SOME OBSERVATIONS ON THE LIFE-HISTORY AND BIONOMICS OF THE KNAPWEED GALL-FLY *UROPHORA SOLSTITIALIS* LINN.

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(With Plates XI and XII and 1 Text-figure.)

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Introduction.

In September 1911, whilst collecting seeds of wild plants at Prestatyn, North Wales, I found galls in many of the flower-heads of the small knapweed, *Centaurea nigra* L., and these on further examination were found to contain dipterous larvae.

On counting the seeds contained in a few of the galled flower-heads, and comparing the numbers obtained with the numbers present in ungalled heads, it was seen that considerably fewer seeds were present in the former than in the latter It therefore seemed probable that

the dipterous larvae present in the flower-heads, by inducing gall-formation, caused a reduction in the number of the seeds normally produced by this troublesome and useless weed, which is very common in many pastures and meadows.

A number of the infected heads were brought to Manchester, and kept until the following spring, when, towards the end of June, imagines commenced to emerge from the galls, and continued to do so during the ensuing three weeks.

The fly was recognised as a Trypetid and specimens for determination were submitted to Mr J. E. Collin, of Newmarket, to whom I am indebted for naming them; they belong to one of the common species of Trypetidae, viz. *Urophora solstitialis* L. Mr Collin also informed me that so far as he knew the larvae and pupae of this species had never been scientifically described.

Early in July some young flower-heads of the knapweed were gathered and a few fertilised female flies were placed on them in a covered glass jar. The females deposited eggs freely, and in eight days from the date of oviposition free larvae were observed within the flower-heads. It was thus apparent that the flies would breed freely in captivity, and Professor Hickson suggested that I might undertake a study of the life-history of this species.

The work was carried out in the Department of Agricultural Entomology of the Victoria University, Manchester, and I wish here to thank Professor S. J. Hickson for his kindness in providing me with opportunities by which I have been enabled to undertake this research; to Dr A. D. Imms my thanks are also due for valuable suggestions and advice given during the later stages of its progress, and to Professor F. E. Weiss for permission to use apparatus belonging to the Botanical Department. My indebtedness to others who have assisted me in various ways, is acknowledged in the text.

Description of fly and classification.

The fly was described by Linnaeus (1758) under the name *Musca solstitialis*; since then it has been frequently referred to and more fully described, under various names, by several entomologists. Loew (1844) discussed the characteristics of this species very fully, and he recognised and described five well marked size and colour varieties. In his monograph *Die europaischen Bohrfliegen* (1862) the same author gives a full description of the species, together with the synonomy;

the description given by Schiner (1864) is more complete however, and of this the following is a slightly abbreviated translation.

"Wings yellowish-white, with brown bands, of these the first and second are always widely separated at the anterior border. Body glossy black; thorax with a brownish-yellow dusted appearance, and with the usual yellow side-stripes as in *Ur. stigma*; scutellum yellow, blackish at the sides. Ovipositor much longer than the abdomen, and swollen from the base to the middle. Head yellow, posterior aspect black or brown; facial aspect paler, frons distinctly brighter in the centre, sometimes rusty-yellow. Antennae, proboscis, and palps, reddish-yellow; proboscis lobes rather narrow, and much elbowed backwards. Legs yellow, in most specimens the anterior femur with a black stripe on the outer border, less frequently a similar stripe is present on the mid and hind femora; terminal tarsal joints brown. Wings with a yellowish-white tinge; at the base and towards the anterior border as far as the stigma, a deeper yellow, with four lighter or darker brown moderately straight cross bands. The first lies near the wing base, is frequently indistinct, and reduced, but always present; it extends backwards at the most into the anal cell, and is always widely separated from the second band. The second proceeds from the point of the brownish-yellow stigma over the discal cross-vein, almost completely straight to the posterior wing-border; the third arises at the anterior wing-border in front of the apex of the marginal cell and proceeds moderately straight over the posterior cross-vein to the posterior wing-border; the fourth is usually narrowly continuous with the third anteriorly, and borders the wing-tip just beyond the fourth longitudinal vein. The clear area between the second and third bands is at least double the width, or frequently only just wider than, the bands themselves. Examples are found in which the bands are very much faded, their position, however, is always distinctly recognisable. Discal cross-vein a little beyond the middle of the discal-cell; 3·1—6·2 mm."

Bezzi (1910, 1913) has recently proposed that the family name should be Trypaneidae instead of Trypetidae, by which name this family of acalypterate flies has been known so long. He divides the family into two sub-families, the Dacinae and the Trypaneinae; the latter is divided into three tribes, Ceratitininae, Myiopitininae, Trypaneininae. The second tribe contains only three genera: *Myiopites* (*Stylia*), *Asimoneura*, and *Urophora*.

Among other characteristics of the tribe Myiopitininae are the

following: "the species are found exclusively in temperate countries, being wanting in the tropics; the larvae live only on plants of the family Compositae, and often make galls" (Bezzi).

The genus *Urophora* was proposed by Robineau-Desvoidy in 1830, one of many that he formed out of the large genus *Trypeta* of Meigen, and from this date onwards the name of the species *Urophora solstitialis* Linn., has been accepted by most entomologists.

The following is a list of the principal synonyms of the species as given in Loew's monograph.

Urophora solstitialis Linn. (1758) ♂ and ♀.

Musca solstitialis Linnaeus, Syst. Nat. x. 601, 98. Faun. Suec. II. 1879. Syst. Nat. XII. 999, 127.
Musca Dauci Fabricius, Mant. Ins. II. 353, 118. Ent. Syst. IV. 358, 187.
Musca solstitialis Cederhjelm, Prod. 318, 1006.
Dacus Dauci Fabricius, Syst. Antl. 277, 22.
Dacus hastatus Fabricius, Syst. Antl. 276, 15.
Trupanea Leucacanthi Schrank, Faun. (Boic.) III. 141, 2507.
Tephritis solstitialis Fallen, Ortal. 6, 5.
Trypeta solstitialis Meigen, Syst. Beschr. v. 324.
Trypeta pugionata Meigen, Syst. Beschr. 330.
Urophora solstitialis Walker, Ent. Mag. III. 7 (ex parte) Macquart, Suit. Dipt. II. 457, 9.
Trypeta solstitialis Loew, Germ. Zeitschr. v. 355.

Geographical distribution.

Urophora solstitialis has been recorded from nearly all the countries of Europe; a list of these records is given by Schiner (1858). Mr J. E. Collin informs me that it is common and widely distributed in England; Fitch (1872) records it from Suffolk; Wingate (1906) from Hesleden, Durham; Connold (1901) from Hastings, Sussex. I have collected the galled flower-heads containing larvae of this species at Prestatyn, North Wales, and also at Port Erin, Isle of Man; and Dr A. D. Imms collected a few galled-heads at Llwyngwril, Merionethshire. Professor J. W. H. Trail of Aberdeen very kindly sent me the following list of localities in Scotland where galled heads containing the larvae have been obtained: Aberdeenshire and Kincardineshire, especially in the valley of the Dee; near Dunkeld and elsewhere in the valley of the Tay, from Glen Falloch, and from Loch Lomond in Perthshire; in these and in other localities the galls are abundant. I am indebted to Professor G. H. Carpenter of Dublin for a note on its occurrence in Ireland;

it has been recorded from Ballyvaughan, Co. Clare; Westport, Louisburgh and Clare Island, Co. Mayo. Professor Carpenter further remarks that probably the species is widely spread in Ireland.

It is worthy of note that specimens belonging to the genus *Urophora* have been recorded only from the old world. In the *Katalog der Paläarktischen Dipteren* (1905) twenty-nine species of this genus are recorded from Europe and Northern Africa; seven of these are listed as British (Verrall) and one species, *U. spoliata* Hal., has not been found elsewhere.

Historical.

Records of detailed observations on the life-history of this species appear to be very scanty, although a few well-known entomologists have studied closely allied forms. Thus Goureau (1845) described the larva and pupa of *U. cuspidata* Meig., and Dufour (1857) those of *U. quadrifasciata* Meig. Until comparatively recently the former was regarded as synonymous with *U. solstitialis* (Schiner, H. Loew); Becker (1902) however, who examined Meigen's type of *U. cuspidata* in the Paris Museum, considers that *U. cuspidata* Meig. is distinct from *U. solstitialis* L. The most complete account of the larva and pupa of a species of the genus *Urophora* was given by Mik (1897) who described those of *U. cardui* L.; the larvae of this species induce galls on the stems of *Cirsium arvense* L.

Boie (1848) obtained *U. solstitialis* in hundreds from galled flower-heads of *Carduus crispus* L.; they emerged from June 8 to July 12. From several thousand pupae only three or four flies emerged in autumn, and his opinion was that this species gave rise to a single brood only, unless exceptional conditions prevailed.

In a paper devoted to the natural history of the Trypetidae, Frauenfeld (1857) refers to this species among others; he states further, that it produces swellings in the receptacles of all the plants that it infects, and he gives a list of its food-plants.

There is a brief paragraph by Kaltenbach (1874) on this species, he gives the names of three hymenopterous parasites reared by Goureau from *U. cuspidata*, as parasites of *U. solstitialis*. He assumed, however, that the two latter were one and the same species.

Fitch (1872, 1879) refers to it in two short notes; it is also referred to by Connold (1901) and by Swanton (1912). Connold gives a short description of the galls together with photographs of these and of the larva and pupa.

Food-plants.

As regards the food-plants Schiner (1858) remarks that:

" The larvae live in the flower-heads of *Carduus nutans* L., *crispus* L. and *acanthoides* L.; they are also found in those of *Cirsium lanceolatum* L., *Centaurea scabiosa* L. and *montana* L., and on other Cynaroideae "; F. Löw (1866) recorded *Centaurea paniculata* L., as a food-plant of the larvae, and Fitch (1872) recorded this species from galled flower-heads of *Serratula tinctoria* L., collected in Suffolk. In a later paper (1879) this observer remarks that in 1872 he added to the list of [British] gall-making Trypetidae, *Urophora solstitialis* L., " which deforms the ovary of the common knap-weed (*C. nigra*) into a hard, woody, but only tactilely noticeable gall."

This is the first record which I have been able to find of the occurrence of this species on *Centaurea nigra*. Curtis (1860) refers to *U. solstitialis* under the name *Tephritis solstitialis* as being abundant on thistle blossoms during the summer, he does not state, however, that he bred the fly from thistles. Connold (1901) and Swanton (1912) both give *C. nigra* as the food-plant of the larvae of this species; Prof. Trail informs me that in Scotland *C. nigra* alone is known as the food-plant.

It is noteworthy that none of the continental authorities, whose writings I have been able to examine, record *Centaurea nigra* as one of the food-plants of these larvae; on the other hand, with the single exception of Fitch's record of *Serratula tinctoria* referred to above, all the records of its occurrence in this country that I have been able to consult, state that *Centaurea nigra* is the food-plant of the larvae here.

Many of the recorded continental food-plants are equally common in this country, whilst *Centaurea nigra* is common on the continent, and it is worthy of remark that there appears to be this difference in the habits of the larvae here and abroad.

The larvae of a closely related species, *Urophora quadrifasciata*, are recorded as feeding in the flower-heads of *Centaurea nigra* (Loew, Schiner); and according to the account of Dufour (1857) the life-history of this species and the effects produced by the larvae on the host-plant, are very similar to those of *U. solstitialis*.

There was just the possibility therefore, that I might be dealing with this species (*U. quadrifasciata*). Through the kindness of Mr J. E. Collin, I have had the opportunity of examining two continental specimens of *U. quadrifasciata* from Bigot's collection, and there is no doubt that the specimens reared here from *Centaurea nigra* are distinct from

the continental specimens of *U. quadrifasciata* that I examined. Possibly in this country *U. solstitialis* feeds also in the flower-heads of various species of thistles, and its occurrence in these food-plants may have been overlooked.

U. quadrifasciata differs from *U. solstitialis* in the following characters. Its average size is smaller. The thorax appears almost black owing to the very slight yellow powdering (Bestäubung) on the surface; all the femora are black also. The ovipositor is not much longer than the abdomen. The four cross-bands on the wings are very broad, dark, and sharply defined; the first band is united with the second, and the third with the fourth at the anterior border of the wing.

Life-history, description of ovipositor, and method of oviposition.

A supply of galled flower-heads was gathered in September, 1912, and one or more of these were examined from time to time in order to find out when pupation commenced. The first indication of change was observed on April 29th, the following spring; in one gall, two larvae were found whose skins were just hardening and changing to a darker colour. On May 3rd, ten individuals were found in one gall, and in nine of these the puparium was hard and definitely formed, whilst the remaining one was still in the larval state. From this date onward pupae were invariably found and in increasing numbers; the latest date on which I found unchanged larvae was May 29th. On June 1st imagines appeared; we may therefore say that the pupal state lasts from four to five weeks.

From June 1st imagines emerged every day until July 3rd; after this date very few emerged and only at intervals of several days, and the last fly emerged towards the end of July. The period of emergence thus extended seven weeks, but the greatest number of flies emerged during the month of June.

The flower-heads from which the flies were obtained were kept inside a cool room during the winter, and in April they were taken into the warmer laboratory. Outside in the open fields, development would probably be slower and the flies would emerge later. In the open, however, flies are on the wing in mid-June.

The number of males and females that emerged between June 3rd and July 3rd, 1913, was counted in order to ascertain the proportion of the sexes to each other. Between these dates 152 male flies and 130 females was obtained. In the early part of June, many more

males than females emerged, but towards the end of the month, this disproportion in the sexes was decreased. Fitch observed that the males emerged before the females, but he only obtained twelve females and eight males; the numbers he dealt with are therefore very small. If the results obtained above should be confirmed by subsequent countings of greater numbers, they might be explained by supposing that the greater numbers of males produced and their early emergence are provisions for ensuring that as far as possible, all the females shall be fertilised.

Four days after emergence, two pairs of flies were observed in copulation, and another pair copulated five days after they emerged (June 5th and 6th). Probably several days intervene between copulation and oviposition, the exact length of time that elapses between these two acts was not determined.

When the female is ready to oviposit she selects an unopened bud; the bracts of this, however, are just beginning to open. If the flower-bud is suitable for the purpose, she is observed to move over it in various directions; at the same time the ovipositor is frequently protruded and inserted at various points between the bases of the scales; she is evidently selecting a suitable place for the insertion of her ovipositor. As soon as this is found she settles down, her head pointing towards the apex of the bud; the first joint of the ovipositor is then bent almost at a right-angle to the abdomen, and pushed between the bases of the lowest and outermost scales; whilst in this position the ova are placed within the flower-head.

If a flower-head which contains eggs is severed vertically into two halves, and carefully examined, the eggs will be found either in the space between the upper surface of the florets and the overlying bracts (Fig. 2) or between the florets themselves. In order to understand how the eggs are placed in these positions, the ovipositor, during the process of oviposition, may be rapidly severed from the abdomen with a sharp pair of fine scissors, and its position in the flower-head observed; or in a fortunate section of an infected flower-head the tunnel made by the passage of the ovipositor may be seen (Fig. 13). Evidence has been obtained by both these methods, and in order to explain the process of oviposition in a more complete manner, a short description of the ovipositor is inserted here.

The female fly possesses the usual corneous, pointed, three-jointed ovipositor which is characteristic of the three closely related families of acalypterate muscids, Trypetidae, Ortalidae and Lonchaeidae (Bezzi).

The first segment of the ovipositor (which appears as the terminal segment of the abdomen) is about 2·7 mm. long ; it is swollen anteriorly, being about 0·6 mm. across in this region, and it becomes narrower in the posterior portion ; near the distal end it is about 0·25 mm. in diameter. The walls are strongly chitinised and it is covered with numerous hairs.

The second or middle segment of the ovipositor is about 2·3 mm. in length, by 0·15 mm. wide along its whole length, and consists of a transparent flexible membrane in which a great number of small chitinous sclerites are partially embedded. This segment is capable of protrusion and retraction, like the finger of a glove.

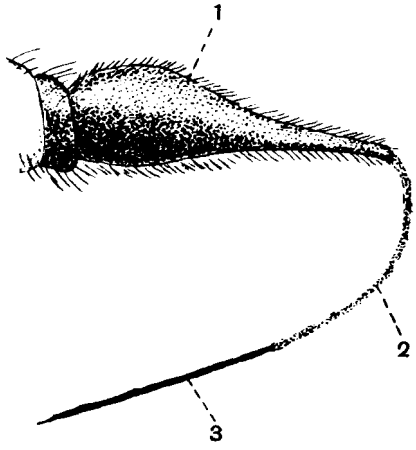


Fig. 1. Extended ovipositor of *U. solstitialis* from left side, × 15. 1, 1st segment of the ovipositor ; 2, 2nd, flexible segment ; 3, 3rd, piercing segment

The third and last segment is the actual piercing portion of the ovipositor ; it is composed of chitin, is about 2·3 mm. long, and except at the extreme narrow tip is about 0·07 mm. in diameter. There are two sharp-cutting blades at the sides of the tip. This segment contains the terminal portion of the oviduct, which opens to the exterior near the tip. During the passage of the ova this segment probably expands slightly.

The ovipositor is extended by pressure, presumably by muscular compression acting on some of the body-fluids. If the swollen portion of the ovipositor is compressed with a pair of forceps, the flexible and piercing segments are readily everted, and they always assume a curved

position which they retain as long as the pressure is applied. The significance of this curvature will be apparent if we consider the structure of the flower-head and the act of oviposition.

As is well known, the young florets of composite flowers are protected by an involucre which is composed of numerous bracts or scales. In the flower-head of *C. nigra* these bracts arise just below the level of the receptacle, and this is the region selected by the fly for the insertion of its ovipositor.

During oviposition the blunt end of the first segment of the ovipositor is placed between the lower scales as described above, and whilst in this position the piercing portion is forced into the tissue of the receptacle. The piercing segment passes downwards and inwards towards the vertical axis of the flower-head, and gradually bends upwards until the tip of the ovipositor finally reaches the space between the tops of the young florets and the overlying bracts. The ova are usually placed in this space; less frequently, however, they are to be found between the young florets. In the latter case the flower-heads are probably older than in the former case, and the florets are longer; consequently the ovipositor is not sufficiently long to reach the space wherein the eggs are usually laid.

Goureau, who correctly described the external appearance and movements of the ovipositor in *U. cuspidata*, believed that the ovipositor was pushed between the florets of open flowers, and that the eggs were then placed on the receptacle of the flower-heads. A similar opinion was also held by Dufour who observed some phases of the life-history of *U. quadrifasciata*. The latter observer, in addition, supposed that the eggs were placed inside the tissue of the receptacle, and further, he believed that the presence of the eggs, and possibly the injection of an irritating fluid at the same time as these were laid, induced " une irritation nutritive du réceptacle transformé alors en placenta "; in other words induced the formation of the gall.

Although the observations of these entomologists refer to species other than the one considered here, yet, as these species are all so closely related to each other, and their larvae also feed in similar flower-heads, it is almost certain that on this point the opinions of these observers were erroneous.

From evidence obtained by opening the flower-heads after oviposition and counting the eggs, and also by counting the number of larval chambers in galled heads, I believe the number of eggs usually laid at one time varies from one to four; where more than four eggs

or larval chambers are present they are probably the result of two or more separate acts of oviposition.

The ovaries of two females were dissected out and the eggs counted in order to determine the number of eggs a female fly is capable of producing. From the ovaries of a female which had laid no eggs, 108 apparently mature ova were obtained, as well as a considerable number of immature ones from the ovarian tubules; the ovaries and oviduct of another female yielded 105 ova; this fly had, however, laid a few eggs. We may safely say that a female of this species is capable of laying at least 100 eggs, and if the immature ova ripen as the season advances, then probably considerably more.

Descriptions of ova, larvae, and pupae.

The ovum of *U. solstitialis* is elongate and usually crescent shaped, with its widest diameter across the centre; the amount of curvature varies, however, examples are met with at times that are almost straight; from the central area the egg tapers towards each end, but more abruptly towards the posterior end which is pointed, than to the anterior or cephalic end which is rounded, and terminated by the prominent micropyle. Bezzi (1913), who discusses the metamorphosis and bionomics of the Trypaneids in general, states that the eggs are "rounded at the two ends"; the egg of this species is therefore exceptional in this respect.

The ova have a glistening white appearance, and when present are readily observed in the flower-heads; the shell or chorion is very thin and quite smooth, and exhibits no sculpturing or pattern on the surface.

In size the ova vary considerably: a number of ova laid by one female varied in size from 0·87 × 0·15 mm. to 1·04 × 0·17 mm.; ova taken from the same fly measured about 0·9 × 0·12 mm. The largest ovum observed measured 1·3 × 0·15 mm.; the average size is about 1–1·02 × 0·15 mm.

Just before deposition the fertilised ovum completely fills the space within the chorion, but shortly after oviposition the embryo commences to diminish in length; in three ova measured one hour after oviposition there was a shrinkage of 0·18 mm., 0·2 mm. and 0·3 mm. respectively, and within twenty-four hours of oviposition the embryo contracts to about two-thirds of its former length. (Fig. 7.) A space thus appears at each end between the embryo and the chorion.

The length of time that elapses between oviposition and hatching, varies somewhat; probably temperature is the controlling factor. In July 1912, larvae were obtained in eight days from the date of oviposition, whilst in June 1913, the shortest time recorded between these two events was eleven days.

The larvae, after hatching, may be found creeping on and between the florets; possibly they feed on these for a short time, but very soon they bore their way through the walls of the corollae and travel down the corolla tubes to the developing ovules. The corollae that contain larvae may be readily distinguished from those that are uninfected. Small circular or elliptical apertures with discoloured margins are visible on florets that contain larvae, and in the majority of cases these apertures are about one-third the length of the floret from the top. Usually each infected floret contains only one larva, but occasionally two larvae may be found, and in one example I found four larvae within a single floret. I have never observed more than a single fully-grown larva in the completed larval chamber; it is therefore probable that where more than one young larva enter a floret all except one eat their way out again and enter other florets. On reaching the base of the corolla tube the young larva bores into the developing ovule and by its activities in this position induces the formation of the gall.

The recently hatched larva measures about 0·5 × 0·1 mm. and has a glistening white appearance; it is cylindrical in shape and slightly thicker at the anterior than at the posterior end. There are two pairs of very small papillae on the anterior segment placed just above the mouth hooks; the lower pair, nearest the mouth, are the sense-organs or palpi, and the upper pair are the antennae (Mik). The pharyngeal skeleton is well developed and very similar in shape to that of the fully grown larva, with the obvious difference that it is very slender and slightly chitinised. At the posterior end of the body the spiracles are visible under a high magnification, as two light-brown spots, and each spiracle possesses three apertures.

The larvae do not grow very rapidly at first; two larvae fourteen days after hatching measured only 0·6 × 0·12 mm., and a larva five weeks old measured 1·3 × 0·4 mm. During the following two or three weeks growth is very rapid; two larvae that were about eight weeks old (Aug. 13th) measured 3·5 × 1·5 mm., and 3 × 1·8 mm. respectively. The posterior surface of the last segment in both these larvae was becoming dark in colour and strongly chitinised; in larvae preserved early in September these characters are fully developed, and in addition

the area round the mouth is changing to a reddish-brown colour, and undergoing chitinisation. A series of fine grooves which radiate in a backward direction from the mouth are very apparent about this stage. These grooves or striations are present on younger larvae (Aug. 22nd) but in order to see them it is necessary to strip off the cuticle from the anterior part of the body and examine it under the microscope ; this area is not chitinised in larvae at this stage ; in those larvae, however, where this area has become chitinised the grooves can be much more easily seen. A series of small channels at the sides of the oral lobes in the larva of *Musca domestica* L. is described and figured by Hewitt (1908). The grooves referred to above may correspond to those of the house-fly larva.

The first appearance of the chitinised area round the mouth aperture probably coincides with the nearly completed feeding period. From mid-September to early October the majority of the larvae are fully fed, and they remain head downwards in the larval chambers until pupation commences in the following spring ; the larvae reverse their position just before pupation. During the period of feeding, and the growth of the gall, an opening of the larval chamber to the exterior is maintained, and this opening is sufficiently wide to allow the imago to emerge ; this opening is situated at the apex of the chamber and is much narrower than the basal part in which the larva hibernates.

The fact that the larva remains head downwards with the strongly chitinised posterior segment uppermost and stretched across the larval chamber where it fits very tightly, suggests the explanation that this is a contrivance for avoiding or preventing the attacks of parasites or other predaceous enemies during the prolonged hibernating period. This suggestion is made by Connold and is, I think, a very probable one. He, however, states that pupation takes place in October. Of course, this may be so in the South of England, although I doubt it.

The larvae of *U. cardui* remain head downwards during the winter (Mik), and Goureau notes that the larvae of *U. cuspidata* also remain in this position until pupation commences. In Dufour's account of the life-history of *U. quadrifasciata* there is no mention of this peculiarity ; it may be inferred, however, that the larvae of this species hibernate in a similar manner to those described.

I have never been able to convince myself that frass is present in the larval chambers. In the galls of *Cirsium arvense* caused by larvae of *U. cardui*, Mik found in the upper portions of the larval chambers " Excrementen in der Form von lichtbraunen Krümchen " ; possibly

the larvae of *U. solstitialis* derive the greater portion of their food from the sap liberated by rupture of the cells which line the larval chamber. If this assumption is correct, then the absence of frass might be explained, as in this case practically all the food would be absorbed.

The evidence obtained leads to the conclusion that there is only one brood produced each year. Early in September, 1912, I obtained young larvae from flower-heads gathered at Prestatyn and then thought that possibly two broods were produced in one season ; as I have never found pupae or empty puparia during the months of August, September, and October, the conclusion arrived at is that the young larvae obtained in September, were the progeny of late-emerged flies and that there is only one brood produced each year in this part of the country. Goureau states that in France *U. cuspidata* gives rise to two broods in favourable seasons.

The life-history of *Urophora solstitialis* may be briefly summarised as follows :

Egg stage. 8–12 days, from end of June, during July and early August.

Larval stages. Feeding period three months or less ; from early July to early October.

Hibernating stage of larva. About seven to seven and a half months, from early October to mid-May.

Pupal stage. About 4–5 weeks. From mid-May to end of June.

Imago. Length of life uncertain, probably at least a month. (I have kept them alive for three weeks.) They emerge from mid-June to end of July and early August.

There is a certain amount of overlapping in the times given above owing to the extended period of emergence of the imagines.

Description of the mature larva.

There is considerable variation in the size of the fully fed larvae ; thus, three examples taken from one gall in November measured 2·8 × 1·5 ; 3·5 × 1·7 ; 4 × 2 mm. respectively ; the average size of five large larvae was 4·4 × 2 mm.

Naturally the variation in size is also exhibited by the pupae as will be seen from the measurements of these given further on. A probable explanation of this variation is that the smaller individuals develop from eggs laid by late-emerged flies and consequently the feeding period is much shorter than in the case of those which develop from eggs laid

earlier in the season ; it is also possible that where several larvae, say eight to ten are feeding together in one flower-head, there is not sufficient nourishment to enable them all to reach a large size.

The larvae are ellipsoidal in shape ; the anterior end is bluntly pointed and the posterior end sharply truncate, and the greatest width is across the anterior third of the body (Fig. 9). With the exception of a very few extremely small hairs on the posterior surface of the last segment, the body of the larva is completely smooth and free from bristles or spines ; Bezzi (1913) in his very useful account of the Trypaneidae states that " the under surface [of Trypaneid larvae] bears transverse rows of small black spines directed backwards," and further, that " the anal end is somewhat impressed, contoured by a variable number of fleshy points or tubercles, some of which bear also chitinous spines." Neither of these characters is present in the fully grown larvae of this species, nor according to Mik in those of *U. cardui* ; in his description of the larvae of this species he says they showed " keine Spur von Dornchen " and " die Larve ist also völlig kahl, glatt " ; as far as can be judged from the descriptions of the larvae of *U. cuspidata* and *U. quadrifasciata* given by Goureau and Dufour, the larvae of these species possess neither spines nor anal tubercles. The larvae of these four species differ therefore from the majority of Trypaneid larvae in these two features, which, according to Bezzi, are possessed by Trypaneid larvae in general.

In colour the fully grown larva is pale creamy white, except at the ends ; the two anterior segments are reddish brown, and the posterior segment is pale yellow round its anterior border, merging into a very dark chestnut-brown, almost black, colour on its posterior surface ; the two areas surrounding the spiracles are lighter in colour.

The segmentation of the larva is well defined except at the anterior end ; Bezzi states that the number of segments in Trypaneid larvae generally is usually fourteen. I have been able to distinguish only thirteen segments in these larvae, and Goureau regarded the larvae of *U. cuspidata* as probably possessing twelve segments, excluding the head ; there may be a fusion of two segments in the cephalic region of these *Urophora* larvae. On the ventral surface of the middle segments there are indications of creeping-pads (Kriechschwielen).

The mouth appears as a slit whose long axis is dorso-ventral ; the antennae and sense-organs are difficult to make out on fully grown larvae, in fact I have never been able to make them out satisfactorily ; probably they are retracted into the body together with the cephalo-

pharyngeal apparatus when chitinisation of the oral segment takes place. They can be observed on larvae about 7–8 weeks old, but they are very minute, measuring about 12μ in length and 8μ in diameter; in larvae of this age there can be seen in addition, a number of small papillae bordering the dorsal and dorso-lateral lobes of the mouth. The fine radiating grooves which surround the mouth have already been referred to.

The complete cephalo-pharyngeal skeleton consists of three pairs of sclerites and an unpaired V-shaped sclerite. The mandibular sclerites or "great hooks" each possess a prominent anterior tooth, a smaller median tooth, and a basal tooth or spur, and each sclerite is perforated near the base by a small aperture; Hewitt (1907) described a similar perforation in the corresponding sclerites of the larva of *Anthomyia radicum* L. The mandibular sclerite articulates with the intermediate or hypostomal sclerite, which in *U. solstitialis* appears to be fused with the posterior or cephalo-pharyngeal sclerite; in this latter sclerite there is a deep indentation posteriorly between its dorsal and ventral prolongations, and these again are frequently bifurcated. With careful observation a membrane can be observed surrounding each prolongation extending some distance behind them; a corresponding membrane is figured by Mik in *U. cardui*.

A V-shaped sclerite is situated beneath the hypostomal sclerites; each free end of the V articulates with a ventral projection of the hypostomal sclerite on each side, and the apex of the V is placed near the bases of the two mandibular sclerites (Fig. 8). It may be called the sub-hypostomal sclerite. The examination of a number of preparations of the cephalo-pharyngeal apparatus reveals numerous slight variations in size, shape, and amount of chitinisation of these structures; these variations are more especially noticeable in the posterior sclerite. Interposed between the mouth and the mandibular sclerites there is found another strongly chitinised body; this only becomes apparent towards the close of the feeding period, and probably consists of the closely apposed and chitinised sides of the oral lobes.

In appearance and structure, the anterior and posterior spiracles are very similar to those of *U. cardui* figured and described by Mik; he described the anterior pair as being situated on the second segment (of the pupa). In *U. solstitialis* the anterior pair are placed dorso-laterally on the third apparent segment, and near its posterior border, about 0·3 mm. apart (Fig. 11). They are yellowish-brown in colour and do not project above the surface of the body; each spiracle consists

of three short papillae joined together at the base ; a slightly elliptical aperture is situated at the apex of each papilla, and these lead into the spongy felted-chamber (Filzkammer) which is in communication with the longitudinal canal. In some preparations I have been able to distinguish a membrane between the inner boundary of the felted-chamber and the longitudinal tracheal canal, and this is perforated by a small aperture 4μ in diameter (Fig. 15).

The posterior segment bears the anus and the posterior spiracles ; it is wider on the ventral aspect, where the anus is situated in the mid-ventral line, than on the dorsal and lateral aspects. A shallow horse-shoe shaped depression is present on the posterior surface of this segment at a short distance from its dorsal and lateral borders, and a slight depression, situated just dorso-median to the posterior spiracles, is also apparent. The surface is marked with a number of very fine grooves or lines which run in various directions ; round the spiracles they are arranged concentrically. A number of small darker-coloured areas may be observed on various parts of this surface, particularly on the ventral portion ; they indicate the points of attachment of muscles (Fig. 12).

The posterior spiracles are situated slightly nearer the dorsal than the ventral aspect, as in the larva of *U. cardui*, and they are about 0·7 mm. apart. They are larger than the anterior spiracles and darker in colour ; anatomically they are very similar to these but the apertures are more definitely elliptical in shape and are arranged in a radiate manner. They project very slightly from the body surface (Fig. 14). In one instance a variation in the number of apertures in the left posterior spiracle of a larva was noticed ; this spiracle possessed four apertures instead of the usual number three.

In concluding this description of the larva, the small number of lobes or papillae of the anterior spiracles as compared with the number on the anterior spiracles of many other Trypaneid larvae may be noted ; Banks (1912) describes nine Trypetid (Trypaneid) larvae whose anterior spiracles each bear a large number of lobes varying from about fifteen in *Ceratitis capitata* Wied. and *Rhagoletis pomonella* Walsh, to thirty-eight lobes in *Dacus ferrugineus* Fab. ; whereas in the larva of *U. solstitialis* and *U. cardui* (Mik) three lobes only are borne on each anterior spiracle.

Description of the pupa.

The pupae vary considerably in size as may be expected from the great variation in size exhibited by the larvae; among ten selected for measurement the largest measured 4·3 × 2 mm. and the smallest 2·8 × 1·4 mm., the average size of the ten pupae was 3·6 × 1·7 mm. In shape they are cylindrical, obtuse or bluntly pointed at the anterior end, and obliquely truncate dorso-ventrally at the posterior end; during pupation there is little or no alteration in length but the pupa is more parallel-sided than the larva (Fig. 10).

The colour varies from light yellow to dark reddish-brown; the majority, however, are of the lighter colour, and in all specimens the first three or four segments and the last one are much darker in colour than the intermediate ones. These anterior and posterior segments vary in colour from reddish-brown to dark chestnut-brown or black. On the surface of the puparium a number of anastomosing wrinkles are seen which vary in direction in different parts of the same; they are more or less parallel to the segmental grooves on the dorsal and ventral aspects of the middle-segments, but at the sides they run obliquely. These wrinkles are darker in colour than the smooth portions of the puparium, and represent wrinkles of the larval skin which become more apparent through shrinkage undergone during pupation.

At the anterior end the radiating grooves which run in a backward direction from the mouth are very noticeable, and the anterior spiracles are visible under a good lens as two brown spots in the position described in the larva.

The posterior aspect exhibits the same features as in the larva and requires no further description; there is a variable amount of wrinkling around the margin of the last segment, but well-marked ridges similar to those figured by Mik on the posterior surface of the pupa of *U. cardui* are not apparent. The pupae have a dull glistening appearance; Mik described the appearance of the pupa of *U. cardui* as "etwas seidenglänzend."

Connold's figure of the pupa of *U. solstitialis* is incorrect; the object figured resembles a syrphid larva.

Effects of larvae on production of seeds in galled flower-heads of Centaurea nigra *L.*

In order to obtain some definite information concerning the effects of the *Urophora* larvae on the production of seeds, a number of plants were collected and a series of counts made. Perfect accuracy is not claimed for the results obtained, as, owing to various circumstances, the conditions were such that a high degree of accuracy could not be expected. The plants were collected on Oct. 1st, 1913, that is to say, late in the season, when many of the seeds had certainly escaped, in addition to those probably taken by seed-eating birds. As the plants, however, were collected within a space of about twenty square yards, it may be assumed that these factors affected all the plants in this area in a more or less similar manner. Fifty plants, single shoots cut off at the ground-level, were selected, and these bore 147 flower-heads; twenty-four of these, however, were immature and therefore disregarded. Of the remaining 123 heads, seventy-four or 60·1 per cent. contained galls, whilst forty-nine or 39·8 per cent. were ungalled. Nine of the galled heads contained no seeds, and these for the purpose of calculation were neglected; from the remaining sixty-five galled heads 1077 seeds were obtained, averaging 16·5 seeds per head.

Twenty-five of the forty-nine ungalled heads were rejected for various reasons; ten contained no seeds whatever, whilst the seeds in the remaining fifteen were more or less eaten by seed-eating lepidopterous and free living dipterous larvae.

From the twenty-four ungalled heads that were considered countable, 755 seeds were obtained, averaging 31·4 seeds per head. Thus showing a reduction of nearly 50 per cent. (31·4 – 16·5) in the number of seeds produced in the galled heads, compared with the number produced in ungalled heads. The number of seeds (31·4) per head obtained from these particular heads is very low, and would be misleading if one were to assume that this was the average number obtainable from normal well-grown flower-heads of *Centaurea nigra.*

It may be explained that the soil on which the above plants were grown was very poor and stony, and the specimens were gathered late in the season when some of the seeds had escaped, as stated above; these considerations may help to explain the small average number of seeds per head.

By way of contrast may be quoted the number of seeds obtained from some flower-heads of the knapweed gathered by Prof. Hickson,

near St Bees, Cumberland, early in September of the same year. These results give a more accurate idea of the number of seeds present in well-developed flower-heads of this weed.

From twenty-seven flower-heads 2045 seeds were obtained; averaging 75·7 seeds per head; one flower-head contained 103 seeds, whilst the smallest number found in one head was sixty-two. A collection of flower-heads was also made at Port Erin, Isle of Man, early in September, and one head yielded the very high number of 109 seeds.

These figures indicate the large number of seeds that may be ripened in a fully-developed flower-head of this plant, and it may be of some interest to make an estimate of the number of seeds that a single plant of this species is capable of producing.

Several plants of the knapweed were grown for experimental purposes last summer, in my garden at Northenden, in Cheshire, and one of them gave rise to several particularly lusty shoots; one of these bore fifty-one flower-heads, and if it is assumed that each head ripened only thirty-one seeds (the average number obtained from heads gathered at Prestatyn) we obtain the number 1581 seeds producible on one single shoot. A vigorous plant growing in good soil would give rise to at least three or four shoots, so that several thousands of seeds may be produced on one plant. Long (1910, p. 175) remarks that "knapweed (*Centaurea nigra* L.) known under a variety of names as Hardheads, Hardhack, Blackhead, is a too common weed of pastures and meadows," and in view of the above estimate of its seed productivity, this is not surprising. Were it not for the fact that several insect larvae and birds feed on its seeds it would be even still more abundant.

A germination experiment was also made to test the difference, if any, between the seeds ripened in galled heads and those in ungalled heads, with regard to their vitality or germinative power.

A large number of seeds from the ungalled flower-heads collected in October were taken and mixed together; after rejecting all seeds that showed evidence of injury, *i.e.* indications of having been partially eaten by other insect larvae, 100 seeds were separated without exercising any selection. These were placed on moist blotting paper in a seed-germinating apparatus, and kept at a temperature of 26° C. From these seeds eighty-nine seedlings were obtained, equivalent to 89 per cent.

In a similar manner 200 seeds were selected from the galled flower-heads that were collected on the same date and these were placed in the germinating apparatus at the same time. That is to say, both lots of seed were collected at the same time and place, and germinated under

similar conditions. Of these seeds only fifty-seven germinated, equivalent to 28·5 per cent.

The percentage of germination in the seeds tested from galled flower-heads was thus reduced 60·5 per cent. owing to the presence of *Urophora* larvae in the receptacles of the flower-heads; probably the nourishment that normally goes to the developing seeds, becomes diverted to the growing larvae and also to the formation of the thick-walled woody gall.

This experimental result coincides with the indications given by the appearance of the seeds usually obtained from galled flower-heads; many of these seeds are shrivelled, and smaller than the majority of those collected from ungalled heads.

Thus in addition to a reduction in the number of seeds produced in the galled flower-heads, the number of seeds capable of germination is also reduced. Taking into consideration the smaller number of seeds obtained from infected flower-heads, and also the reduced vitality of those actually ripened, as indicated by the above experiments, it may be stated that the presence of the larvae of *Urophora solstitialis* in the flower-heads of *Centaurea nigra* reduces the number of effective seeds in these infected heads at least fifty per cent.

Although the Trypaneidae or fruit-flies are justly regarded as injurious from the economic standpoint because many of them are very destructive to various cultivated fruits and to vegetable life in general, yet those species whose larvae feed on, or in, the stems, leaves, flower-heads and seeds of the weeds of cultivated land, may be regarded, from the agricultural point of view, as beneficial. The result of the activities of their larvae is that the plants fed upon are affected adversely, and in many cases, as in the case of the species considered in this paper, the production of seeds is directly checked; the distribution of the weeds attacked is therefore restricted, even if only to a moderate extent.

The question occurs as to whether destructive weeds could be appreciably reduced by encouraging certain species of insects which attack the seeds thereof. It is hoped that the present paper will suggest to others the possibilities for further research and experiment in this field of enquiry, which is fully worthy of attention from the economic entomologist.

Parasites.

Three species of Chalcids and one Braconid emerged from the flower-heads in May 1912 and 1913, but in very small numbers; presumably some of these were parasitic in the *Urophora* larvae. The Chalcids have not as yet been identified; Mr Claude Morley, however, has kindly named the Braconid, it is *Bracon minutator* Fab., and probably parasitic on the lepidopteron *Parasia metzneriella* Stt. Brischke (1882) records this parasite from the larvae of *Sesia* (*Bembecia*) *hylaeiformis* Lasp. (not a British species); Marshall (1885) states that Elisha bred two females of this Braconid from the lepidopteron *Argyrolepia zephyrana* Tr. It therefore appears probable that *Bracon minutator* is parasitic on lepidopterous hosts. Under the description of *Bracon variator* Nels., Marshall says "It is doubtful whether this *Bracon* is a parasite of certain small curculios (*Cionidae*) or of flies of the genus *Trypetâ*" and further on he states that "Giraud records *B. nigripedator* Nees, from *Urophora solstitialis* L.; and Fitch once obtained a Bracon, now lost, from galls of *Centaurea* inhabited by the same fly."

With regard to these records of parasitic hymenoptera obtained from flower-heads of *C. nigra* and other composite plants, I would remark that unless it is proved that dipterous larvae and pupae alone are present therein, it is incorrect to state definitely that they are the hosts of the parasites obtained, inasmuch as a single flower-head may contain the larva or pupa of a lepidopteron in addition to those of diptera.

Kaltenbach states that *Eurytoma aterrima* Schr. (*verticillata*) is parasitic on *U. solstitialis*, and probably also *Trigonoderus amabilis* Walk. and *Semiotellus* (*Semiotus*) *diversus* Walk. Walker (1833–37) records these three Chalcids from near London but does not give their hosts.

Mr C. Morley (1908), from a quantity of dried heads of *Centaurea nigra* gathered in March, 1907, beneath fir-trees, obtained both sexes of a *Pteromalus* in May, and numerous *Bracon minutator* ♂ in April; he also obtained one specimen of *Pimpla sagax* Htg. on April 26th, and of this specimen he says (p. 81) "Its host was undoubtedly *Urophora solstitialis*, many of which emerged during the following June; unless, of course, its presence there were purely accidental and its true association were with the overhanging conifers, in which case it would surely have shown itself in the jar in the course of the preceding month." In view of the fact that with one exception, viz. *Anthonomus pomorum* L. all the recorded hosts of this ichneumon are lepidopterous, and as the

larvae of at least three species of lepidoptera have been recorded from *Centaurea nigra*, the evidence adduced by Mr Morley that *U. solstitialis* is a host of *Pimpla sagax* is hardly conclusive. It seems more probable that the single specimen obtained by him either emerged from a lepidopterous host, or that its presence in the flower-heads was accidental, as he indeed suggests.

Five hymenopterous larvae, probably of a Chalcid, were obtained from 259 larval chambers examined in October, 1913, equivalent to two per cent. Each of these larvae occupied a chamber that had previously contained a *Urophora* larva. In one case there was direct evidence that the hymenopteron had fed on the dipterous larva, as the parasitic larva was inside a portion of the cuticle of the *Urophora* larva and had evidently been feeding on the latter. From material in hand I hope to be able to breed out a further supply of these Chalcids, to get them identified, and to obtain the percentages.

Remarks on Gall-formation and on other inhabitants of the flower-heads of Centaurea nigra.

The process of gall-formation in the flower-head of the host plant exhibits some very interesting features. To determine whether the formation of this gall is induced mechanically by the feeding habits of the larva, or whether the latter secretes an irritant fluid which causes the abnormal growth, would require further observations. The tissues of the receptacle near the ovule attacked commence to swell up shortly after the larva begins to feed, and in a comparatively short time the size and shape of the future hibernating chamber of the larva are marked out in the gall, although the larva is far from its full size. In a longitudinal section of a gall that contained a larva about four weeks old and 1·3 mm. in length, the outline of the future hard-walled chamber could be clearly distinguished. A thin layer of woody tissue is developed within the hypertrophied tissue that the larva is feeding on, and a thick layer of soft nutritive tissues is left within this woody layer and the space occupied by the larva (Fig. 5); this nutritive layer is connected at the base of the chamber with the vascular system of the plant.

During the period that elapses between this stage and the attainment of the fully fed one, the larva gradually eats away this layer of soft tissue, until finally when the growth of the larva is complete the layer of soft tissue has been absorbed and the hard wall of the chamber reached (Fig. 6); meanwhile the wall becomes more lignified and

harder, and the tissue between adjacent chambers that have fused together also becomes drier and harder, and in this manner the hard plurilocular gall is produced (Figs. 3 *a* and 4).

The interesting fact revealed during this process is that the stimulus produced by the presence of the larva in the embryonic tissue of the developing ovule, and in the hypertrophied receptacle, induces a reaction of the plant to form a structure that is possibly protective to the plant itself, but which is also at the same time exactly suited to the requirements of the fully-grown larva, forming as it does a very efficient means of protection to the larva during the prolonged period of hibernation.

Several larvae, pupae, and imagines of *Parasia metzneriella* Stt. were obtained from the flower-heads during this investigation; 30 % of the heads examined were found to contain these lepidopterous larvae. By far the greater number of larvae were found in chambers that had originally been made by *Urophora* larvae, and it is a subject for further investigation to find out what becomes of the original occupants of these chambers.

Eleven larvae of an unidentified dipteron were found feeding on the ripening seeds; they were found in 9 per cent. of the heads examined. Small orange-coloured larvae of a Cecidomyid were very abundant, almost every flower-head examined contained several specimens.

A lepidopterous larva which differed from that of *P. metzneriella* was found feeding on the seeds in 25 per cent. of the flower-heads collected by Prof. Hickson at St Bees; as the moth has not yet emerged, I have not been able to identify the species to which it belongs.

The larvae of two species of *Coleophora*, *C. alcyonipennella* Koll. and *C. conspicuella Z.* are recorded from *Centaurea nigra*. The larvae found at St Bees may belong to one of these two species.

SUMMARY.

1. A description of *Urophora solstitialis* L. and an account of its systematic position and geographical distribution are given, together with an abstract of the work of previous observers on this species.

2. A list of its British and continental food-plants is given; the records of the latter show that on the continent the larvae feed on various species of thistles, and on three species of *Centaurea*, but not on *Centaurea nigra*, whereas with the exception of one record of their occurrence on *Serratula tinctoria*, the larvae in this country are recorded as feeding exclusively on *Centaurea nigra*.

3. The life-history, ovipositor, and method of oviposition are described, and descriptions and figures of the ova, larvae, and pupae are given. The life-history is summarised on p. 148.

4. It is shown that owing to the formation of galls induced by larvae of *U. solstitialis* in the flower-heads of this weed a reduction in the number of seeds is effected amounting to about 50 per cent. in the heads examined. The germinative capacity of the seeds produced in these galled heads was also adversely affected. In the germination experiment described 60·5 per cent. fewer seeds germinated from galled flower-heads of *C. nigra* than from ungalled ones. At a moderate estimate the number of seeds rendered non-effective in galled flower-heads of *C. nigra* is placed at 50 per cent. It is pointed out that Trypaneids, whose larvae adversely affect the weeds of cultivated land, may be regarded as beneficial.

5. A short account and discussion of the recorded parasites of *U. solstitialis* is given.

6. Some interesting features observed in the process of gall-formation are referred to, and a few notes are added on some other insect inhabitants of the flower-heads of *C. nigra*.

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Summary of results obtained from the examination of 50 *shoots of* Centaurea nigra *gathered Oct.* 1*st*, 1913, *at Prestatyn, North Wales.*

45 of the 50 shoots carried galled flower-heads, *i.e.* 90 % were infected.

No. of heads obtained from 50 shoots, 147 ; average, 3 per shoot. 24 were immature ; of the remaining 123, 74 (60·1 %) contained galls and 49 (39·8 %) were ungalled.

No. of heads	No. of larval chambers per head
1	11
1	10
1	9
2	8
3	7
5	6
6	5
13	4
14	3
10	2
18	1
74	Total 66

Total No. of larval chambers, 259 ; average, 3·5 per head

Total No. of larvae obtained, 170

No. of chambers found either empty or containing hymenopterous or lepidopterous larvae, 89.

No. of seeds obtained from 65 galled heads, 1077 ; average 16·5 seeds per head.

No. of seeds obtained from 24 ungalled heads, 755 ; average, 31·4 seeds per head.

200 seeds from galled heads on germination yielded 57 seedlings (28·5 %).

100 seeds from ungalled heads yielded 89 seedlings (89 %).

Remarks. The greatest number of larval chambers found in a single flower-head of the above fifty examined was eleven, and this number occurred only once ; eighteen heads contained only one larval chamber each. The greatest number of chambers found in one head during the investigation was thirteen.

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EXPLANATION OF PLATES.

PLATE XI.

Fig. 1. *Urophora solstitialis.* Female, ×5; ovipositor partially extended.

Fig. 2. Vertical section through young flower bud of *Centaurea nigra*, showing eggs *Ov.* of *U. solstitialis in situ.* 24 hours after oviposition. ×9.

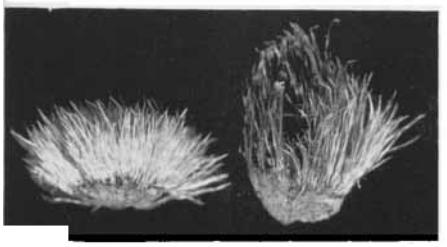
Fig. 3. A. Ungalled receptacle of *C. nigra.* × 2.
B. Galled „ „ „ „



1



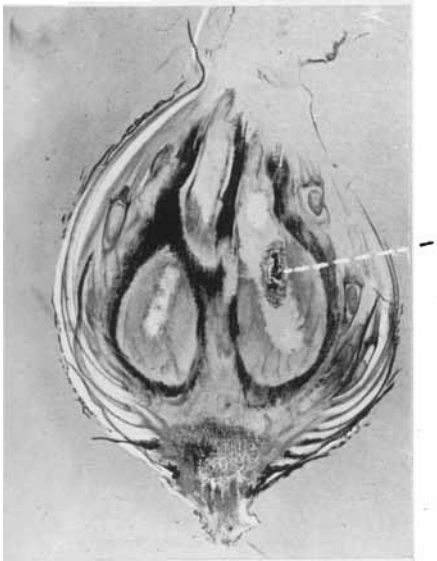
2



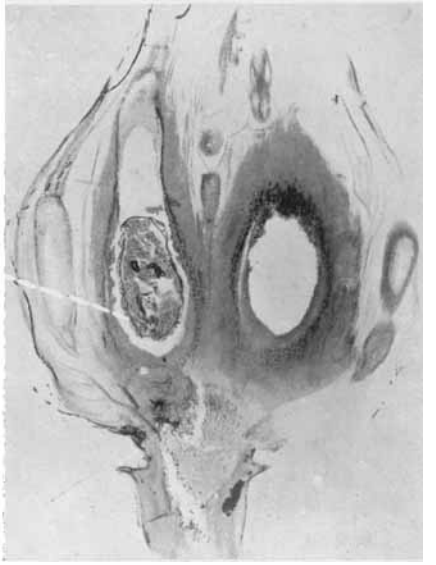
A 3 B



4



5



6

J. T. W. phot.

Urophora solstitialis.

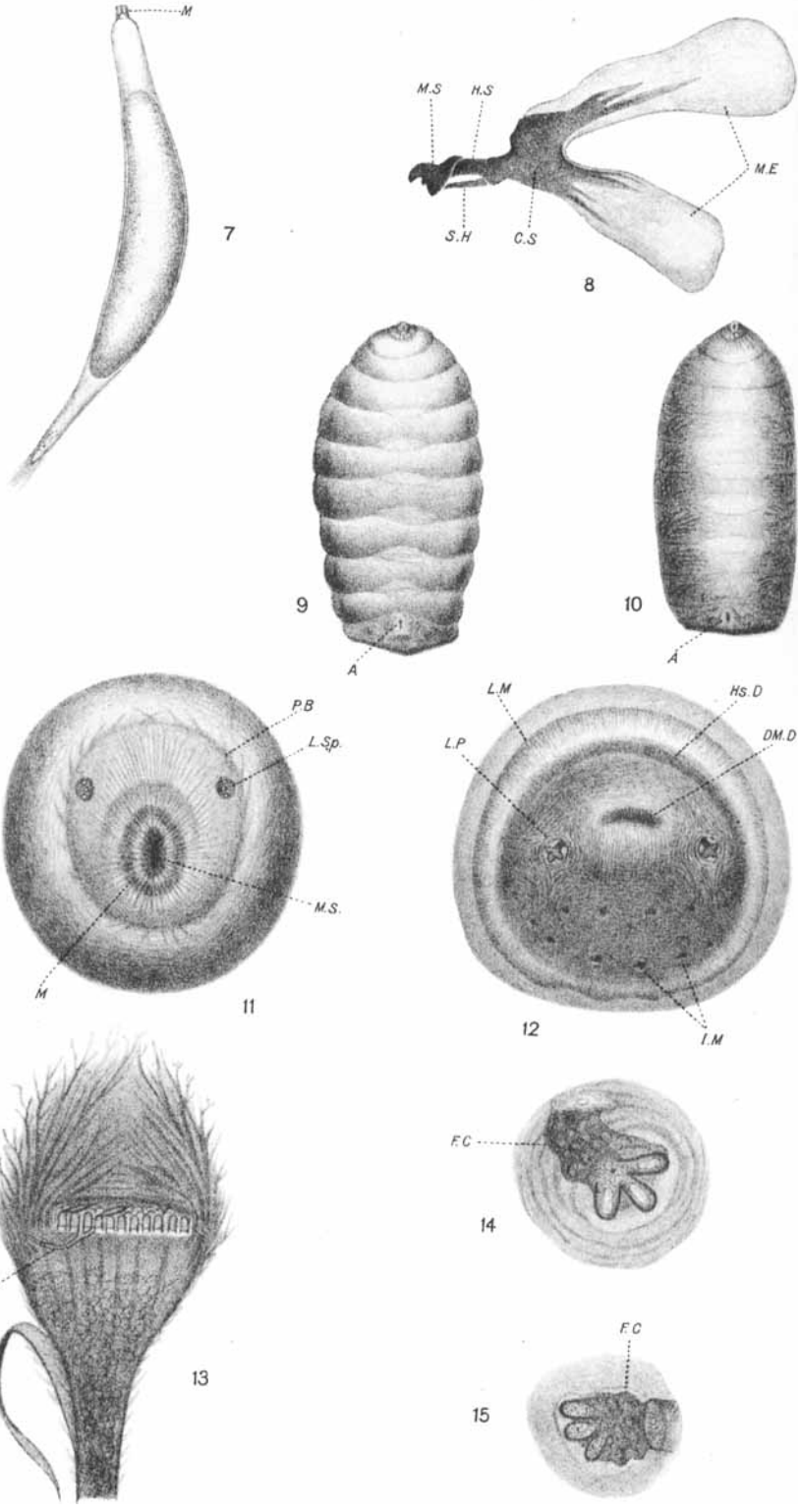

M
7
M.S
H.S
M.E
S.H
C.S
8
9
A
10
A
P.B
L.Sp.
M.S.
M
11
L.M
H.S.D
L.P
DM.D
12
I.M
P
13
F.C
14
F.C
15

Fig. 4. Vertical section through three galled flower-heads of *C. nigra* showing the chambers in which the larvae hibernate during winter, and where pupation takes place. The left hand one contains a pupa. ×2.

Fig. 5. Vertical section through a galled flower-head of *C. nigra*; the section shows the hard woody walls of two chambers; the right chamber contains a section of a larva and shows the thick layer of nutritive tissue that is separated from the remainder of the receptacle when the woody layer is developed. The section is slightly tangential, and the larva is younger than the one in Fig 6. ×5. *l.* section of larva.

Fig. 6. Section similar to Fig. 5 containing an older larva in the left chamber, the nutritive layer has been almost eaten away by the larva, and the woody wall reached. ×5. *l.* section of larva.

PLATE XII.

Fig. 7. Egg of *U. solstitialis*. 24 hours after oviposition. ×50; *m.* micropyle.

Fig. 8. Cephalo-pharyngeal skeleton of mature larva from the left side. ×120. *m.s.* mandibular sclerite; *h.s.* hypostomal sclerite; *c.s.* cephalo-pharyngeal sclerite with deep indentation between dorsal and ventral processes which exhibit further bifurcations; *s.h.* sub-hypostomal sclerite; *m.c.* membrane surrounding each process of the cephalo-pharyngeal sclerite.

Fig. 9. Mature larva, ventral aspect. ×10. The larva was slightly lifted upwards anteriorly bringing into view the mouth-slit and the anterior spiracles. *a.* anus.

Fig. 10. Puparium, ventral aspect. ×10. *a.* anal scar.

Fig. 11. Anterior view of mature larva. ×45. *p.b.* posterior border of third segment. *l.sp.* left anterior spiracle. *m.s.* mouth-slit with the dark chitinised sides of the oral-lobes. *m.* posterior margin of the chitinised area surrounding the mouth.

Fig. 12. Posterior view of last segment of mature larva. ×50. *l.m.* lateral margin of last segment *hs.d.* horse-shoe shaped depression. *dm.d.* dorso-median depression. *l.p.* left posterior spiracle. *i.m.* indications of muscle-attachments which appear as dark areas on the surface.

Fig. 13. Vertical section of flower-bud of *C. nigra* showing the passage *p.* made by ovipositor during the process of oviposition. ×5. The ovipositor had passed on both sides of the third floret from the left-hand side, as indicated in the drawing.

Fig. 14. Right posterior spiracle of mature larva viewed from above. ×200. *f.c.* felted-chamber (Filzkammer).

Fig. 15. Left anterior spiracle of nearly mature larva viewed from above. ×200. *f.c.* as Fig. 14.

NOTE. In figs. 14 and 15 the felted-chamber (*f.c.*) is displaced laterally. In the larva the chamber is directly beneath the spiracular openings.

Figs. 7, 8, 11, 12, 14, and 15 were drawn by the aid of the Zeiss-Greil drawing apparatus.