, W. E. Sharp(22) also records *A. lineatus* as "Common in haystack refuse, etc., during winter."

So far as *A. sputator* is concerned, this habit is not universal, the beetles having been turned up in the soil during winter, though they had probably left the pupal cell previously.

In the case of *A. obscurus*, my observations in the open inclined me to the belief that this species also left its pupal cell and hibernated in the neighbouring soil. Good observers, however, have assured me that they have seen the mature beetle in the cell in winter and early spring, so that there may be a difference in habit in this respect between *A. obscurus* and the other two species named. Probably the friable nature of the soil in the locality where my observations were made is responsible for the breaking-up of the cell before the beetle was discovered.

Athous haemorrhoidalis (and it may also be mentioned *Corymbites cupreus*, F.) similarly remains in the soil during the winter, but whether within the cell or not, has not been ascertained.

In the spring the beetles emerge from their winter quarters, according to my observations, about the middle of May. Adrianov(1), observing at Kaluga in Russia, in the same latitude as Yorkshire, came to the conclusion that they had emerged earlier than May. Local climatic conditions may perhaps account for this, but during four years' observation in Hertfordshire, scarcely any *Agriotes* have been found abroad before the 15th May, although in Westmorland *A. obscurus* has been taken under stones in the first half of April.

At the end of May Adrianov found them in great numbers on the rye and wheat plants. Later they appeared on the stems and ears, very active in bright sunlight, and he considers that the pollen of rye is their favourite food. At sunset, or on cold and windy days, he found that they were hiding in the grass, under lumps of soil and so forth.

So far as *A. obscurus* and *A. sputator* (two of the species referred to by Adrianov) are concerned, my observations do not quite coincide with his. Comparatively few specimens of these two species have been taken by sweeping, either on corn or other plants. They have however been taken in great numbers on occasion under heaps of cut grass and it has been noticed that the largest numbers have been taken in dull or showery weather, as might be expected from reading Adrianov's account.

Vassiliev(23) also refers to a similar habit of hiding during the day on the part of *A. lineatus*, but says that the beetles remain in holes made by themselves, especially in hot weather—a habit which has not been observed in this country.

In contrast to the habits of the said three species, *A. sobrinus* and *A. pallidulus* and also *Athous haemorrhoidalis* are commonly taken from leaves and flowers (especially flowers of *Caucalis anthriscus*) by sweeping growing corn, clover and hedgerow plants. As to the food taken by the adults, little has been observed. *A. sobrinus* and *A. pallidulus* are evidently feeding on the nectar when found on *Caucalis* and *A. sputator* has been observed to do the same in the laboratory, though it is so seldom found on flowers in the field. Vassiliev supposed that *A. lineatus* and the other species dealt with by him (*Athous subfuscus*, *Melanotus rufipes*, *Prosternon holosericeum*) feed chiefly on the nectar of flowers, though *P. holosericeum* eats the petals of *Cytisus*.

A number of different Elaterids in America and *Limonius minutus* in Russia(19) have been recorded as damaging fruit blossom, while *Adrastus limbatus*, Brit. Cat. (= *nitidulus*, Marsh) has been known to attack Strawberries (Carpenter(5)), but so far as *Agriotes obscurus*, *A. lineatus* and *A. sputator* are concerned, little is known of the nature of their food at large beyond the statement of Adrianov.

THE EGG.

The eggs of the four *Agriotes* species, *lineatus*, *obscurus*, *sputator* and *sobrinus* are laid in the soil at varying depths from a quarter of an inch down to two inches. Up to the time of going to press those of *A. lineatus* have not been procured at Rothamsted, but Adrianov obtained eggs of that species, together with *A. sputator*, in his breeding pots at depths of, approximately, $\frac{3}{4}$ to $1\frac{3}{4}$ inch, so that the site for oviposition in the four species named may be considered the same. Ova of *Athous haemorrhoidalis* have also been obtained from one of the breeding pots in a similar situation at a depth of $\frac{1}{2}$ to $\frac{1}{3}$ inch below the surface of the soil.

Adrianov found that eggs deposited too near the surface became desiccated and Graf(13) in America also found that those of *Limonius californicus*, Mannh. became desiccated when kept in a dry vial. Probably therefore the beetle descends into the soil for the purpose of obtaining a sufficiently moist nidus.

Oviposition takes place from towards the end of June to the middle of July. The ova have not been found in the open, but in the breeding pots in which the beetles have been confined from the end of May until

their death, no ova have been discovered before the early days of July. From a comparison of the time of hatching of some of the ova with that of the maximum incubation period (which is about one month) it would appear nevertheless that some of the eggs are laid in June.

Ova of both *A. obscurus* and *A. sputator* have been found in burrows excavated by the beetles in the soil, in one case the burrow appearing to be more or less horizontal, in another vertical. It is possible that this may be commonly the case but the friability of the soil when it is examined renders it uncertain whether the burrow will remain intact. The friability of the soil also makes it difficult to say whether the eggs are always laid in clusters. Certainly this is frequently the case, 52 eggs of *A. obscurus* having been taken in close proximity, but many have also been taken singly and in twos and threes and these have almost certainly not always been detached from larger clusters. In the case of *A. sobrinus*, only a few eggs have yet been taken and no clusters were

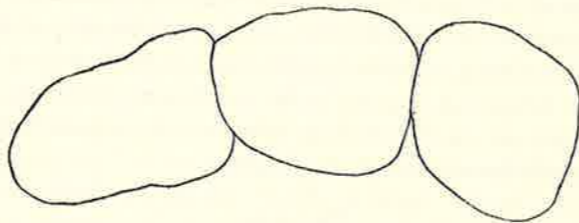


Fig. 1. Coherent ova of *Agriotus sobrinus*, Kies. Magn. $\times 50$ approx.

found, but in the cases of each of the other two species of *Agriotus* observed, as well as in that of *Athous haemorrhoidalis*, clusters of eggs have been found.

The eggs in a cluster do not generally cohere at all fast, and no evidence has been forthcoming that they are in any real sense glued together, or to the soil in which they are laid, by any special material produced by the mother for the purpose, as is the case with some insects. Text-figure 1 is an outline drawing showing three eggs of *Agriotus sobrinus* which were coherent when dug up from the soil. One of them, which appeared to have cohered to the others in a plane at right angles to their long axes, eventually became detached under manipulation.

The actual environmental condition necessary for oviposition is a matter of the greatest practical importance and it is one which cannot at present be considered entirely solved. It seems from extrinsic evidence however to be probable that the presence of grasses, either cultivated or as weeds, is nearly, if not quite, an essential factor. Thus the typical situa-

tion in which wireworms are found in large numbers is grass-land, which has been laid down a considerable time. They may be present in arable land, but their number seems to bear a direct relationship to the state of cultivation of the land, making allowance for a ley of "seeds" or clover which will occur in the rotation.

It is concluded therefore that the eggs are laid about the roots of grasses and that such an environment is only provided by grass- or waste-land, a temporary ley (after which the wireworms found should be nearly of a size) or badly cultivated land on which couch or other grass weeds have been allowed to multiply.

THE LARVA.

No difficulty was experienced in hatching the young larvae, by allowing the ova to remain either on damp soil or moss. Possibly, however, there would have been trouble from desiccation, as Adrianov found, if care had not been used to supply a certain amount of moisture. The young larvae, when first hatched, at once make their way downwards into the soil and, as in the case of older larvae, appear to dislike a strong light. Except in pots where they have been known to be present, they have not been found in the soil and it is doubtful whether larvae, at least those of *lineatus*, *obscurus* or *sputator*, are ever found by farmers or gardeners in their first year of life. They are extremely small up to this age; they are pale in colour and possibly their food is not of quite the same nature as that of older larvae, so that there seems sufficient reason for their being overlooked.

Vassiliev⁽²³⁾ fed young larvae, up to a month or six weeks old, on rotten dung, while Adrianov found pieces of beetroot and carrot eaten to some extent and also found evidence of the larvae having eaten into the small roots of rye and wheat. In my own investigations young larvae have been kept for some weeks in tubes containing turfy soil and the gut, which is plainly visible through the cuticle, was found to be filled with a dark brown substance, evidently partially-decomposed vegetable matter. In the same way also larvae, kept in moss, have been found to have the gut filled with a green substance, the chlorophyll of the moss on which they had fed.

Some slight evidence of potato having been eaten was obtained, but it was not quite satisfactory and certainly larvae in the first instar have not been discovered boring tunnels into potato tubers in the manner of the older larvae. Tests made with growing barley at the end of the first, and during the second, instar afforded no positive evidence

of damage. Ten larvae of *A. obscurus* were enclosed in a pot with plants just above the ground. At the end of six weeks, no evidence of attack could be found and the plants appeared in no wise inferior to those in the control pot. Possibly the smaller rootlets may have been attacked, but though the length of the larvae was doubled during the experiment, the plants appeared quite healthy.

The rate of growth of the young larvae in the first instar I have found to be exceedingly slow, differing in this respect from the experience of Adrianov. His specimens of *A. lineatus*, from a length of 1.25-1.75 mm. at hatching, had obtained a length of about 4.5-5.0 mm. in eleven weeks, while *A. sputator*, from 1.0-1.5 mm., had grown in a few cases to 6 mm. or even more. As he points out, however, the total number of specimens of the latter species examined was only small and he does not regard them as typical. Other tables for the two species, reared more nearly under field conditions, show *A. lineatus* on 25th September (? 7th October by Western Calendar) to be of an average length of 4.3 mm. and of *A. sputator* 3.5 mm.

As will be seen from the data given when dealing separately with the two species, larvae of *A. obscurus* and *A. sputator* were in general found to be larger than Adrianov's at the time of hatching (2-2.75 mm. for *A. obscurus*, 1-2.5 mm. for *A. sputator*), while *A. obscurus* barely attained to the length given by Adrianov for *A. sputator* in September—October of the year of hatching by the end of the first instar (in the following June).

Larval specimens of *A. sputator* from the 1916 brood have unfortunately been few in number, but so far as the information gathered from them goes, this species appears to keep pace with *A. obscurus* in rate of growth. At the end of twelve months, either species reaches little beyond the maximum length of Adrianov's laboratory-fed specimens of only eleven weeks' growth. Possibly *A. lineatus* may be of more rapid growth than *A. obscurus*, but the few laboratory-fed *sputator* of Adrianov which reached so great a length as 6 mm. must be regarded as quite exceptional; though even the average (3.5 mm.) of the large number (44) measured by him from his outdoor cultures considerably exceeded that of either *sputator* or *obscurus* in anything approaching a similar period at Rothamsted.

At the first ecdysis, which takes place in June, the larvae of *A. obscurus* had grown but little, but during the second instar their length was about doubled. The second ecdysis occurs at the end of July and in the beginning of August, so that growth at this point is rapid. After

the second ecdysis the larva grows a little before the winter and then moults again about April or May of the following year. It is at this stage that the young larvae are generally first recognised in the field and they are then of a length of some 6.5-8.5 mm.

At the end of the second year of life, after two more ecdyses, the larvae have attained an average length of 10-11 mm., and are then very distinctly yellow. From this stage onwards observations have been made only on wild-caught larvae, but for *A. obscurus* it appears to be probable that the rate of growth is somewhat as follows:

3rd year from	11 mm.	to	17-18 mm.
4th " "	18 " "		20-21 " "
5th " "	21 " "		23-25 " "

Such an estimate tallies with Bierkander's statement (Marsham (17)) that he had kept the larvae in confinement for five years. Ford (11) p. 101) considers this period too long, but as will be noticed from his argument on the subject, he did not take into consideration the smallness of the larvae in the first year of life—the earliest stage known to him being larvae of 7 mm. in length—nor the fact that growth in the last year is very small. The figures given above are approximate only but are taken from data of measurements of wild-caught larvae together with laboratory observations on their subsequent development.

The fact does not appear to have been generally recognised that the larvae normally moult twice in the year, in April and May and again between July and September. It appears to be true both for *A. obscurus* and *A. sputator*; also for some other species of Elaterid larvae. The summer moult is the most noticeable, since all the larvae appear to be at ecdysis at nearly the same time. At this time the larvae under natural conditions are deep in the soil, possibly as a protection from the appetites of those few which are not in the same condition and of other predaceous insects. The spring moult does not appear to take place amongst all the larvae at one time to the same extent, but there is no doubt about its occurrence. A number of cases have been noted among laboratory-fed larvae; but in addition exuviae, evidently freshly shed, have been found out-of-doors in April and larvae brought into the laboratory from outside in May have moulted within a short time afterwards. Graf (13) found the same in the case of *Limonius californicus*, an American pest of sugar-beet, but he records it in rather a tentative manner (p. 30), though evidently expecting that subsequent experience will confirm the results which he obtained in 1912.

Evidence has also been obtained that the larvae of *Athous haemorrhoidalis*, *Corymbites cupreus* and others which are believed to be *C. pectinicornis*, L., undergo two ecdyses in the course of the year, but this cannot yet be certainly stated.

Agriotes larvae will feed upon almost any crop and apparently upon a good many weeds, apart from grasses, which were probably their original food-plants. They are not however indifferent to the species of plant which they attack and though mustard does not appear to be absolutely immune, as was once supposed, it is probably only attacked in the absence of some more palatable plant. Charlock on the other hand appears to be favoured, larvae having been found boring into the root in cornfields, where it might be supposed their choice would be exercised otherwise. Beans usually do not suffer so much as other crops, but wireworms will on occasion attack the seed beans in the ground. Attacks in pots are difficult to induce, but in a test on a small scale, one bean out of four sown was found somewhat eaten, there having been ten wireworms in the pot. The other three beans were not affected and all four plants subsequently developed equally well.

Potatoes are often much damaged by *Agriotes* larvae and to some extent also by *Athous haemorrhoidalis*, but much of the damage done to potatoes and attributed to wireworms is in reality wrought by slugs and millipedes. *Athous haemorrhoidalis*, and also *Agriotes*, have been reported as pests of tomatoes grown in glass-houses (Carpenter⁽⁶⁾), the latter of course being a well-known trouble to the grower. The larvae enter the plants below the ground-level and, boring their way up the stem, kill the plants, frequently at a time when it is too late in the season to replace them. The fondness of *Agriotes* for the roots of Dock (*Rumex*) has been noted by Curtis (⁽⁷⁾ p. 159) and both it and *Athous haemorrhoidalis* have been found in or about them.

It is hardly necessary to mention the propensity of *Agriotes* for attacking young growing corn, but we do not appear to suffer seriously in this country from attacks on the sown seed, though experimentally larvae have been found to hollow out corn seed in the laboratory. In the United States and other parts of America the attacks of *Agriotes* and other genera on seed is serious and they are also stated to be injurious to maize seed in Russia (Vassiliev⁽²⁴⁾). Probably in this country the seed of cereals is sown too late in the autumn and too early in the spring to be much affected by wireworm attack before the plant develops.

Apart from the capacity of the larvae for fasting, there is no doubt that they can subsist in any ordinary soil for a very lengthy period with

no food other than humus and decaying vegetable matter. Graf⁽¹³⁾ records an experiment made by H. M. Russell on *Limonius californicus* to test the capacity of the larvae for subsisting, as he supposed, without food. "Ordinary soil" alone was given, and, for the first thirteen months of the experiment, it was regularly watered. At the end of this time seven larvae were alive and healthy. The soil was then allowed to become dry for some two months and during this time all the larvae died except one, their bodies being removed as they died from desiccation, to prevent them from being used as a source of food by the survivors. Watering was then resumed and the one survivor continued to live until it died through an accident twenty months after the commencement of the experiment. This treatment was not of course in any sense normal to the larvae and the species dealt with of a different genus from any of our native species known to be injurious. Nevertheless the experiment throws light on the capacity of "wireworms" to withstand starvation by following, *per se*, or by the use of mustard as a "starvation crop" on infested land. I have made no experiment lasting over so long a period, but from observations made in the laboratory and in pot cultures, there can be little doubt that *Agriotes* larvae would succeed in maintaining life in similar conditions for a very considerable time, if not actually for so long as *Limonius californicus*. Larvae have been kept for some months on a diet of vegetable compost during the spring and summer and in the laboratory have frequently been kept in boxes for prolonged periods with no food other than decaying roots and the humus contained in the soil. They do not thrive under such a treatment as the last named, but life is maintained and it is certain that nourishment is derived from the organic matter contained in the soil. On the other hand, provided that sufficient moisture is supplied, *Agriotes* larvae (and those of other Elaterids) are able to fast for a considerable time without apparent inconvenience. In order to test this, three larvae of different sizes were isolated in wide glass tubes containing only moistened sand which had been previously sifted and treated with acid. One larva was able to reach the cork of its tube and was found gnawing it about a week after the commencement of the experiment. At the end of one month all the larvae were found to be alive and active, having apparently suffered no ill effects from the treatment. It should be added that the experiment took place in February and March, so that there was probably no excessive reserve of fat in the bodies of the larvae such as might have been the case at the end of summer.

In the course of experiments to test the toxicity of certain substances

as insecticides, several instances of the power of the larvae to withstand starvation have also been noted. In one case, the larva was evidently affected by the insecticide, which was not of a concentration sufficient to kill it. Treated on the 21st June it still remained, three months later, in much the same condition as immediately after treatment. It was supplied with pieces of potato, but these were not eaten and eventually the larva died—whether from the effect of the insecticide or from starvation could not be ascertained.

Larval *Agriotes* can withstand immersion in water for a very long time. In glazed pots which have remained filled with rainwater for at least a few days, they have afterwards been found alive. Bierkander⁽¹⁷⁾ found they could live in water for four days, but Del Guercio⁽⁸⁾ found that death only took place after twenty to thirty days' submersion and that, as he points out, at a time (June—July) when metabolism may be considered at its height.

Graf⁽¹³⁾ at p. 27) notes that some of the beet fields which have suffered the most from the attacks of *Limonius californicus* are those which almost every year are quite thoroughly flooded for two or three days. It appears therefore that irrigation for any reasonable period is hardly likely to have any controlling effect.

It has been stated by Del Guercio⁽⁸⁾ that the larvae (of *A. lineatus* and *A. obscurus*) feed during the winter between October and March, on decaying vegetable matter and it is probable that such is often the case. When grass-land has been newly ploughed, wireworms may be found, in winter, still in the sod at or quite near the surface, even in hard weather, provided that the sod remains sufficiently damp. They have also been found repeatedly in winter, when digging in the sod heaps mentioned above or on grass-land, amongst the roots of grasses growing on the surface, even during the continuance of frost and snow. Such larvae may be contracted and sluggish at the time, but appear to suffer no permanent damage and revive quickly when brought under milder conditions. At the same time that these larvae are found near the surface on grass-land, others may be found at considerable depths below. Thus, for example, in a hole dug to a depth of 31 inches in one of the sod heaps at the end of December, 1917, 14 *Agriotes* larvae were taken. Of these nearly half were taken amongst the roots of plants growing on the surface or in the first spit (9 inches) of soil, but the remainder were found lower, at depths from the surface of 14 down to 24 inches.

In the case of arable land, which has not been recently ploughed out of grass, the larvae are not found near the surface in winter, unless

perhaps in very mild weather. In a series of tests made in a field known to be infested, none were found nearer the surface than six inches, while several were found in the subsoil, which in this field was at some 10–12 inches from the surface. It is possible that larvae at such a depth might move in their burrows nearer to the surface through the influence of rain and mild weather, but it seems likely that little food, if any, would be taken between the time when they went deep into the soil and that when they returned to feed at the surface in spring. Probably therefore in many cases we have a condition of hibernation similar to that obtaining with many lepidopterous and other larvae, though in others the larvae remain in the sod at or near the surface, feeding on the roots.

As mentioned above, the larvae in the course of their movements through the soil construct burrows, so that in case of necessity they are able to retreat fairly rapidly. These burrows impress the observer when a large number of larvae are kept together in the confined space of a pot and the soil is of such a character that they remain undamaged, when it is lifted out in blocks. The burrows are then seen to honeycomb the soil, ramifying up and down and in all directions.

In the burrow the larva changes its skin, sometimes enlarging the burrow in the process to form a similar cell to that in which pupation takes place. Such cells are also frequently formed for hibernation and the larvae in a sluggish condition may be found in them in winter.

Mention must also be made of the propensity of *Agriotes* larvae for animal food alive or dead. Probably in nature little opportunity occurs to most larvae to indulge their tastes in this direction, but in captivity, as is well known, they will readily feed upon one another, even in the presence of vegetable food. Except in case of injury or at the time of ecdysis, the thick chitin of the cuticle is usually sufficient protection. At ecdysis however the larva is helpless both before and immediately after the moult takes place, so that in the case of larvae kept in a confined space the mortality is very great.

PUPAL STAGE.

Pupation takes place in the ground, within a cell prepared beforehand by the larva. So far as my observations extend, the pupa is placed erect in the cell, with the head uppermost. This habit has also been observed by Hyslop⁽¹⁶⁾ in the case of the American species *Agriotes mancus*, Say.

The pupal instar extends over a period of about three weeks, while

pupae have been found from the latter end of July up to the middle of September.

It is often stated, for instance by Miss Ormerod⁽¹⁸⁾, that the larva descends for a considerable distance beneath the surface to pupate. Reh⁽²⁰⁾ however says that it pupates close to the surface ("in geringer Tiefe") up to a depth of 10-15 cm. This also has been my experience, principally with *A. obscurus*, the following being records from my note book of two tests made by digging in the sod heaps at Windermere, each to a depth of one foot.

5. viii. 18.	2 pupae at 1" from surface	6. viii. 18.	1 pupa at 1" from surface
	1 pupa " 2" " "		2 pupae " 1-2" " "
	1 " " less 3" " "		1 pupa " 2" " "
	1 " " 3" " "		1 " " 3" " "
	1 " " 4" " "		2 pupae " less 4" " "
	1 " " 7½" " "		1 pupa " 4" " "

Larvae pupating in pots at Rothamsted were similarly found in some cases quite near the surface and though they are found to a much greater depth than those mentioned, the habit of pupating deep in the soil, beyond the depth of a plough, is by no means universal.

NATURAL ENEMIES.

This subject has been so thoroughly dealt with in the paper by Ford⁽¹¹⁾ already quoted, that there is but little to add. In confirmation of the value of birds in reducing the number of "wireworms," reference may be made to the work of Miss Laura Florence at Aberdeen⁽¹⁰⁾ especially in regard to the quantity consumed by other gulls than the black-headed gull, which has been well-known as an ally of man in this respect. Hammond's work⁽¹⁴⁾ on the food of birds in the Eastern Counties of England is also of great value, bringing out, amongst other points, the fact that the skylark is of assistance in the control of these pests. Berry⁽³⁾ found many wireworms in the crops of pheasants in Scotland, but Evershed and Warburton⁽⁹⁾ appear to have found but few. Probably local and temporary conditions account for the difference.

There is no doubt that birds are one of the most important factors in the natural control of wireworms and it is probable that under conditions where such a course is possible, their numbers might be appreciably reduced if poultry, especially those of good foraging strains, were run for a time on land newly ploughed out of grass.

Wireworms do not appear to be attacked by internal parasites to any great extent. Marsham⁽¹⁷⁾ records that Bierkander found six out of

thirty wireworms parasitised by an ichneumon (possibly a Proctotrupid) and Mr Fryer, as noted by Ford, has obtained Proctotrupids from *Agriotes* larvae.

In June, 1916, there emerged eleven larvae of a Proctotrupid from a larval *Athous haemorrhoidalis* taken at Windermere in the preceding April. A few days later the larvae were found to have pupated with their heads distal to the body of the host and the eyes showing dark

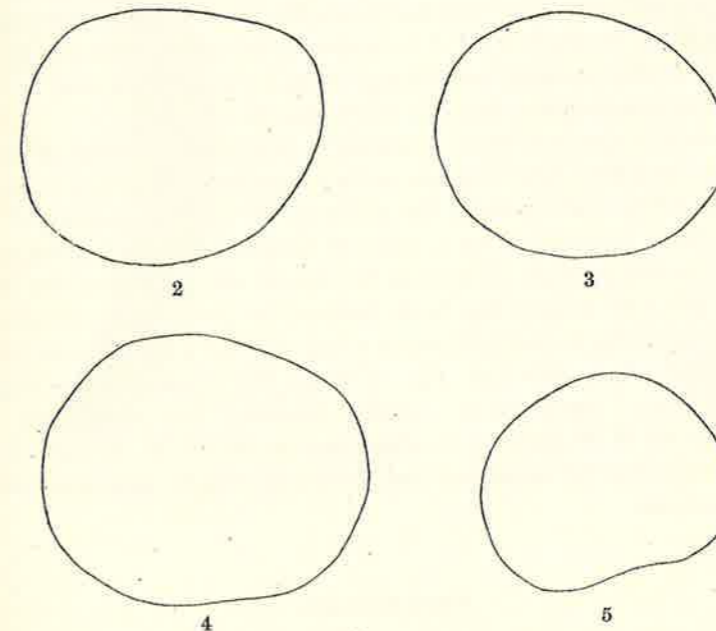


Fig. 2. *Agriotes sibiricus*, Kies.: ovum. Magn. x 75 approx.
 Fig. 3. *Agriotes sputator*, L.: ovum. Magn. x 75 approx.
 Fig. 4. *Agriotes obscurus*, L.: ovum. Magn. x 75 approx.
 Fig. 5. *Athous haemorrhoidalis*, F.: ovum. Magn. x 75 approx.

through the creamy white integument. At this stage they resembled the figure given by Sharp⁽²¹⁾ of pupal Proctotrupids, parasitic on an unknown beetle larva. On July 9th nine imagines emerged, one larva having been killed and one pupa having died without emerging. Five of the imagines were submitted to Mr James Waterston, of the Imperial Bureau of Entomology, who, with Dr R. C. L. Perkins, examined them and reported that all were females of a species of the genus *Phaenoserphus* (Kieff., 1908), probably *P. fuscipes* (Haliday, 1839). To these

two gentlemen my thanks must be expressed for their careful examination.

The only other case of parasitism by an insect occurred in the case of a larval *Agriotes obscurus*, probably also from Windermere, handed over to Dr Malcolm Laurie, of this station, for examination of the internal anatomy. Within the larva he found several larval parasites, which he believes are also referable to the family *Proctotrupidae*.

Wireworms are apparently parasitised by a fungus of the genus *Isaria*, as has been already stated in the Board of Agriculture leaflet (4). Critical work on the subject is necessary to be certain that the fungus is not in reality a saprophyte, though from my experience with it there is a strong presumption that it is truly parasitic.

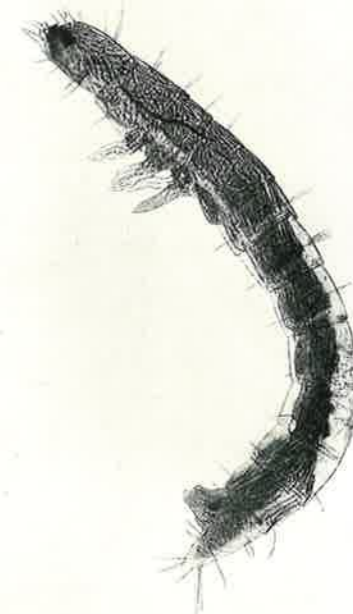
In one of the sod heaps previously mentioned portions of larval *Agriotes* have been found on one or two occasions, consisting of a thin layer of external chitin only, the whole of the interior portions of the larvae being represented by a mass of fungus hyphae. Similar cases have occurred amongst laboratory-fed larvae obtained from the same source and the fungus has been induced to grow upon apparently healthy larvae by enclosing them in a box with an affected larva, upon portions of which they fed. Fig. 3 (Plate IV) represents the fungus growing from a specimen of *Agriotes obscurus*. The photograph was taken by Mr W. F. Bewley, to whom and to Mr W. B. Brierley I am greatly indebted for assistance and advice in dealing with this branch of our subject.

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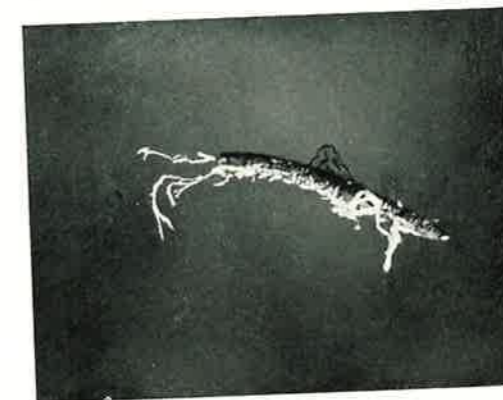
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EXPLANATION OF PLATE IV

Figs. 1 and 2. *Agriotes obscurus*, L. Larvae in 1st instar: about six weeks old.
Magn. $\times 40$ approx.

[Photos. by Flatters & Garnett, Ltd.]

Fig. 3. Larva of *Agriotes obscurus* attacked by *Isaria* sp.
[Photo. by W. F. Bewley.]