THE FAUNA OF WRACK BEDS.

Henry J. Egglishaw

Thesis for the degree of Ph.D.

September, 1958.

CONTENTS

PART I.

THE ENVIRONMENT

Chapter I

THE WRACK BEDS.

Wrack beds are accumulations of seaweeds of various kinds that have become detached from the rocks on which they have grown and have been cast up on to the sea-shore. If such accumulations are formed beyond the high tide level, they may remain but little disturbed for several days or even for months. Here, as they gradually decompose, these wrack beds become the home and breeding place for many invertebrate animals. It is with these animals that this thesis is concerned. The most prominent of them are various species of flies, beetles and amphipods, and with them there occurs, less obviously, various mites, oligochaetes and nematodes. Over and above these regularly occurring animals there are numerous incidental visitors to the wrack beds.

Previous work on wrack fauna.

Wrack beds have long been known as good collecting grounds for insects and mites, and several lists of these two groups of animals found in them and in their vicinity have appeared in the literature. In Great Britain such lists, along with some ecological information, have been published by Yerbury (1919-22) (Diptera), Halbert (1920) (Mites) and Keys (1918) (Coleoptera); and similar papers dealing entirely or partly with wrack animals have appeared in other countries (e.g. Madsen (1936) studied various groups in Greenland, and Lindroth (1931) studied wrack insects in Iceland).

No serious study of the fauna or consideration of its special attributes appeared until 1945, when Backlund published the results of his observations on the wrack fauna of Sweden and Finland. Backlund's paper is extensive, the work for it being carried out, on and off, over a period of eleven years, and it deals with nearly three hundred samples taken from various places covering almost the whole of the Finnish and Swedish coasts where wrack beds occurred.

Types of wrack beds.

In his paper Backlund divides the wrack beds he investigated into three types according to size, calling them wrack strings, wrack flakes and wrack banks. These terms are very appropriate in describing the shapes of wrack beds and are adopted in the present work. Backlund's definitions are altered slightly to suit the wrack beds encountered in this study of their fauna.

Wrack strings are long, continuous or broken, stretches of wrack usually less than eight inches deep and twelve inches wide (photos. on page 4). They are usually found along the length of the high tide line and are formed perhaps only where there is a gently-rising shore extending several yards beyond the high tide line. Wrack strings never become soft because they cannot retain water, and at times during dry weather their wrack may be hard and brittle.

Wrack flakes have about the same depth but are broader than wrack strings (photo.on page 5). They are formed either on fairly level parts of the shore or in shallow depressions.

Wrack banks are larger accumulations of wrack, more than eight inches deep and twelve inches wide (photos. on pages 5 and 6). They are most often formed at the foot of cliffs and boulders where the wrack piles up because it cannot be pushed farther back or scattered to form wrack strings or flakes. Wrack banks decompose rapidly and soon become very soft. Their deepest layers are always wet.

Although the three types of wrack beds approach each other in size, the physical differences and the differences in fauna between the extreme forms - wrack strings and large wrack banks - are very distinct.

<u>The wrack beds studied.</u>

Most of the field work for this thesis was carried out

WRACK STRINGS

Whitburn

Whitburn

Llandudno

Llandudno

WRACK FLAKE

Whitburn

WRACK BANKS

Whitburn

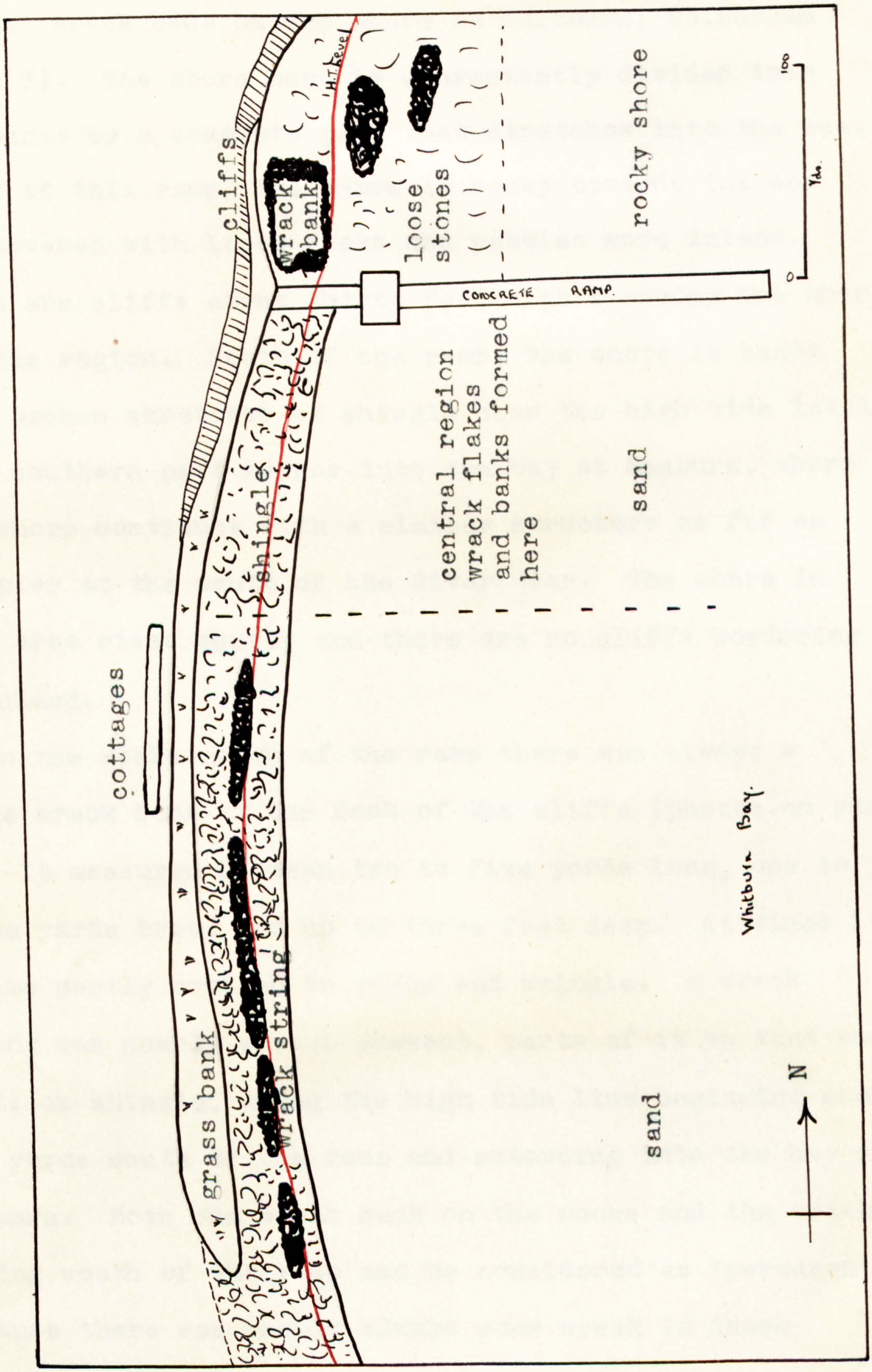
WRACK BANKS

Whitburn

Whitburn

St. Mary's
Island

Plan of the shore at Whitburn, Co. Durham.



on the wrack beds on the shore at Whitburn, Co.Durham (page 7). The shore here is conveniently divided into two parts by a concrete ramp that stretches into the sea. North of this ramp, the shore is rocky towards the sea and covered with loose rocks and pebbles more inland. There are cliffs about thirty feet high flanking the shore of this region. South of the ramp, the shore is sandy with broken stretches of shingle near the high tide level. This southern part merges into the bay at Seaburn, where the shore continues with a similar structure as far as the pier at the mouth of the River Wear. The shore in this area rises gently and there are no cliffs bordering it inland.

On the rocks north of the ramp there was always a large wrack bank at the foot of the cliffs (photos.on page 5). It measured between two to five yards long, one to three yards broad and up to three feet deep. At times it became partly covered in rocks and shingle. A wrack string was nearly always present, parts of it on sand and parts on shingle, along the high tide line beginning about 150 yards south of the ramp and extending into the bay at Seaburn. Both the wrack bank on the rocks and the wrack string south of the ramp can be considered as 'permanent' because there was nearly always some wrack in these positions. Other wrack banks were found seawards of the 'permanent' one on the rocks (photos. on page 6), but they remained for only a few days at the longest.

Between the positions where this wrack bank and wrack string were formed is a stretch of shore, 150 yards long, on which all three types of wrack beds were continually being formed at various intervals between the high tide and low tide levels. This region is referred to here as the central region of the Whitburn shore. The wrack beds formed in this region remained for varying periods lasting from several hours to about three weeks. The shore here rises more gradually than the rest of the Whitburn shore and, at times, even contained large, shallow depressions. It was the only region where wrack flakes were formed at Whitburn (photo. on page 6).

The variation in type and permanency of the wrack beds found within a stretch of about 400 yards of shore at Whitburn made this locality a very suitable one for carrying out a study of wrack fauna.

The wrack beds at Whitburn were visited regularly once or twice a week throughout the period October,1955 to April,1958.

Other wrack beds investigated were found on the mainland opposite St.Mary's Island, Northumberland, some 10 miles north of Whitburn. Here, large wrack banks, two to three feet deep, were formed at the base of some cliffs (photo. on page 6). No wrack strings or wrack flakes were ever found here, and the occasional small clumps of wrack which were sometimes seen on the shore remained for only short periods. These wrack banks near St.Mary's Island were visited once or twice a week from September,1955 to March,1956, and thereafter occasionally until April,1958. Since only large wrack banks were formed here, their fauna could easily be compared and contrasted with the fauna found in the three kinds of wrack beds occurring at Whitburn.

All of the wrack beds found at Whitburn and near St. Mary's Island were composed entirely, or almost entirely, of Laminaria and Fucus. Sometimes there were small amounts of other seaweeds present and sometimes various amounts of other organic and inorganic tidal debris.

All of the Durham coast and the Northumberland coast south of St.Mary's Island was examined at some time, but no other large area of wrack beds, similar to that occurring at Whitburn, was seen. Small stretches of wrack strings were sometimes found, and on the shore at Hart there once occurred a bank of debris among which was scattered a small amount of wrack. Temporary wrack banks were sometimes seen in the harbour at Cullercoats.

In August,1956, a wrack string at Llandudno, Wales, was examined (photos.on page 4). It was about 400 yards long and was composed of Laminaria and Fucus.

In August,1957, a wrack string on the Furness coast, Lancashire, was examined. It was made up entirely of a filamentous green alga, in clumps of about one foot long and four to six inches deep.

At Bamburgh, Northumberland, a wrack string of Laminaria and Fucus was examined on 3rd September, 1957.

The temperature of the wrack beds.

Backlund (1945) discussed the physical and chemical properties of wrack and wrack beds fairly thoroughly and mentioned other works on the subject that may be consulted. Only the temperature of the wrack beds at Whitburn was measured in the present study.

Because of the decomposition of the wrack and the breakdown of complex organic compounds, the temperatures of the various wrack beds were higher than those of the surrounding air. When the wrack beds were first formed and before decomposition had taken place, the temperature was roughly the same as that of the air. In the wrack banks after two or three days, however, when decomposition was taking place, the temperature rose to as much as 17°C. above the surrounding air. The greatest increase occurred in compressed wrack where the decomposition products could not drain away.

If the wrack banks ~~banks~~ became contaminated with sand, as those formed in the central region at Whitburn frequently did, the temperature fell to about that of the air. The sand separates the wrack, aids drainage, and absorbs heat from the decomposing wrack, all of which lowers the temperature of the wrack banks.

Wrack strings and flakes being shallow wrack beds lying on sand and shingle at Whitburn were well drained and were usually about the same temperature as the surrounding air. On warm, sunny days, however, they were up to 5°C. higher than the air temperature, having presumably absorbed radiated heat.

Some actual temperatures of the wrack beds taken with a mercury thermometer are now given.

Date.	Temperature in degrees C.		
	Air	Wrack	
1. Fresh, wet wrack banks.			
11.ix.56	15.0	14.5	
24.ix.56	14.5	14.5	
2. Decomposing wrack banks in summer.			
10.ix.56	15.0	32.0	12 ins. from top and 12 ins. from side.
		25.0	4 ins. from top and 4 ins. from side.
11.ix.56	14.0	31.0	6 ins. from top
1.vii.56	13.0	21.0	6 ins. from top

3. Decomposing wrack banks in winter.

17.xii.56	5.0	21.0	6 ins. from top
24. i.57	6.5	13.0	do.
25. ii.57	4.5	20.0	do.

4. Parts of wrack banks contaminated with sand compared with parts uncontaminated.

17. ix.56	15.0	16.0	contaminated
	15.0	24.0	uncontaminated
1. x.56	16.5	15.0	contaminated
	16.5	27.0	uncontaminated

5. Wrack strings

11.ii. 57	3.5	2.5	
6.vi. 56	7.0	6.5	
16.vii.56	18.5	23.0	a sunny day
8.vii.57	17.0	22.0	a sunny day

Seasonal alterations in the amount of wrack.

The 'permanent' wrack beds at Whitburn were largest after the high autumn equinoctial tides had cast up a great deal of wrack that had grown in the summer months. For several weeks previous to these tides the large amounts of wrack could be seen floating in the sea in the bay and large temporary wrack banks were formed below the high tide level on the shore. Eventually the wrack was cast up beyond the high tide level. The wrack beds formed remained throughout the winter. Additional wrack was added to them now and again, but in general they gradually decreased in size. By April the wrack string was dry and brittle and remained very much in this state until the autumn.

Methods.

Between two and three hours were spent observing and collecting animals on each visit to the wrack beds at Whitburn and to those near St.Mary's Island. Adults were collected from the wrack beds with an aspirator and insects in flight were caught with a kite-net. Wrack material containing larvae etc. was removed with a trowel and placed in 2-lb.size Kilner jars.

These jars were found the most suitable for field work and also for rearing larvae in the laboratory. They were a convenient size to handle, and their large mouths enabled the entangled wrack materal to be placed easily inside the jars. The glass lids of the jars could be removed and replaced by perforated cardboard when necessary. The jars were large enough to allow larvae that had been collected with wrack material to mature without further attention.

The photographs were taken with a Nicca 3-S camera fitted with an f.2 Nikkor lens on Ilford FP3 film which was developed in Johnson's Fine Grain developer. They were printed on Kodak bromide paper. The diagrams of the young stages are printed on Kodak bromide airmail hard paper.

Scope of the present work.

The thesis has been divided into a number of parts. Part I, which is concluded by this section, is concerned with the environment studied. Barts II, III and IV will deal with the animals that breed in the wrack beds or are closely associated with them in some other way and part V will deal with some effects of the environment on the animals present. The thesis concludes with part VI, a list of the animals found in the wrack beds.

Although all the groups of animals that were found in the wrack beds receive some mention, it is with the insect fauna that the thesis is most concerned. Of the insects present, the most intensive studies were carried out on four species of the fly family Coelopidae and on other three flies belonging to different families. All or some of the young stages of these seven species are described and figured in the thesis from material collected in the field or bred in the laboratory, and the field life-history of each species is discussed. Less intensive studies were carried out on several other species of flies closely associated with the wrack beds, on the beetles and on the mites present. Mention is made of the activities of the nematodes, amphipods and oligochaetes occurring in the wrack beds. The parasites and predators of the wrack animals are also dealt with.

PART II.

STUDIES ON THE FAMILY COELOPIDAE.

Chapter II

SYSTEMATICS.

1. Introduction

The Coelopidae are a small family of acalyptrous flies, species of which breed in wrack beds found on the shores of temperate and sub-arctic regions of both the Northern and Southern Hemispheres. Five species of the family occur in Britain. Their classification is as follows, synonyms being placed in brackets.

Family COELOPIDAE (Phycodromidae)

1. OEDOPAREA (Heteromyza, Heterochila) buccata (Fallén).
2. ORYGMA luctuosa Meigen.
3. MALACOMYIA (Phycodroma, Malacomyza) sciomyzina (Haliday).
4. COELOPA pilipes Haliday (frigida Meigen).
5. COELOPA (Fucomyia) frigida (Fabricius) (gravis, simplex, parvula Haliday, eximia Stenhammar).

This list differs from the one given by Kloet and Hincks (1945). Heterochila is added as a synonym of Oedoparea to concur with various authors; C. eximia Stenhammar is given as a synonym of C. frigida (Fabricius) according to the thesis of Mayhew (1939); and C. parvula is also given as a synonym of C. frigida (Fabricius) since its description (Haliday 1833) falls within the variation of structure now known to occur in the latter species.

Malacomyia sciomyzina was the only species of the five not encountered while the present study was made. This thesis is concerned with Coelopa frigida, C. pilipes, Orygma luctuosa and Oedoparea buccata.

2. The general appearance of the adults.

The diagnostic features of the family Coelopidae are given by Hennig (1937), by Seguy (1934) and in less detail by Colyer and Hammond (1951). The only detailed morphological investigation carried out on the adults of the family is that of Mayhew (1939) on Coelopa frigida and C. pilipes. Hennig (op. cit.) gives short descriptions of the adults of these two species and also of Malacomyia sciomyzina and Orygma luctuosa. Hennig, unlike other dipterists (e.g. Oldroyd (1954) and Seguy (op. cit.)) does not consider Orygma luctuosa or Oedoparea buccata to be species of Coelopidae, although he deals with O. luctuosa in his paper on that family. Oe. buccata (as Heterochila buccata) is described briefly by Czerny in his work on the Dryomyzidae (1930). Seguy (op. cit.) gives the distinguishing features of each of the genera and species and includes a key to their identification which is suitable for students in the British Isles.

It is necessary here to give only an indication of the appearance of the flies and to mention the variation in size that was found in wild specimens.

Coelopa frigida, which is a very bristly, dorso-ventrally flattened black fly, is the most variable of the Coelopids in size and appearance. Males measured between 3 mm. and 9 mm. in length (from the front of the head between the antennae to the tip of the abdomen) and females between 3 mm. and 7 mm. (Mayhew (op. cit) showed that the larger flies had proportionately longer bristles, thus giving them a different appearance, which probably accounts for the several synonyms used for this species.)

C.pilipes closely resembles C.frigida, but instead of being bristly C.pilipes is covered with a fur of fine hairs. The females are most alike, but can be distinguished by their tibiae. The tibia of C. frigida bears a preapical bristle which in C. pilipes is only slightly developed and is obscured by dense hairs. C. pilipes is less variable in size than C. frigida, specimens found measuring between 4.5 and 7.5 mm.

Orygma luctuosa is also a black, dorso-ventrally flattened fly but it is not so hairy and bristly as the two species of Coelopa. It is more constant in size, males measuring 5.5. to 6.75 mm. and females 4.75 to 6.0 mm. long. It differs, too, in having a few long hairs on its metathoracic spiracles.

Oedoparea buccata is a light-brown to orange-coloured fly with a grey thoracic region and it is a little less flattened, dorso-ventrally, than the other three species. Male specimens ranged from 4.5 to 7.5 mm. long (less than one-fifth were under 6.5 mm.) and females from 4.5 to 6.0 mm. In May, 1957, however, a small group of this species was caught all of which were only 3.5 mm. long and had the abdomen grey as well as the thorax.

The males of each of the species are in general more hairy or bristly than the females, but the bristles used for purposes of classification in the Diptera are usually more developed in the females and more distinct since they are not so obscured by the general covering of bristles and hairs present in the males.

3. The young stages.

The young stages of each of these four species of flies consist of the egg, three larval instars and a pupa which is contained within a puparium.

The only detailed account of the external structure of these stages was given by Mayhew (1939) and concerned only C. frigida and C. pilipes, though he failed to find any real distinguishing features between the two species. A less detailed study of the stages of C. frigida was made by Elwes (1915) and brief descriptions of the mature larva and puparium were given by Hennig. The young stages of the other two species have received only little attention. Backlund (1945b) gave a brief account of the third instar larva and puparium of Oedoparea buccata and the only useful information available concerning Orygma luctuosa is the short description of a damaged puparium by Scott (1920).

Concerning C. frigida, it is sufficient here to give a description only of its third instar larva and puparium so that they may be compared with those of the other species of Coelopidae. This description will be followed by a discussion of the features that distinguish the larvae and puparia of C. pilipes and C. frigida, and a detailed account of the young stages of O. luctuosa and Oe. buccata.

4. The larva and puparium of Coelopa frigida.

The following account of the structure of the third instar larva of C. frigida is based on the thesis of Mayhew (1939). Further details have been added, particularly about the structures which differ from those found in the other genera of the family.

THIRD INSTAR LARVA.

Length 5.0 - 13.75 mm. When food plentiful, attains 10.0 - 13.75 mm. Breadth 1.6 - 1.8 mm. at widest point : greatest depth 1.7 - 1.9 mm. Shape cylindrical, anterior third tapering to head; blunt posteriorly. Colour white save for brown to black sclerotised regions. Body composed of the normal twelve segments, first segment indicated dorsally by the projecting antennae, segments 3 - 11 subequal in length (c. 1 mm.), segment 2 shorter and segment 12 only about half their length. First segment consists of two lobes separated by a median ventral groove at posterior end of which is mouth. In front it bears, one on each lobe, a pair of small, forwardly-directed, two-segmented antennae.

Posterior to these, on antero-ventral margin of each lobe, are the pair of 'maxillary palps', each appearing to consist of a sclerotised ring surrounding a central transparent segment. A third pair of sensory organs, the smallest and just visible at X100, are found, one on each lobe, lateral to the anterior margin of the grooves in which the bifurcate mouth-hooks are found. Each lobe bears a number of rows of sclerotised teeth; at sides of mouth-hooks are three rows of 9 - 10 teeth stretching right along ventral surface; anterior to mouth-hooks are a further two distinct rows of 12 - 15 teeth and anterior to these the teeth are in less distinct and gradually shortening rows to a point level with the maxillary palps. The teeth diminish in size anteriorly and laterally so that the largest teeth are found immediately to side and front of mouth-hooks.

Anterior spiracles situated laterally near posterior margin of second segment; each composed of 13 - 19 digitate processes at tip of which are found the spiracular openings. Posterior spiracles borne on backwardly directed projections from dorsal part of segment 12; peritreme dark brown and roughly kidney-shaped, the convex side directed outwards; from inside peritreme arises a ring, broken in region of cicatrix of about fifty branched processes; proximally each process is broad and thin but distally becomes more hair-like; there are three, roughly semicircular, spiracular slits, each of which is closed by a fine sclerotised grating.

Spines: ventral surface slightly swollen at margins of each segment 3-12; the swellings run transversely across larva and on them are borne, about twelve broken rows of small spines; those on segments 2, 3 and 4 are smaller than those on more posterior segments whilst in each group of rows the more anterior spines are slightly smaller than those posteriorly; usually the anterior (c.9) rows of each group are curved forwards whilst posterior (c.3) rows are curved backwards; anal lobe bears spines in rough circles round lobe, pointing outwards. These ventral groups of spines extend round anterior margin of segments 3-5, whilst traces of the spines are found dorsally on the anterior margins of segments 6, 7 and 8. Anus opens on ventral lobe of last (12th) segment; is a longitudinal slit dividing lobe into two lateral portions and an anterior one, at end of anus are three large sclerotised processes each composed of 4-10 spines.

PUPARIUM

Length, from full grown larva c.7.5 mm. Dark-brown to black; outline ovate, tapering anteriorly, posterior end blunt; in side view ventral line straight, may be very gently sinuous, dorsal line convex tapering anteriorly, deepest in region of segments 8-9; first segment completely introverted, so that larval anterior spiracles are situated almost at anterior end of puparium; to allow emergence of adult, split occurs round anterior end, laterally; part of puparium dorsal to this split breaks off by a tranverse split three-quarters way along segment 4, usually leaving ventral part intact.

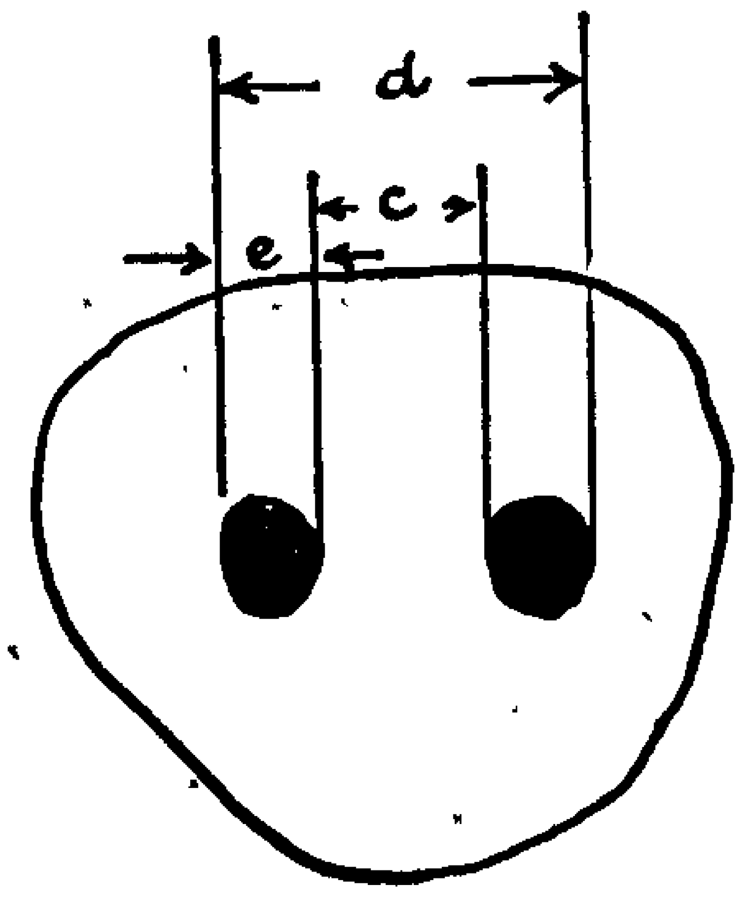
Remarks. It is difficult to decide whether the antennae of the larva of Coelopa frigida and the other species of Coelopidae described in this thesis are two-segmented and placed on a projection of the head lobes or whether they are three-segmented, the projections of the head lobes being in fact third segments. They are described here as being two-segmented.

5. Differences between the larvae of the two species of Coelopa.

The above description of the larva of C.frigida could also apply to the larva of C.pilipes, there being only slight differences between the two. The differences given by Hennig (1937) are not genuine and the use of his key to the identification of Coelopa larvae would lead to error on many occasions.

To determine the difference between the larvae of the two species, each was bred in similar conditions (p.48) at the same time of the year (August and September, 1957). All the larvae were supplied with adequate food (Laminaria stipes) and were etherised after one or two had begun to pupate. When killed, parts of the larvae, particularly the sides between segments 5 to 11, the digitate processes of the anterior spiracles and the rim of the posterior spiracles turned black (i.e. the cuticle became tanned) within a few minutes. Each larva was extended to full length by being gently pressed between the thumb and first finger. Thus the specimens examined were freshly-killed, mature third instar larvae in the fully extended position.

Measurements of fifty specimens of each of the two species were noted and are given in the following tables.



The lengths of the larvae are given in millimetres. The measurements of b,c,d and e were taken with a micrometer eyepiece at a magnification of x 16. when 24 divisions of the micrometer eyepiece were equal to 1 mm. of the object.

Table 1. Measurements of third instar larvae of C. frigida.

Length	Width of last segment	Shortest distance between spiracles	Distance between outside edges of spiracles	Width of spiracular plate	Ratio $\frac{c}{e}$	Number of digitate processes on anterior spiracles.	
a	b.	c	d	e		L. side	R. side
11.5	62	21	39	9	2.3	16	17
11.5	59	19	39	10	1.9	16	15
12.0	62	21	41	10	2.1	15	16
11.5	63	21	40	9.5	2.2	19	18
12.5	63	24	43	9.5	2.5	14	18
12.5	65	23	43	10	2.3	14	16
12.5	66	23	42	9.5	2.4	16	17
11.5	65	21	40	9.5	2.2	14	16
13.0	67	23	44	10.5	2.2	16	17
12.5	66	21	42	10.5	2.0	14	16
12.5	65	23	44	10.5	2.2	16	16
11.0	62	22	41	9.5	2.3	15	15
11.5	61	20	39	9.5	2.1	17	17
13.5	69	23	45	11.0	2.1	16	16
12.0	61	21	38	8.5	2.5	16	15
11.5	61	21	40	9.5	2.2	17	16
12.0	64	22	40	9.0	2.4	16	16
12.5	65	20	39	9.5	2.1	18	13
12.0	62	18	39	10.5	1.7	16	15
11.0	57	19	36	8.5	2.2	18	19
12.5	60	16	37	10.5	1.5	17	17
14.0	65	23	44	10.5	2.2	17	15
12.5	62	19	37	9.0	2.1	16	18
12.5	62	21	40	9.5	2.2	17	16
12.0	61	21	40	9.5	2.2	15	18
11.5	60	21	39	9.0	2.3	19	15
11.0	57	18	36	9.0	2.0	16	17
11.0	55	21	38	8.5	2.5	17	16
11.5	56	19	38	9.5	2.0	16	16
12.0	56	21	40	9.5	2.2	17	14
11.5	62	20	40	10.0	2.0	18	15

a.	b.	c.	d.	e.	Ratio $\frac{c}{e}$	L.side	R.side
13.0	64	21	42	10.5	2.0	15	15
12.5	66	22	37	7.5	2.9	16	16
12.0	61	18	37	9.5	1.9	16	18
11.5	59	18	36	9.0	2.0	19	14
12.0	60	21	39	9.0	2.3	16	15
11.5	59	18	36	9.0	2.0	14	17
11.5	56	20	40	10.0	2.0	16	15
12.5	70	23	42	9.5	2.4	17	16
11.5	61	19	38	9.5	2.0	13	18
11.5	60	18	38	10.0	1.8	16	14
13.0	66	21	41	10.0	2.1	16	15
12.0	65	23	42	9.5	2.4	16	15
11.5	62	21	40	9.5	2.2	17	16
12.5	65	20	41	10.5	1.9	16	16
12.0	64	20	38	9.0	2.2	13	18
12.0	60	19	39	10.0	1.9	16	17
12.0	62	21	42	10.5	2.0	15	16
13.0	68	21	41	10.0	2.1	16	19
11.5	63	21	43	11.0	1.9	17	16

mean $\frac{c}{e}$ = 2.14 s.d. = 0.1

Table 2. Measurements of third instar larvae of C.pilipes.

13.5	75	32	48	8.0	4.0	14	13
13.0	77	29	44	7.5	3.9	13	13
12.5	76	31	46	7.5	4.1	15	15
12.5	75	32	48	8.0	4.0	14	14
13.0	78	33	49	8.0	4.1	13	15
13.5	79	35	52	8.5	4.1	14	13
13.0	77	33	49	8.0	4.1	15	15
13.5	78	32	48	8.0	4.0	15	14
13.5	78	33	50	8.5	3.9	15	13
13.0	76	31	47	8.0	3.9	13	14
12.5	73	31	46	7.5	4.1	13	16
13.5	75	32	48	8.0	4.0	13	15
12.5	74	32	49	8.5	3.8	14	13
14.0	81	35	52	8.5	4.1	14	15
13.0	76	32	48	8.0	4.0	17	14
12.5	74	30	45	7.5	4.0	13	14
13.0	77	32	48	8.0	4.0	15	15
13.0	78	31	47	8.0	3.9	15	13
13.5	78	33	50	8.5	3.9	13	16
12.5	74	32	48	8.0	4.0	15	15

a	b.	c.	d	e	Ratio c/e	L.side	R.side
12.5	75	31	45	7.0	4.4	14	13
14.0	80	34	50	8.0	4.2	13	13
13.0	76	32	48	8.0	4.0	14	15
13.0	75	32	48	8.0	4.0	15	13
12.5	74	31	46	7.5	4.1	14	13
13.0	78	33	49	8.0	4.1	13	14
13.0	77	32	48	8.0	4.0	15	15
13.5	79	33	50	8.5	3.9	15	13
13.0	78	32	48	8.0	4.0	13	13
13.5	80	34	51	8.5	4.0	14	15
12.5	74	32	48	8.0	4.0	15	13
13.0	77	32	49	8.5	3.8	16	13
13.0	77	31	46	7.5	4.1	14	13
14.0	81	35	53	9.0	3.9	15	14
12.5	73	31	46	7.5	4.1	14	14
13.0	78	32	48	8.0	4.0	13	16
13.5	79	33	49	8.0	4.1	14	15
13.0	79	32	48	8.0	4.0	14	14
13.0	77	32	48	8.0	4.0	13	16
12.5	74	31	47	8.0	3.9	15	15
13.5	77	33	50	8.5	3.9	14	15
12.0	74	29	44	7.5	3.9	15	14
12.5	76	32	48	8.0	4.0	14	15
13.0	77	33	50	8.5	3.9	13	15
13.0	78	33	50	8.5	3.9	14	15
13.0	76	32	48	8.0	4.0	16	14
12.5	75	31	47	8.0	3.9	13	13
13.5	78	33	49	8.0	4.1	16	14
13.0	76	32	48	8.0	4.0	13	13
13.5	78	34	51	8.5	4.0	15	13

mean c/e = 4.00 s.d. = 0.23

(1) The ratio of the width of one of the spiracular plates to the distance between them.

It will be seen from tables 1 and 2 that in C. frigida the two spiracular plates of the larvae were separated by a distance of about twice their width, whilst those of C. pilipes were separated by about four times their width. This difference became noticeable as soon as the measurements were taken, and was used later as the easiest and surest way of identifying wild third instar larvae of these two species.

(2) The shape of the larvae.

Although the larvae of the two species were almost equal in length, the larvae of C. pilipes were broader at the posterior end. As can be seen from the tables, the last segment of the C. pilipes larvae was over 20% wider than that of C.frigida larvae. This feature, too, soon became obvious.

(3) The number of digitate processes on the anterior spiracles.

Of the fifty larvae of each species examined, forty-four specimens of C. frigida had a total of more than thirty digitate processes, and forty-one larvae of C. pilipes had less than thirty. Thus about 80% of Coelopa larvae could probably be identified to specific level by examination of the number of digitate processes. Since the larvae of the two species do not intermingle (p. 71) fairly certain identification could be obtained with even a small number, provided they were found together.

(4) The shape and arrangement of the digitate processes on the anterior spiracles.

More significant than the number of digitate processes are their shape and arrangement. In C. frigida the processes are longer and more separated than in C.pilipes. The knob-like swellings at their distal ends being held away from the body in the former species (fig.1 p. 31) but close to the body in the latter (fig. 2). In C. frigida the processes on each side are arranged in two rough fan formations, but in C. pilipes this formation is less obvious.

These differences in shape and arrangement of the digitate processes on the anterior spiracles are the most useful ones for identifying preserved larvae of the two species.

(5) The length of the 'hairs' on the posterior spiracles.

In C. frigida the longest 'hairs' are about 0.15 mm., measured from the outside edge of the peritreme, and in C. pilipes they are less than 0.1 mm long. In many specimens, however, the length of the 'hairs' is difficult to measure accurately as they are often curved towards the larvae.

These differences may be summarised to form a key to the identification of the species.

Third instar larva with the two posterior spiracular plates separated by at least 3.5 (usually about 4) times their width; larva broader at posterior end; with usually less than a total of 30 digitate processes on the two anterior spiracles; digitate processes short and their distal swellings close to body, roughly in a straight line; length of hairs on posterior spiracles 0.1mm. or less,

............C. pilipes.

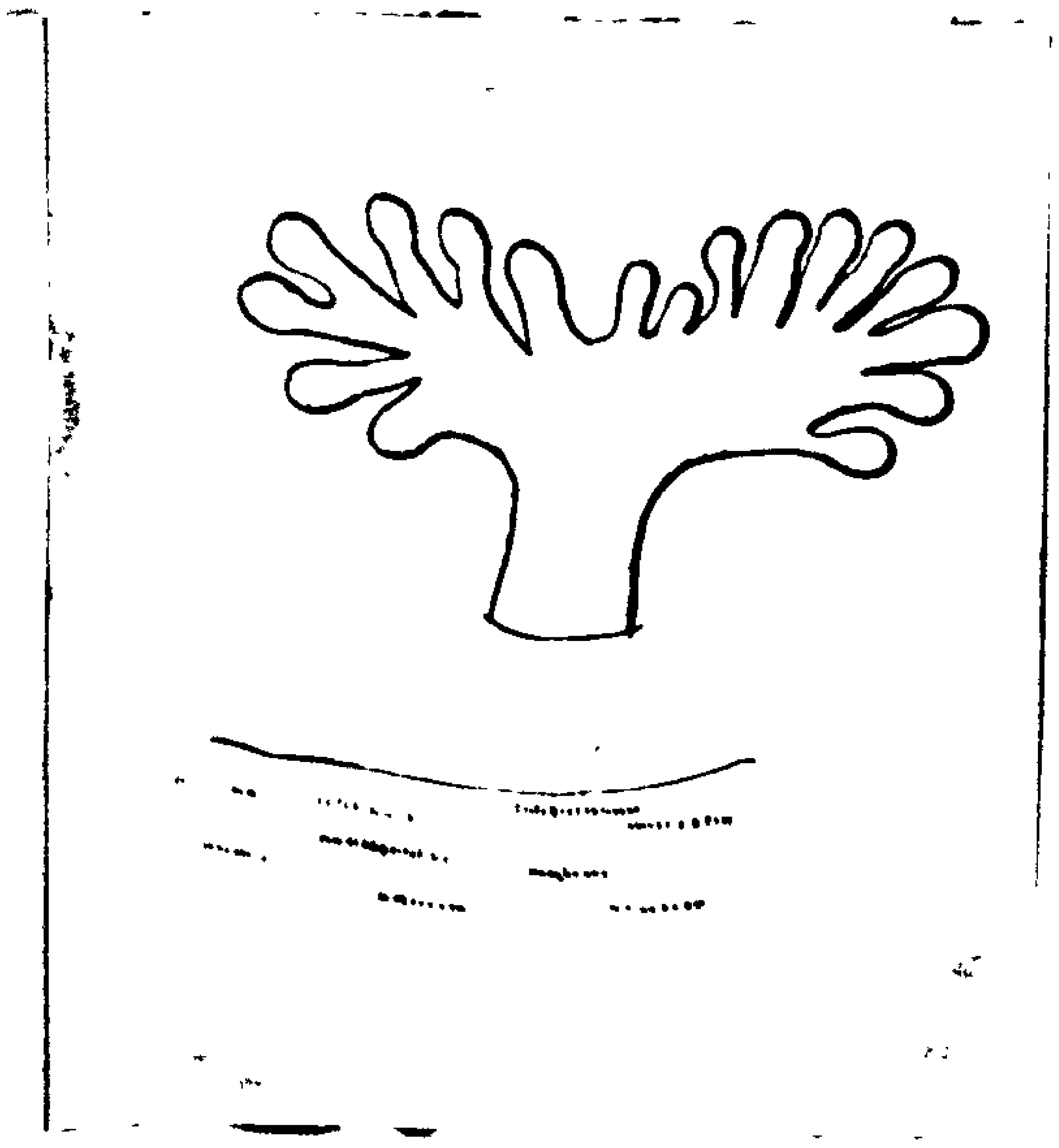
Larva with the two plates separated by a distance less than 3 (usually about 2) times their width; more cylindrical; usually with more than 30 digitate processes; processes longer, more separated, their distal swellings not close to body, roughly grouped into two fans; length of hairs on posterior spiracles about 0.15mm... C. frigida.

The puparia of the two species are also very much alike but the distinct difference in the ratio of the width of the posterior spiracles to the distance separating them in the larvae of the two species hold good in the puparia. The length of the hairs on the posterior spiracles can sometimes be measured in well-preserved specimens.

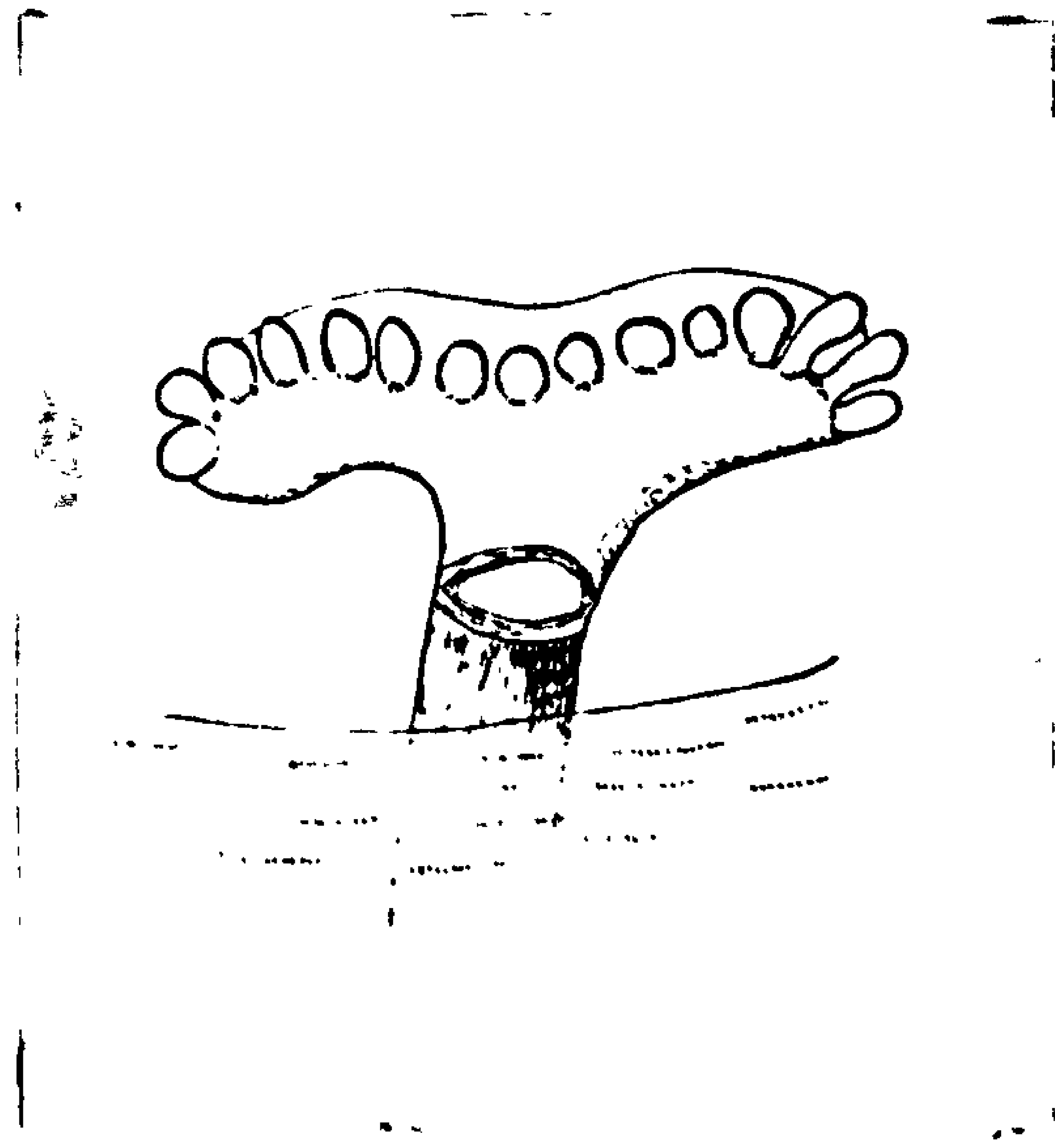
6 The young stages of Orygma luctuosa.

EGG

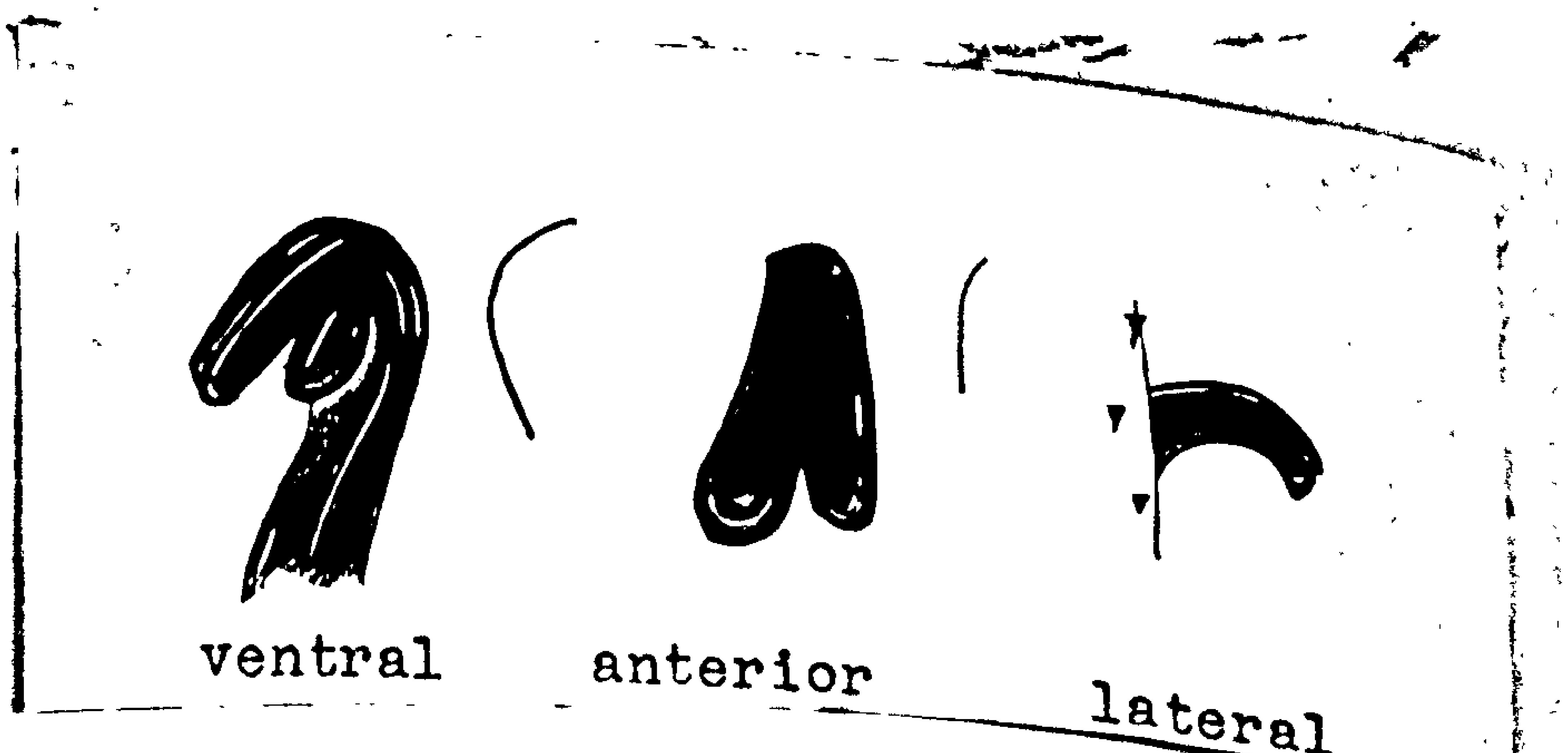
Length 0.8 mm. In dorsal view elongate-ovate; in side view dorsal surface convex, ventral surface almost straight. With two long (1 mm.) thin, white filaments attached to anterior end; the filaments cylindrical, slightly narrowing near distal end before gently swelling into a small bulb. Between filaments at anterior extremity of egg is a small funnel-shaped structure through which a fine passage (micropyle) leads into egg. Colour white. Whole chorion covered in white reticulation of hexagons of roughly same size, except for some smaller ones at anterior end on ventral side.



Coelopa frigida
Anterior spiracle



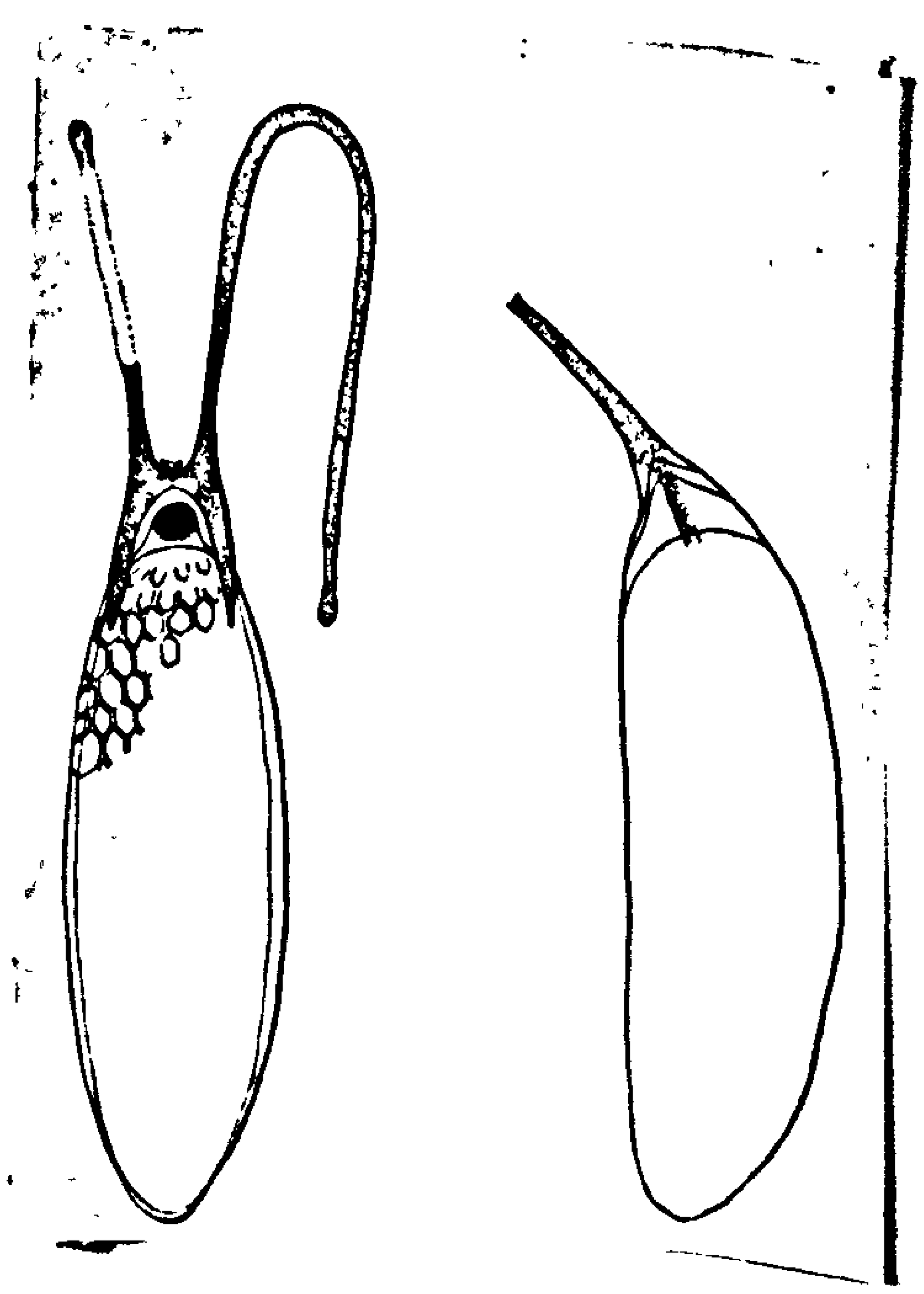
Coelopa pilipes
Anterior spiracle



Coelopa frigida mouth hooks

Orygma luctuosa

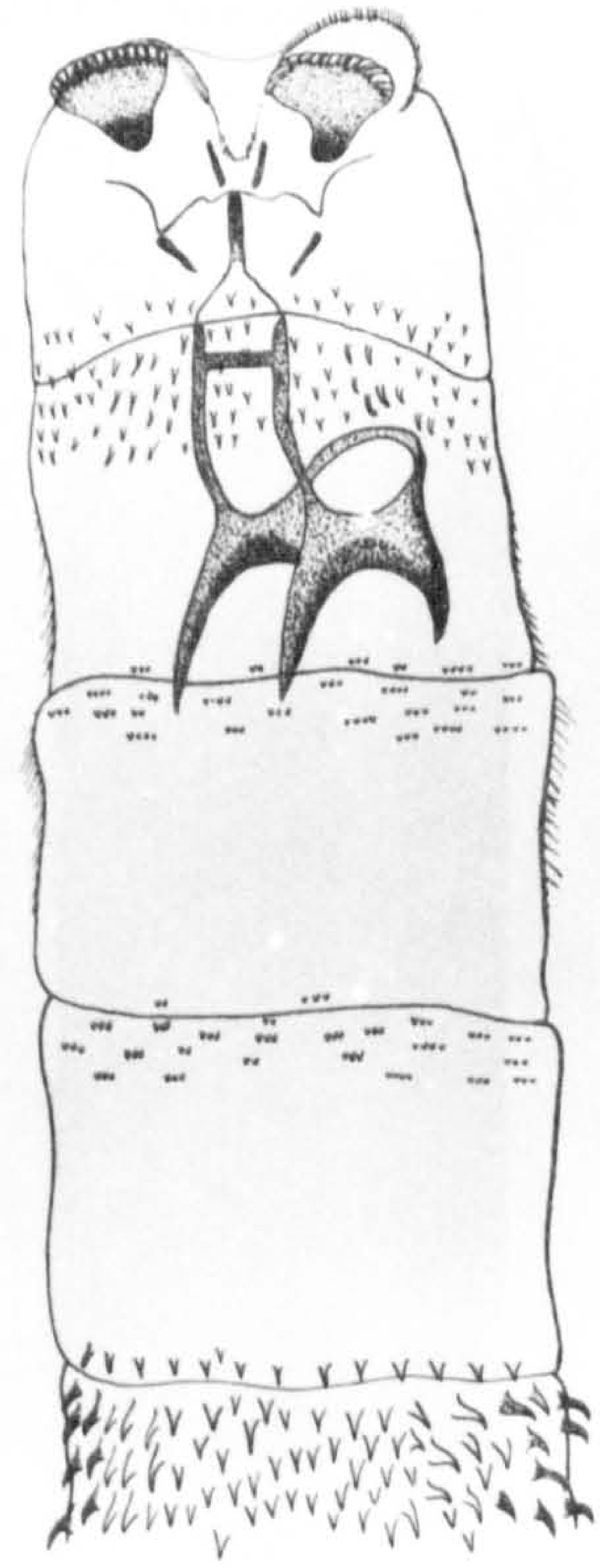
Egg



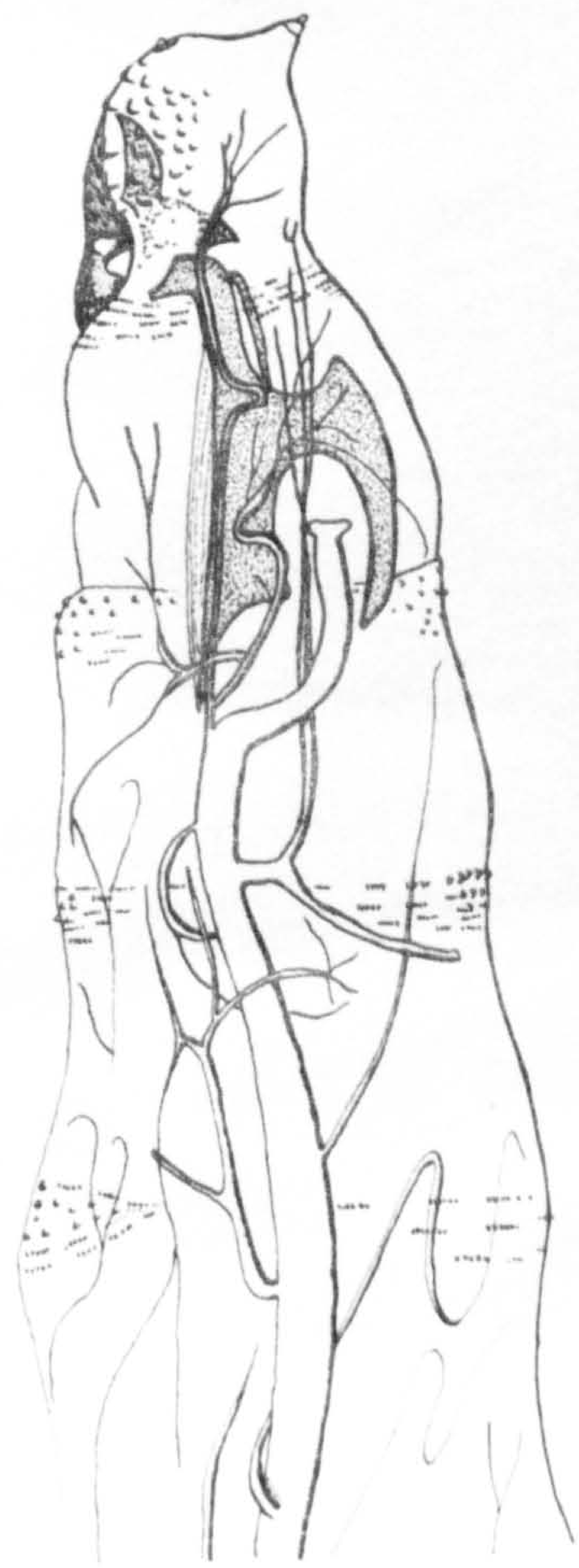
FIRST INSTAR LARVA

Length 1.5 - 3.25 mm. when extended. First segment bears, in front of mouth, a pair of large comb-like mouth-hooks, each with about twenty teeth curved ventrally and slightly inwardly. Each mouth hook covered by a hood of transparent skin which bears on its free, anterior margin a fringe of fine hairs. Posterior spiracles borne on two backwardly-directed processes of last segment; each with four rough groups of hairs, 3-6 hairs per group, directed laterally or lying along sides of processes. Spines found in marginal positions on all segments 2-12 on ventral surface. Small, backwardly-directed, simple spines on anterior margin of segment 2; smaller ones in groups of 3-5 at anterior margin of segments 3 and 4. Spines on segments posterior to these are larger and borne on transverse swellings at anterior and posterior margins of each of the segments. Each swelling bears a group of 4-6 rows of spines, first row of each group being at posterior margin of a segment and the other rows of a group are towards the anterior margin of the segment behind. Nearly all of the spines curve backwards but those in the single row at posterior margin of each of segments 8-10 are curved forwards. Fine, hair-like spines found on dorsal and lateral surfaces of segments 2-12.

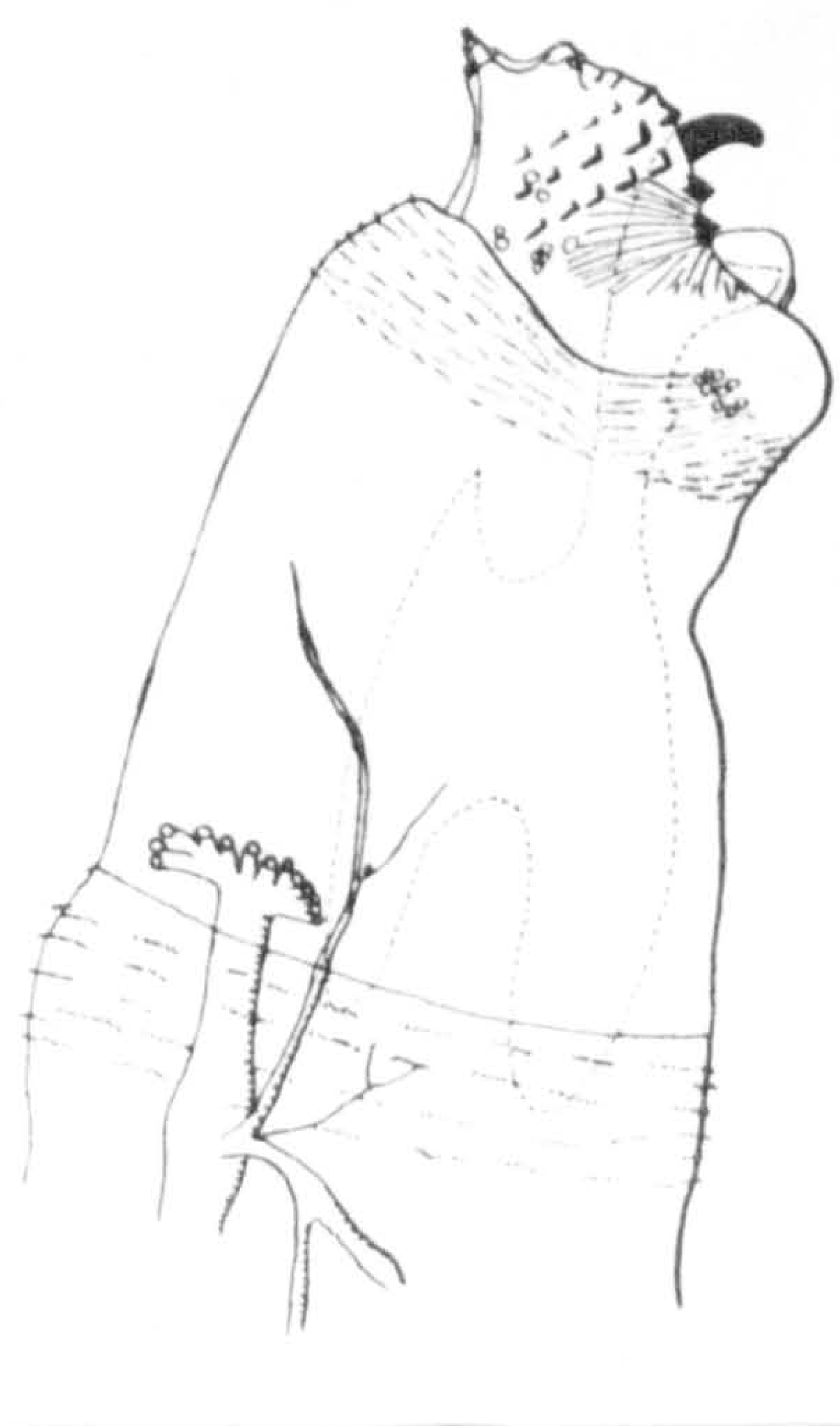
Orygma luctuosa



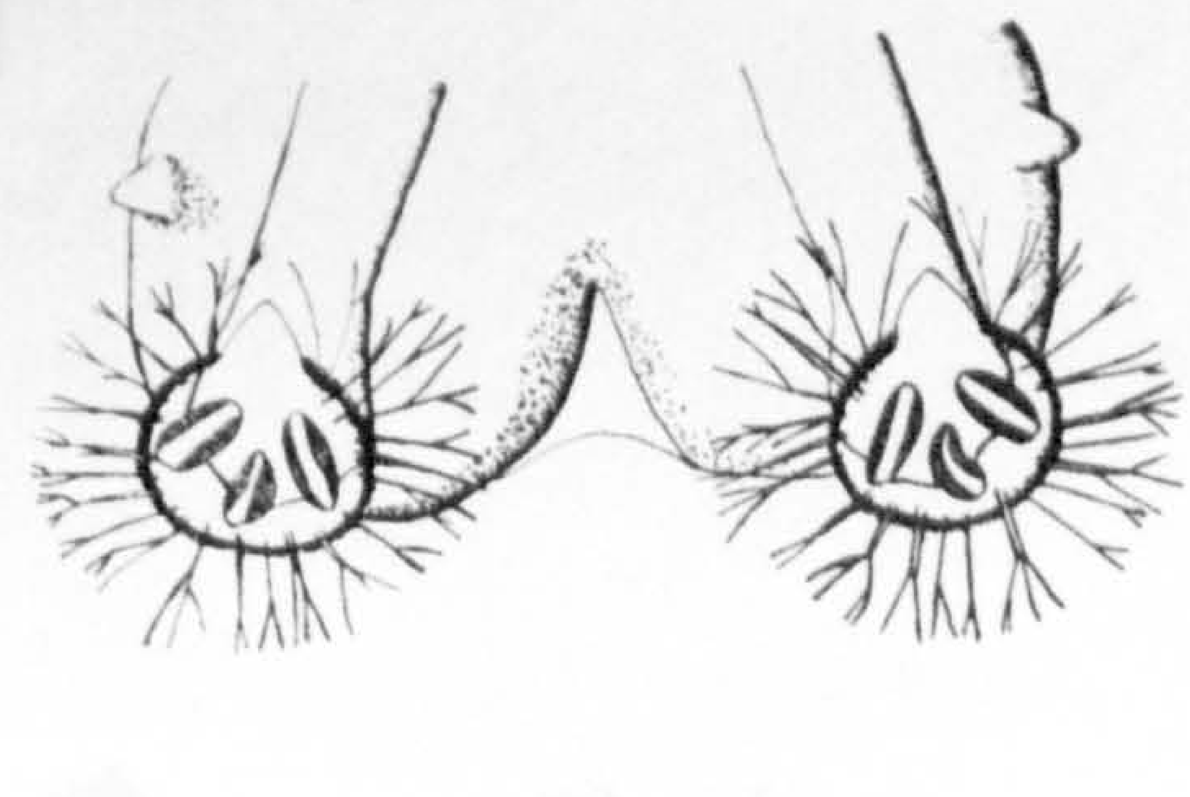
First instar larva
ventral view



Second instar larva
lateral view



Third instar larva
anterior end, lateral view



Second instar larva
posterior spiracles

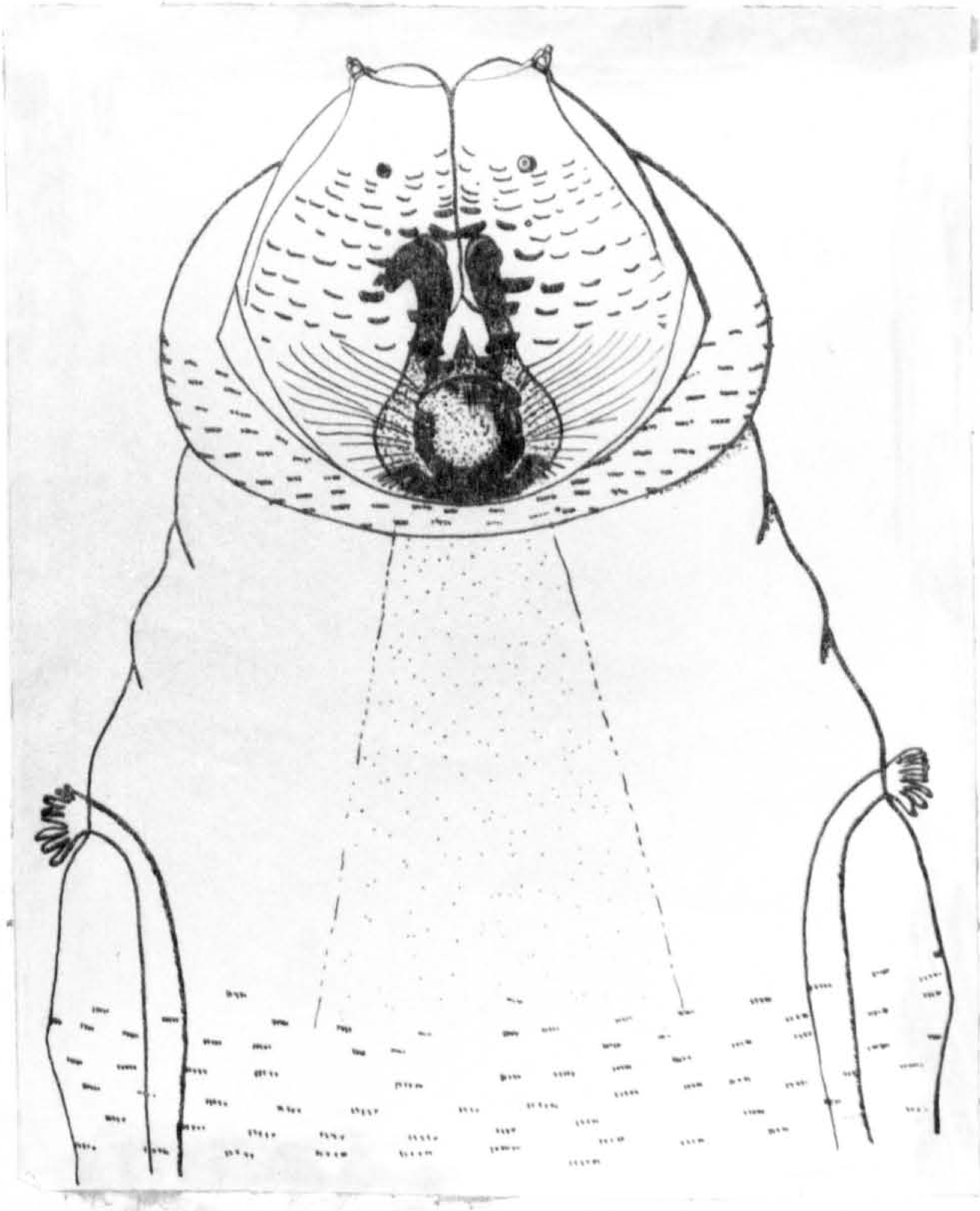
SECOND INSTAR LARVA

Length 2.75 - 6 mm. Anterior spiracles situated laterally near posterior border of second segment; knob-like, fan-shaped without digitate processes. Posterior spiracles each with circlet of 25-30 hairs, nearly all of which are branched, round peritreme. Each hair one-half to two-thirds of the width of the stigmal plate in length.

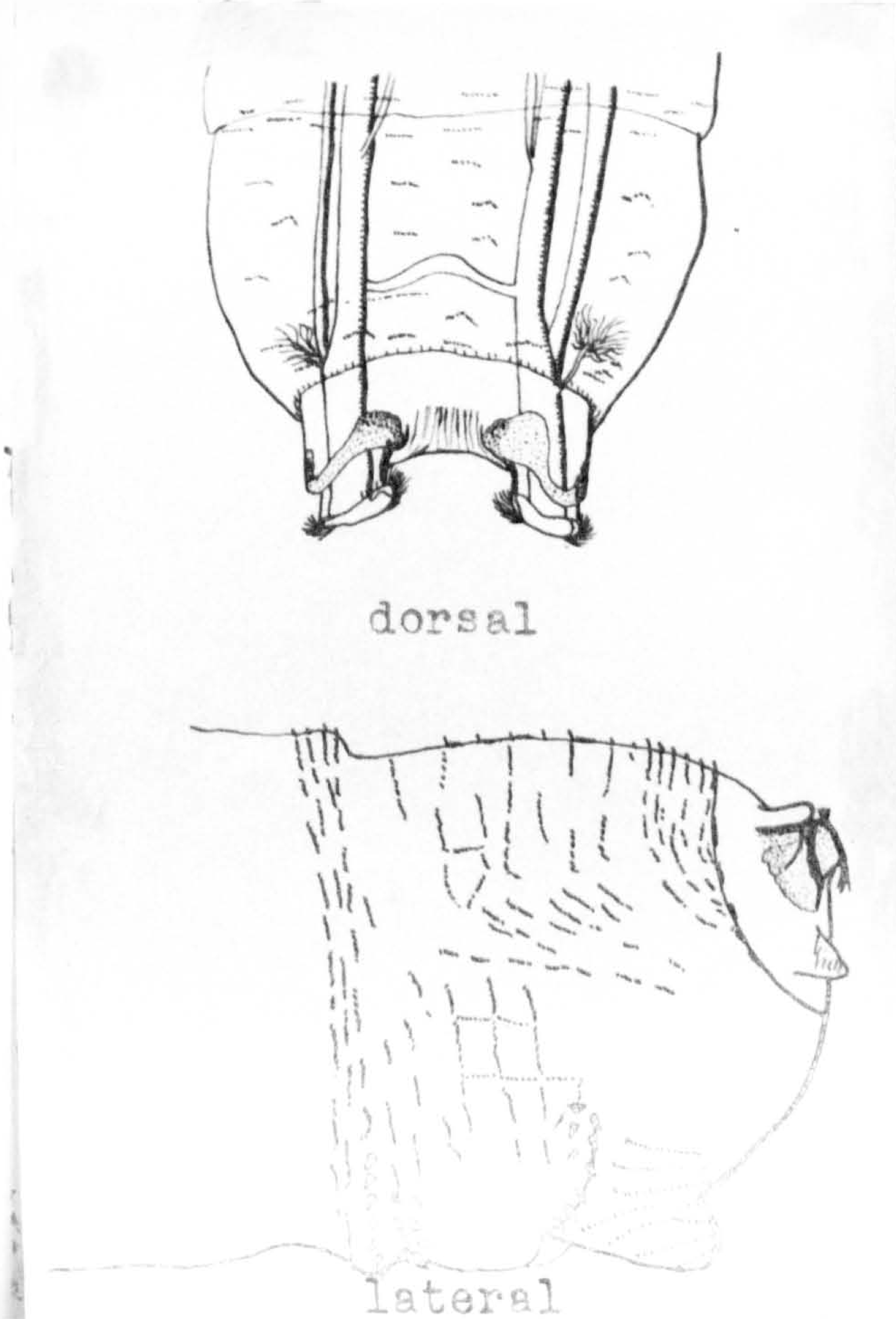
THIRD INSTAR LARVA

Length 6.0 - 16.0 mm, mature larvae 14 - 16 mm. Breadth at widest point (in region of segment 9) 1.8 mm. Greatest depth 2 mm. Shape almost cylindrical, narrowing slightly towards posterior end, and more so towards anterior end. Colour white save for brown sclerotised structures. Body composed of the normal twelve segments; segments 3 - 7 and 12 subequal in length (c. 1 mm.) segments 8 - 11 subequal and longer (c. 1.6 mm.); each segment 3 - 6 slightly concave on dorsal surface, straight in segments 7 - 11. First segment consists of two lobes separated by a median ventral groove at posterior end of which is mouth. In front it bears, one on each lobe, a pair of small, two-segmented, forwardly-directed antennae each situated on a fleshy projection from lobe; proximal segment of each antenna cylindrical, distal one hemispherical, its base half diameter of former. Posterior and ventral to antennae are the two single-segmented 'maxillary palps' each on a slight swelling of lobe. The third pair of sensory organs, the smallest, are clearly visible in an antero-lateral position to the mouth hooks. Each lobe bears a number of sclerotised teeth the largest, placed near the mouth-hooks, being flat plates pointing backwards at about 45° and the smallest appearing as brown sclerotised ridges in the lobes. Each lobe has 1 - 2 large teeth anterior to its mouth-hook; about four large teeth lateral to it getting progressively larger in size posteriorly; about five smaller teeth in a row at the side of each large tooth; and two long rows of about 10 small teeth and four short rows of four small teeth anterior to the large teeth. Anterior spiracles situated laterally near posterior margin of second segment; each composed of about fifteen laterally directed digitate processes. Posterior spiracles borne on backwardly-directed projections (0.4 mm.) of segment 12; peritreme light brown and circular in shape; stigmal plate sloping inwards and upwards, bears three arch-shaped spiracular openings; with three fringes of small hairs (less than one-third width of stigmal plate), each fringe being opposite a spiracular opening. Closely applied to the latero-dorsal surface of each process is a fleshy lobe

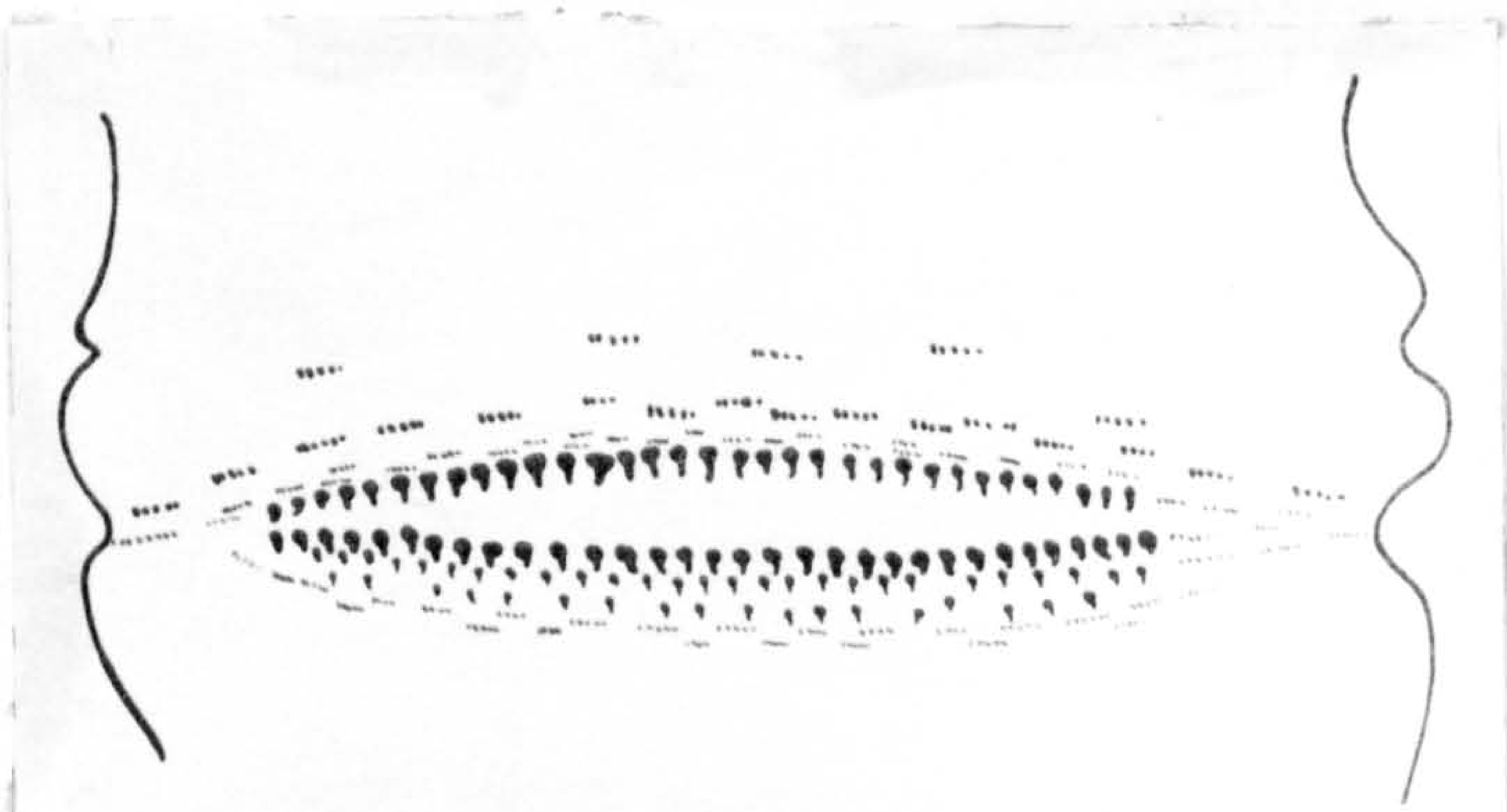
Orygma luctuosa



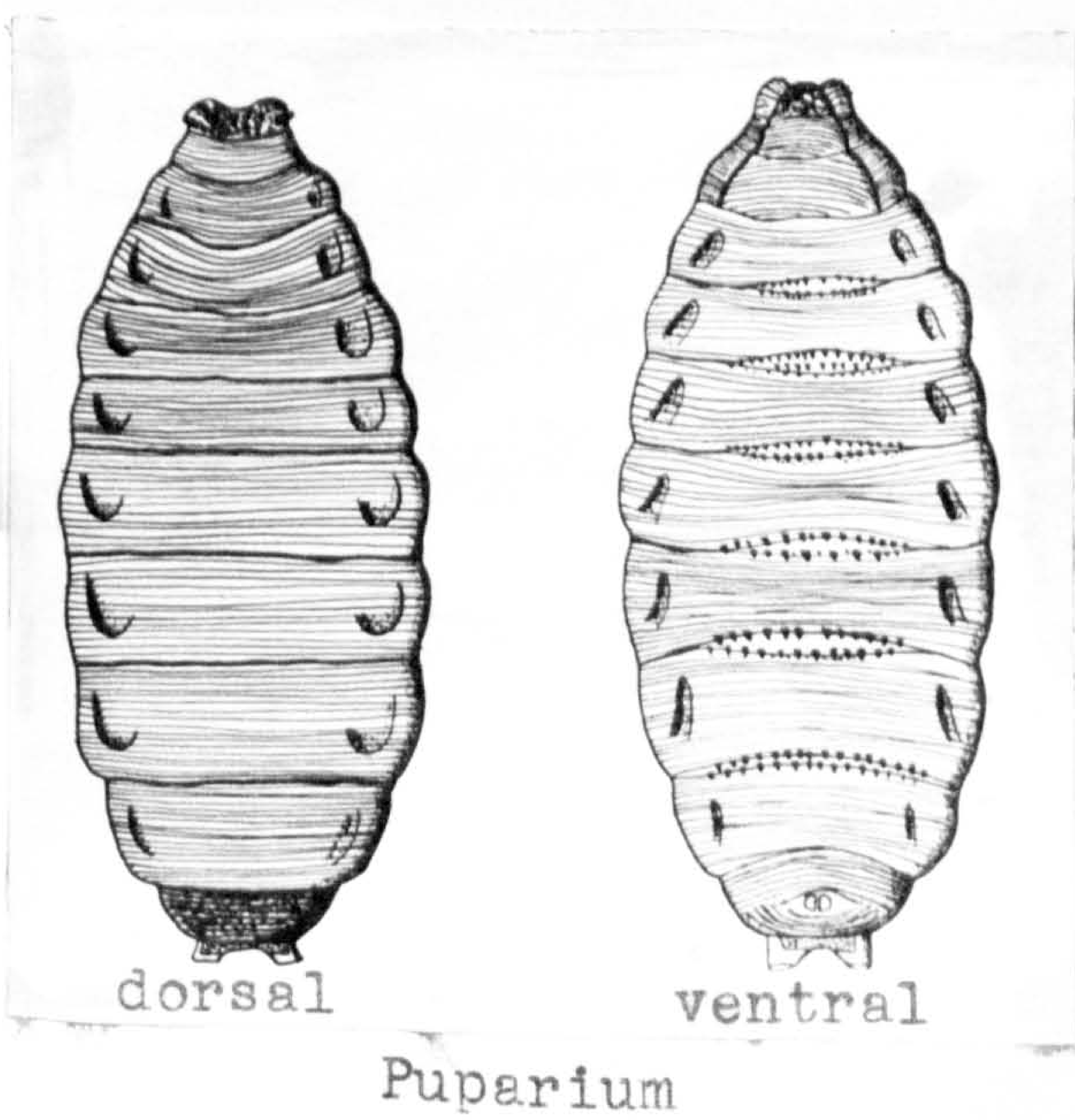
Third instar larva
anterior end, ventral view



Third instar larva
posterior end



Spines on segment 8.



Puparium

and ventral to each process is a fleshy transparent cone-shaped papilla pointing ventro-laterally. Spines of various sizes occur but largest and smallest are easily distinguished from the intermediate ones; largest single and found only on ventral surface, smallest in groups of 2 - 12. Individual larvae vary slightly but are similar to following. Segments 2, 3 and 4 bear a number of rows of small spines in groups which extend right round at its anterior margin. The segments posterior to these bear spines arranged similar to that shown in diagram for segment 8. Following description refers to spines in order on ventral surface unless stated otherwise. Segment 5 with 6-7 rows of small spines in groups of 1-3 in first row, 3-5 in second row and 5-10 in other rows, with 16 groups in first row and twelve in second, these two rows being in centre of segment and slightly arched forward, the other rows extending round dorsal surface; segment 6 with 2 rows each of 24 groups of 8-12 small spines, 2 rows of 31 large spines, 1 rough row of about 35 slightly smaller spines, 1 row of 24 groups of 4-10 small spines, the rows of small spines extending round to dorsal surface; segment 7 with 2 rows each of 24 groups of 8-12 small spines, 2 rows of 33 large spines, 1 rough row of 44 slightly smaller spines, 1 row of 27 groups of 4-10 small spines, the rows of small spines extending round to dorsal surface; segment 8 with 2 rows each of 24 groups of 8-12 small spines, 2 rows of 33 large spines 1 rough row of 45 slightly smaller spines, 1 row of 26 groups of 4-10 spines, a few small spines in groups on sides and dorsal surface; segment 9 with 2 rows each of 12 groups of 6-10 small spines, 2 rows of small spines in groups, which extend round sides of larva, 1 row 35 large spines, 1 row 28 large spines, 1 rough row of 46 smaller spines, 1 row of small spines in groups, very few groups on dorsal surface; segment 10 with 4 rows of small spines 1 row of 31 large spines, 1 row 27 large spines, 1 rough row 50 smaller spines 1 row of 17 groups of 2-6 small spines; segment 11 with 2 rows of small spines in groups, 1 row 28 large spines, 1 row 24 large spines, 1 rough row 57 smaller spines, 1 row of 15 groups of 2-8 small spines, only a few groups on sides and dorsal surface; segment 12 with 1 row of small spines in groups, 1 row 22 large spines, 1 row 19 large spines, 1 row small spines in groups, many groups of small spines on sides and dorsal surface, and some large spines near anal lobes. Anus opens at posterior end of segment 12, lateral to it are two roughly triangular-shaped (in side view) fleshy lobes each bearing small spines on its margin and outer surface.

PUPARIUM

Length 7.0 - 7.5 mm; greatest width 3.5 - 4 mm. greatest depth (at segment 8) 3.0 - 3.3 mm. Colour black except for brown anterior two segments and posterior spiracles; surface dull. Outline elongate ovate, with width of segments 6-10 roughly equal, tapering anteriorly and posteriorly to these to about one-third to one-quarter greatest width; in side view ventral line slopes down to segment 6 and is then straight to middle of segment 12 where it quickly rises to the posterior respiratory processes; dorsal line convex, tapering at anterior end. Segmentation clearly defined, constrictions being between segments and larval segmental spines obvious. First segment completely introverted so that larval anterior spiracles are situated only short distance from anterior end. Skin in ridges which extend right round body, about 20 ridges to each segment. Shallow longitudinal cavities found towards lateral margins of each segment 5-11, one dorsal and one ventral on each side, each rising slightly from anterior to posterior margin of segment. Puparium covered in white calcareous layer (can be dissolved in weak acid for examination of puparium); thickest all over first three or four segments and last segment and between segments on ventral surface, present to less extent between segments on dorsal surface. For emergence of adult puparium splits half-way along segment 5 and laterally from here right round anterior end, the so-formed two parts are either pushed apart or break off.

7. The young stages of Oedoparea buccata.

EGG

Length 0.8 mm; in dorsal view elongate ovate, in side view dorsal surface convex, ventral surface concave: anterior end more tapered than other which is more rounded; colour white; whole surface of chorion covered with sculptured hexagons of roughly same size.

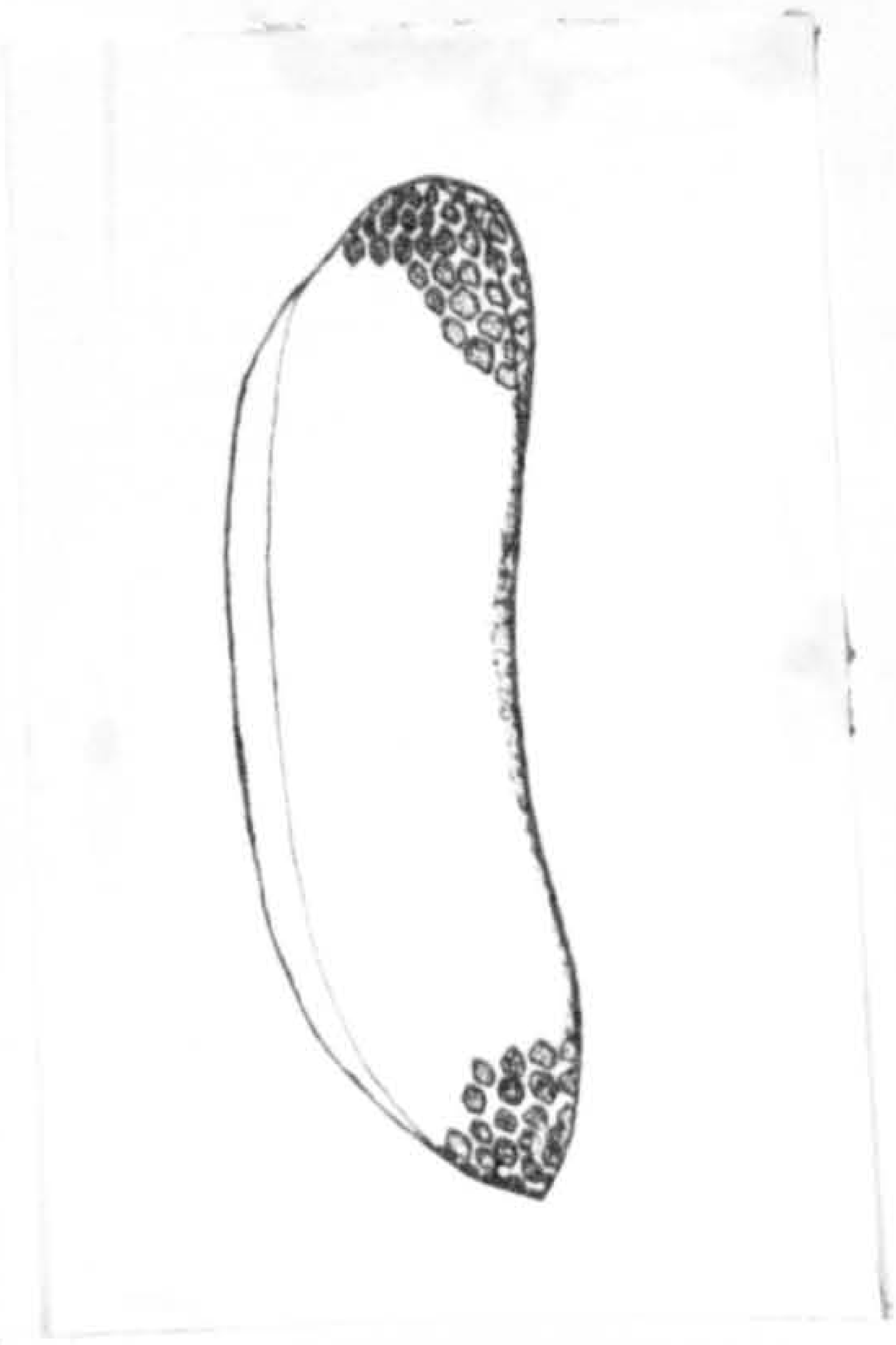
SECOND INSTAR LARVA.

Length 2.5 - 4.5 mm. Anterior spiracles situated on second segment near posterior margin in a lateral position; each a small knob-like structure, projecting from larva laterally, surrounded by a flap of transparent skin; without digitate processes. Posterior spiracles on backwardly-directed processes of segment 12; peritreme black-dark-brown, with small hairs in three groups - one lateral, one dorso-lateral and one ventro-lateral.

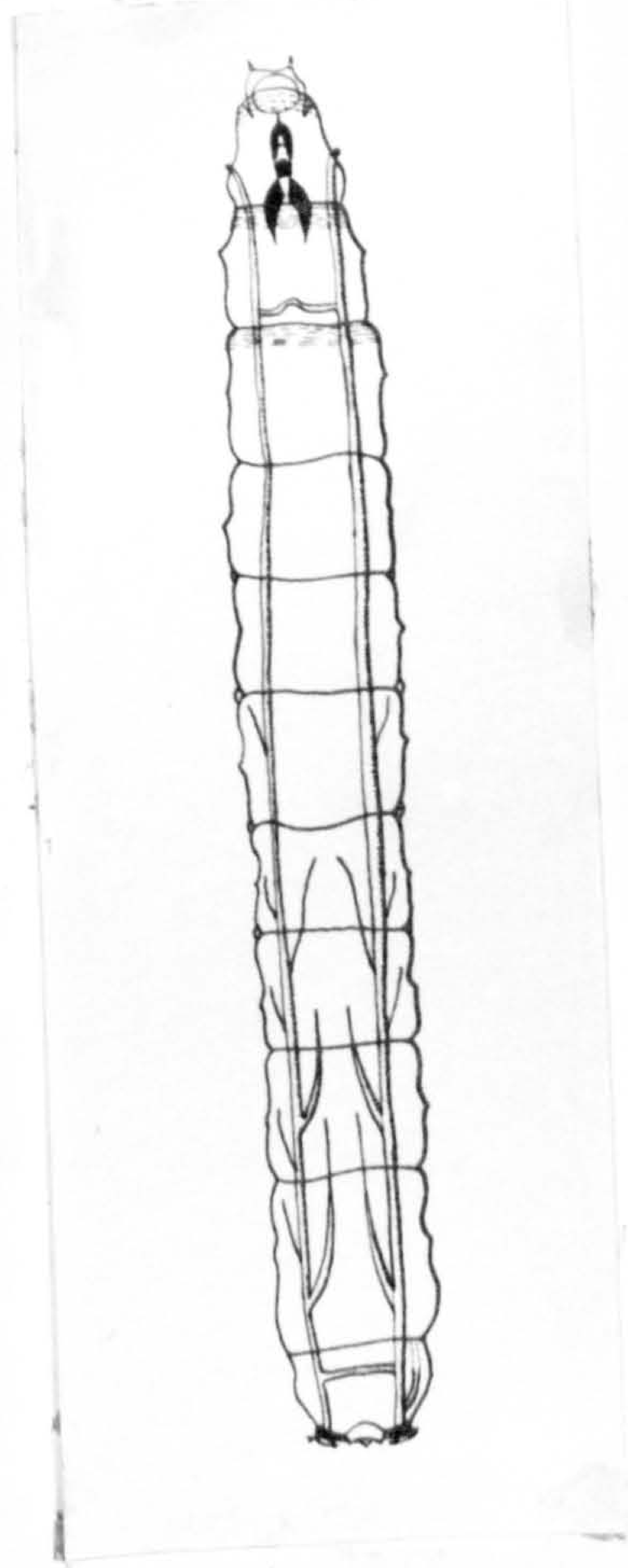
THIRD INSTAR LARVA.

Length 4.5 - 10 mm. When food plentiful attains 9 - 10 mm; greatest width (in region of segment 8) 1.5 mm; greatest depth 1.5 mm. Shape almost cylindrical, narrowing only very slightly posterior to segment 9, more so anterior to segment 5. Colour white save for brown sclerotised structures. Body composed of the normal twelve segments;

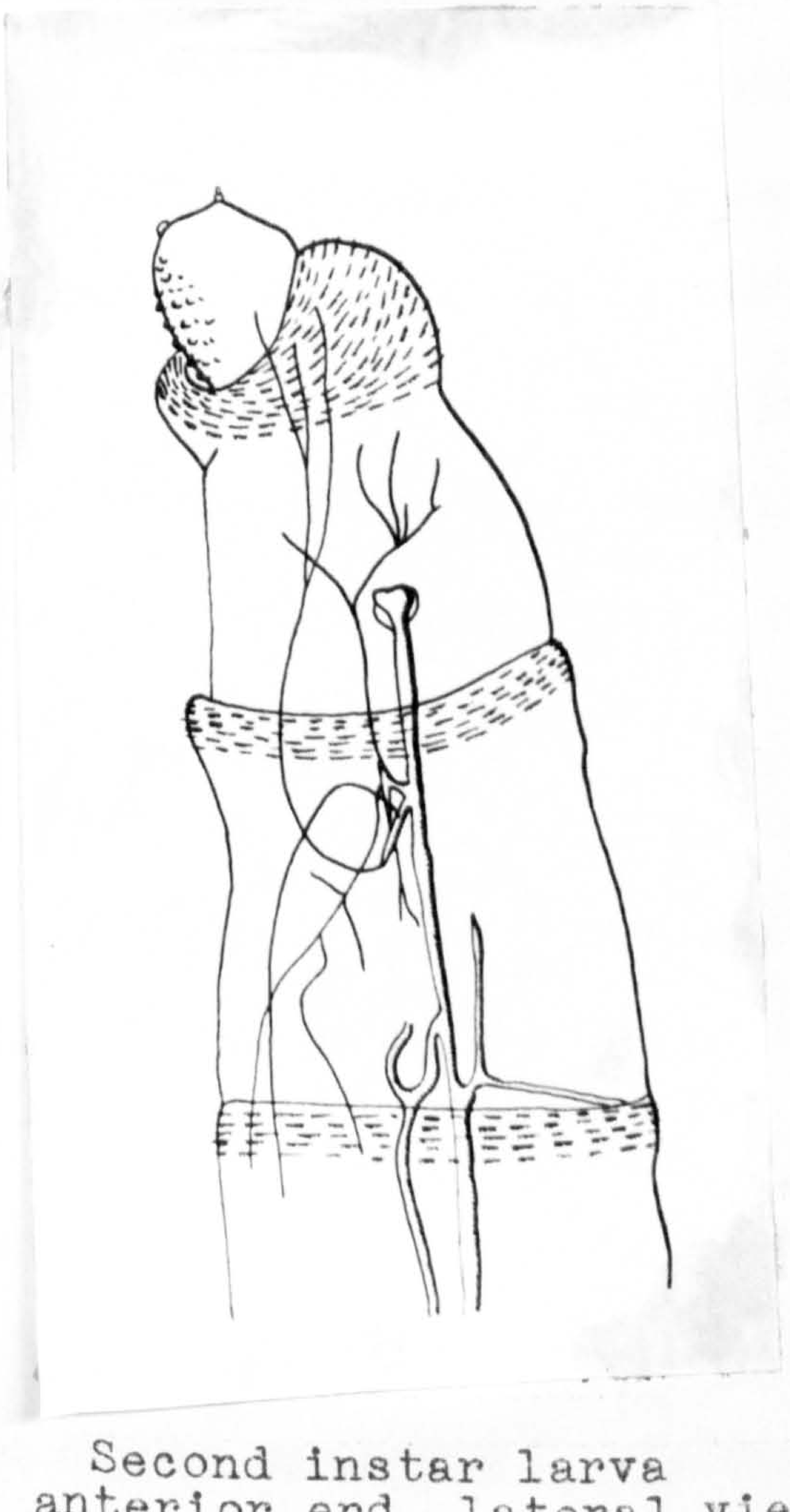
Oedoparea buccata



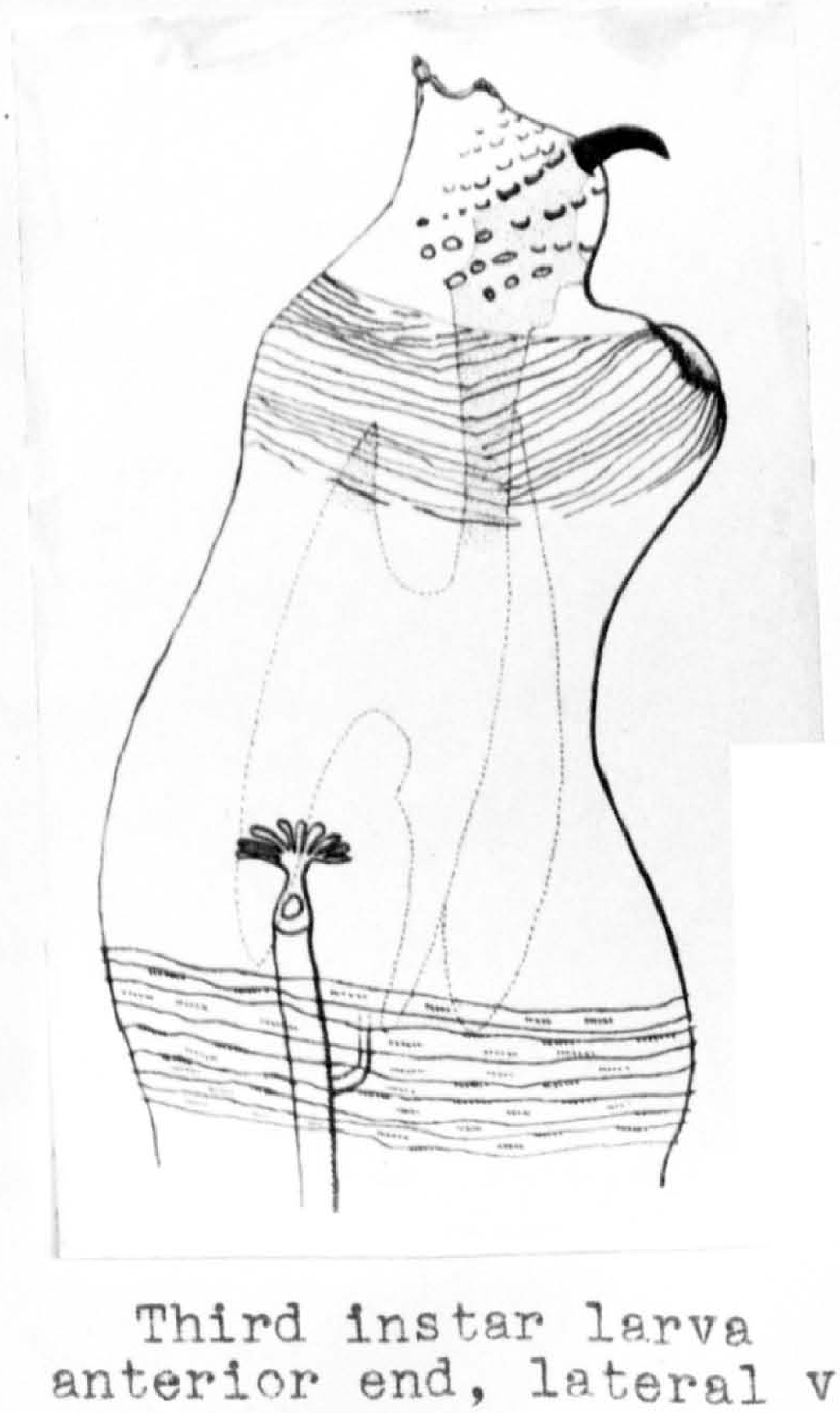
Egg



Second instar larva
dorsal view



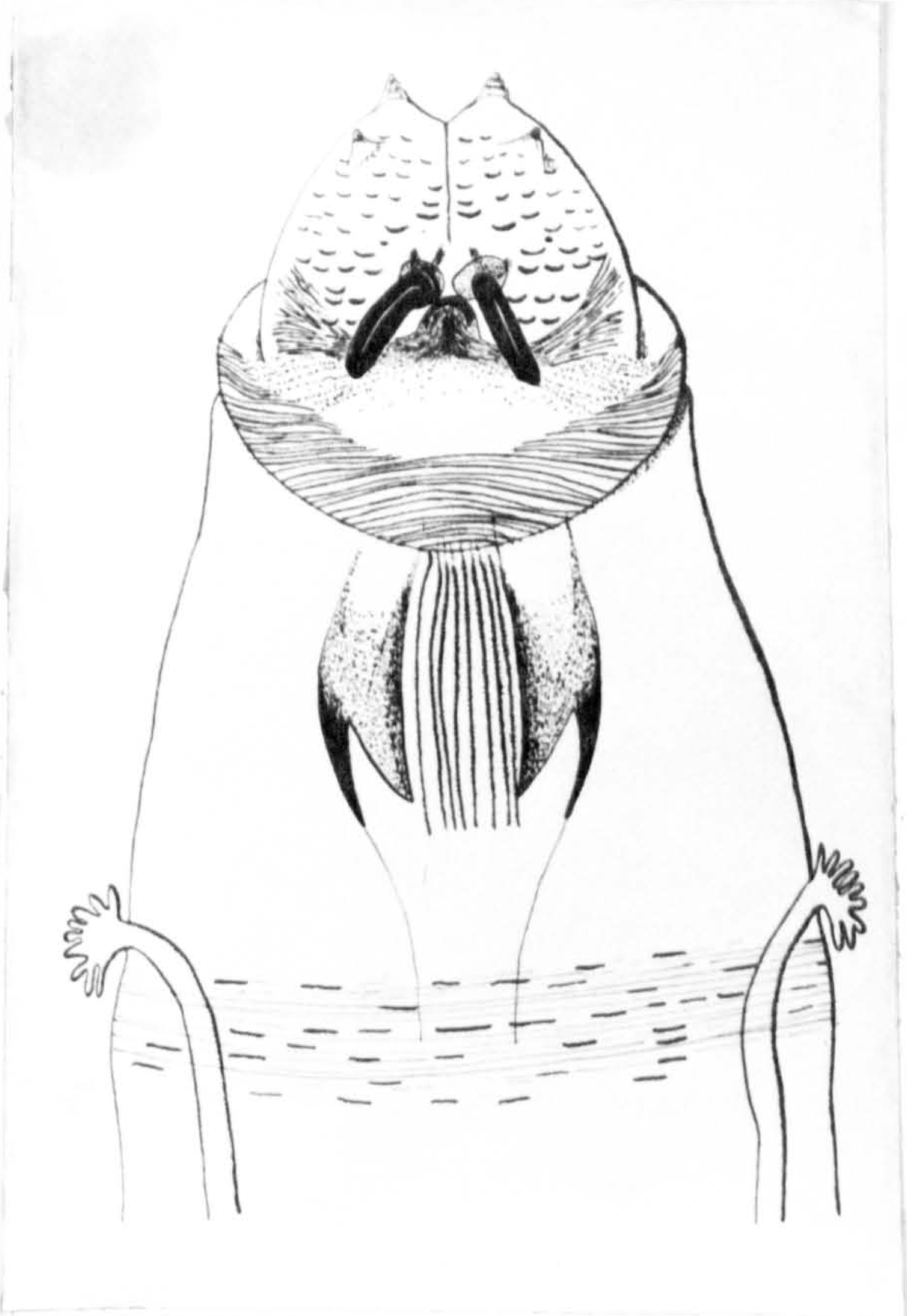
Second instar larva
anterior end, lateral view



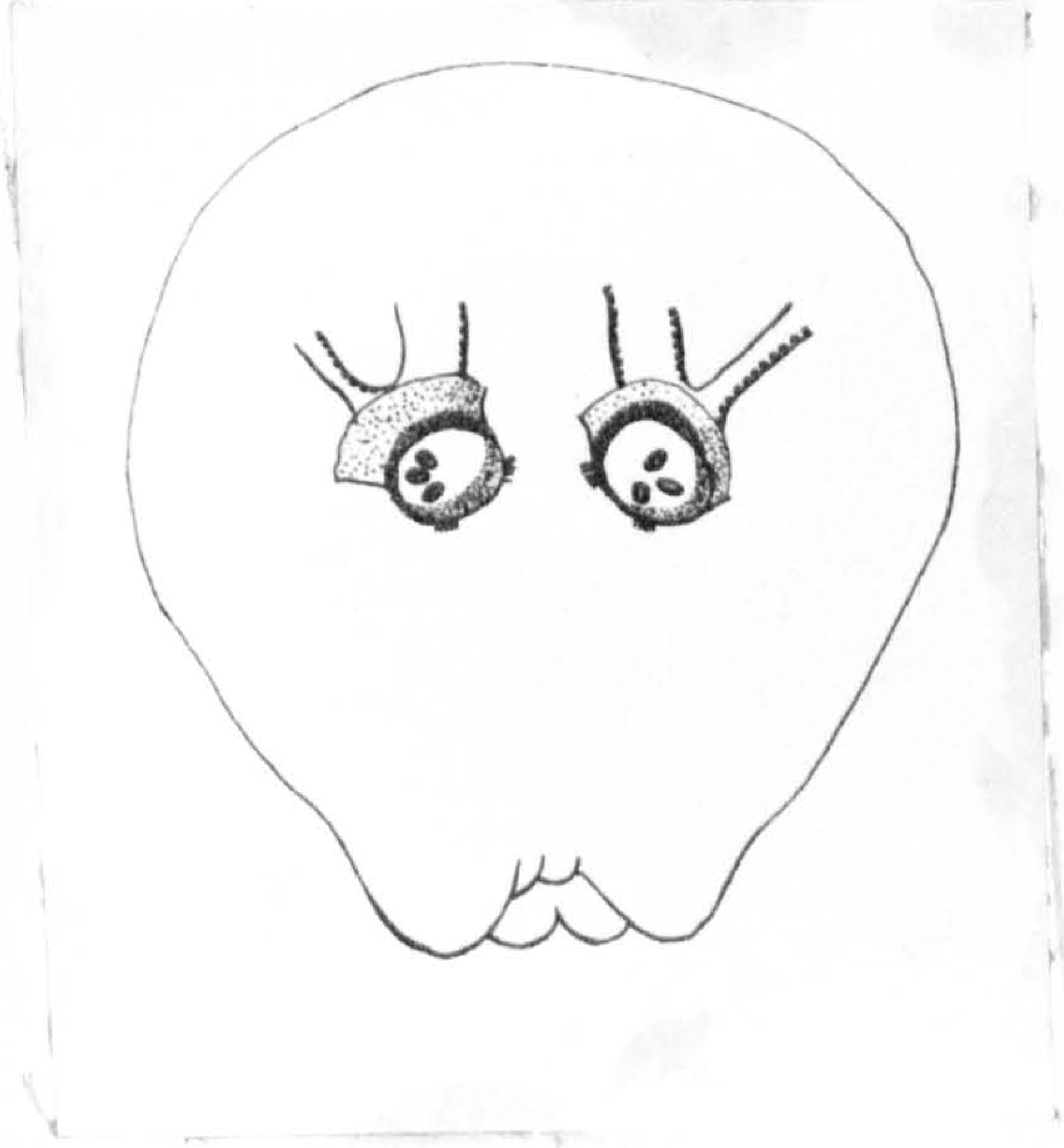
Third instar larva
anterior end, lateral view

3-8 subequal in length, 9-11 subequal and longer; all segments clearly indicated ventrally by swellings at both anterior and posterior margins of segments 2-11 and at anterior margin of 12; not so clearly indicated dorsally as swellings at margins are gentle; slight rise in middle of each segment 3-11. First segment consists of two lobes separated by a median ventral groove at posterior end of which is mouth. In front it bears, one on each lobe, a pair of small, two-segmented, forwardly-directed antennae, each situated on a fleshy projection from lobe; proximal segment of each antenna almost cylindrical, only very slightly tapering to base; distal segment hemispherical. Posterior and ventral to antennae are, one on a swelling of each lobe, the single segmented "maxillary palps". A third pair of sensory organs, the smallest, are found antero-laterally to the grooves in which the mouth-hooks are found. Each lobe bears five rows of sclerotised teeth at sides of mouth-hooks with 3-6 teeth in each row, and about five rows anterior to mouth-hooks; teeth diminish in size anteriorly and laterally so that the largest teeth are found nearest to the mouth-hooks. Anterior spiracles situated laterally near posterior margin of second segment; each composed of 7-10 digitate processes. Posterior spiracles borne on backwardly-directed projections of segment 12; peritreme

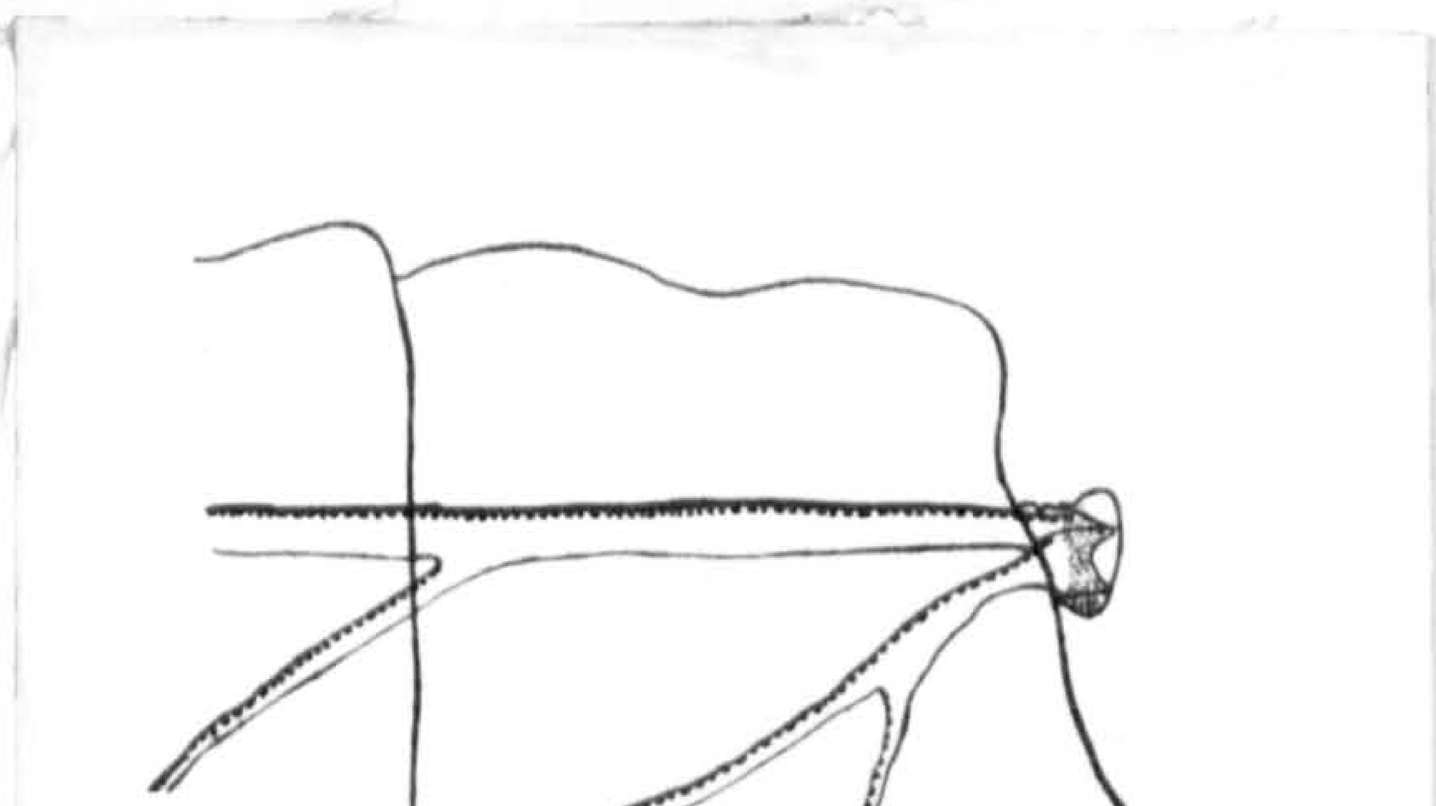
Oedoparea buccata



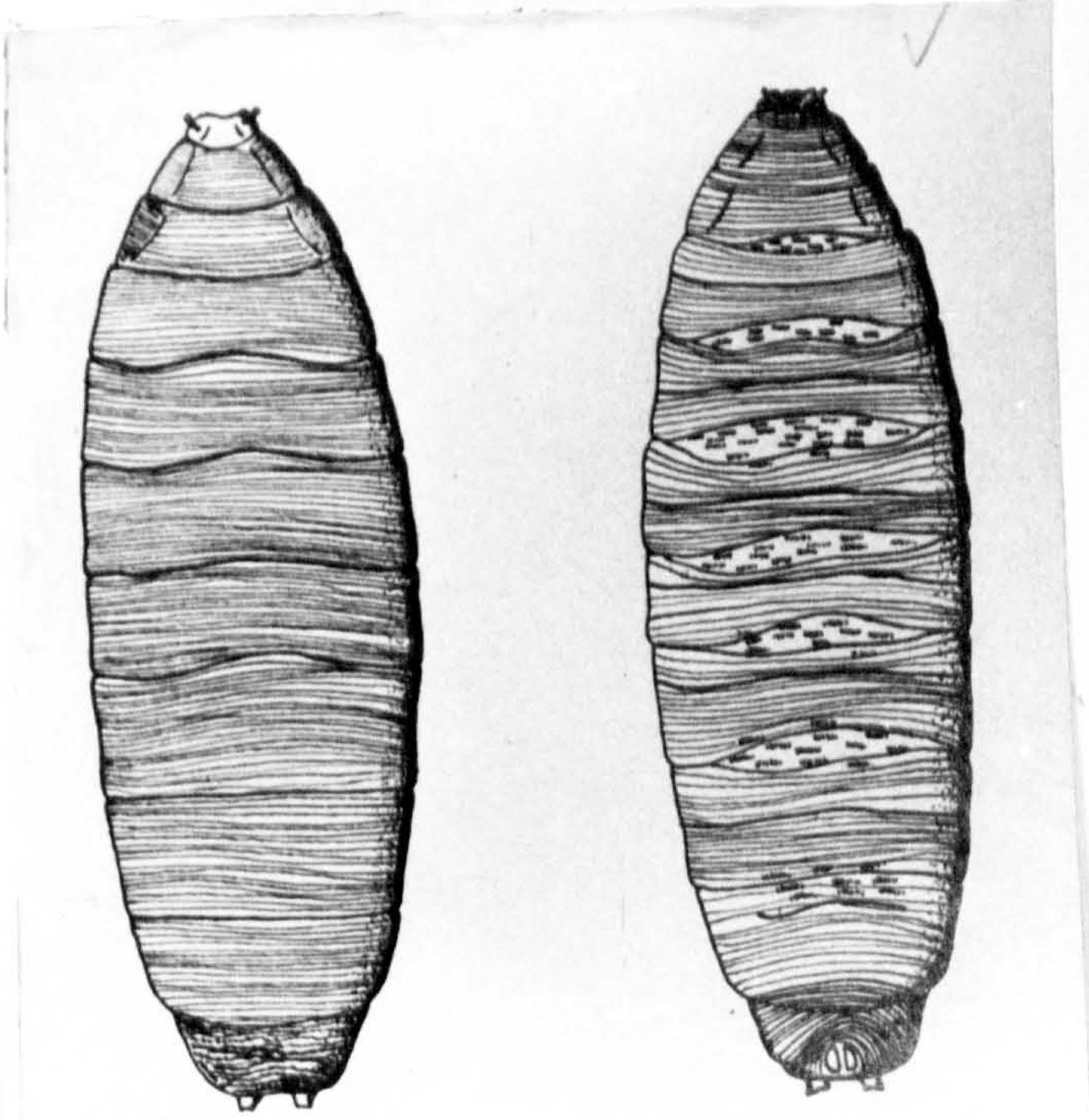
Third instar larva
anterior end, ventral view



Third instar larva
posterior end, posterior view



Third instar larva
posterior end, lateral view



dorsal ventral

puparium

light brown and roughly circular; stigmal plate has 3 roughly oval spiracular openings and two or three groups of very small, fine hairs, set at right angles to length of body. Spines. There are rows of groups of very small backwardly-directed spines on ventral surface at margins of segments 3 or 4 to 12; they are white to very light brown in colour. Anus opens towards end of 12th (last) segment; surrounded by four fused lobes; two - the largest - at the sides, one in front and the fourth - the smallest - behind; front one saddle-shaped giving appearance of being two lobes. There are some very small spines on inside face of the posterior lobe.

PUPARIUM.

Length from full grown larva, 6.5 - 7 mm; greatest depth (in region of segment 8) 1.6 - 1.8 mm; greatest width 1.6 - 1.8 mm. Light to dark brown with black lines between each segment on dorsal surface and (larval) posterior respiratory spiracles light brown; surface shining. Outline more cylindrical than ovate, tapering posteriorly and anteriorly to about one-third greatest width; in side view ventral line slopes down to segment 6 and is then straight to segment 11 where it rises slightly to end of segment 12; dorsal line convex, tapering at anterior end. Segmentation not clearly defined but there is usually a black edge to each segment on dorsal surface. First segment completely introverted; so that larval anterior spiracles are situated only a short distance from anterior end. Skin is thrown into fine transverse ridges each extending right round puparium; segments 3, 4 and 5 have whole skin ridged; 6-10 inclusive have the ridges (between 10 and 15 per segment) towards the centre of each segment; 11 and 12 all surface thrown into ridges. To allow emergence of adult, splits occur round anterior end, laterally and round sides at posterior margin of segment 4, so forming a dorsal and ventral flap and the emerging fly forces either one or the other open leaving the opposite flap more or less intact.

8 Remarks concerning the systematic position of Oe.buccata.

Some little doubt seems to exist over the systematic position of Oe.buccata, most dipterists placing this species in the family Coelopidae, but Hennig (1937) excludes it from this family and states that it is a species of Dryomyzidae. Fortunately, there is a species of wrack-breeding fly, Helcomyza ustulata, which is an undoubted species of Dryomyzidae and which, therefore, can be used as an indicator of the morphological features present in species of that family.

Backlund (1945b) briefly compared the third instar larva of Oe.buccata with a description of the supposed larva of H. ustulata which had been given by Gadeau de Kerville (1894) and came to the conclusion that the larva of Oe.buccata was so different from that of H. ustulata that Oe. buccata and H. ustulata could not possibly belong to the same family. Since Gadeau de Kerville did not rear adults from the larvae he described, there was some doubt over their identification and Backlund's conclusions could not go further than this. At this stage the larva described by Gadeau de Kerville need not have been that of a species of Dryomyzidae, in which case Oe. buccata could be a member of that family.

H. ustulata occurs at Whitburn and its larvae which have been found in the wrack beds there have been reared through to the adult stage. This has shown that the larva described by Gadeau de Kerville was not that of H.ustulata. The true larva of this species is described later (Ch.VII). However, the larva of Oe. buccata is, at least, as different from the true larva of H. ustulata as it is from the larva described by Gadeau de Kerville and Backlund's conclusion that these two species must belong to different families remains valid. Therefore Oedoparea buccata cannot possibly be a species of Dryomyzidae.

As can be seen from the descriptions and figures provided, the larva of Oe. buccata differs a good deal from that of the species of Coelopa, but this could still be only an intrafamilial difference. There seems no reason why Oe. buccata should not remain a member of the family Coelopidae, at least until further studies on the affinities of acalyptrous flies show that it is otherwise.

Chapter III.

LABORATORY CULTURES AND OBSERVATIONS.

Cultures of the four species of Coelopidae were maintained in jars containing split Laminaria stipes in a manner similar to that described for culturing C. frigida by Mayhew (1939) and Thompson (1951). For her genetical work Thompson found it most convenient to use small milk bottles which were stoppered with a plug of cotton wool. The present writer, for reasons given earlier, used 2-lb. size Kilner jars, the glass lids of which were replaced by circular pieces of perforated cardboard.

To prevent the split Laminaria stipes from drying up and withering they were placed on wet sand or cellulose wool. If there were no larvae feeding in the culture the Laminaria often became mouldy or covered in a thick opaque slime within a few days. Since eggs were not normally laid on weed in either of these conditions, it was either scraped and washed free of slime and mould or replaced by fresh weed. With larvae feeding on the Laminaria stipes, neither the mould nor the opaque slime developed, instead the weed decomposed quickly, a brown semifluid running from it. If this became too deep it was removed with a pipette to prevent the larvae from drowning.

Firm Laminaria stipes were collected from temporary wrack beds formed below the high tide level and which were free of animal life other than small nematodes which were usually present. The stipes were washed and examined in the laboratory to avoid accidently introducing other animals or their eggs into the cultures, but no attempt was made to free the Laminaria of the nematodes as they helped in the initial breakdown of the wrack tissues and when present in large numbers prevented the formation of moulds.

Because the wrack beds were visited frequently there was never any need to store Laminaria stipes for more than a day or two. If storage for longer periods is required it should be tightly packed in screw-top jars and kept in a cool, dark place (Thompson).

The cultures were kept at room temperature on a bench in the laboratory or in a room with a controlled temperature of 24°C.

Coelopa frigida.

Under the conditions described above most of the female flies eventually laid eggs. Usually one or two batches of between sixty and eighty eggs were laid but two females each laid a third batch. The eggs of a batch hatched within a few minutes of each other and the young larvae made their way into the soft Laminaria tissue. Here they could be found while in their first and sometimes in their second instars, their bodies immersed in the soft wrack and only their posterior spiracles visible. The third instar larvae were found both on and in the Laminaria stipes and wandering over the inside of the jar. They pupated in clusters in the upper, drier parts of the jar or on the top of the remaining stipes.

Thompson (1951), who bred a large number of samples, found that at 24°C. the time from egg laying to the emergence of the adult was between eleven and twelve days.

Coelopa pilipes.

Unlike C. frigida, females of C. pilipes were very reluctant to lay eggs in the described conditions. Of fifty-three jars, each containing one to four females and several males, set up at various times throughout the period during which the flies were found in the field, only five batches of eggs were laid. All five batches of eggs were laid on the outside surface of the Laminaria stipes.

The resulting larvae, however, thrived on the Laminaria stipes in much the same way as C. frigida and those larvae not killed and preserved eventually pupated in clusters in the same way.

At room temperature the total time from the laying of the egg until the emergence of the adult was from seventeen to twenty-five days. Various conditions which differed from those described above with regard to the amount of water in the culture jar, the state of decomposition of the wrack and the kind of wrack offered (i.e. Fucus instead of Laminaria) were found to be no more suitable for egg-laying. Since C. pilipes was being cultured chiefly to procure examples of its young stages for comparison with those of C. frigida and adequate material had been obtained for this purpose no further attempts were made to find better egg-laying conditions.

Orygma luctuosa.

Since the eggs of O. luctuosa were embedded in the wrack tissue, the most suitable Laminaria stipes for egg-laying was that which was soft but firm. Wrack in this state was quickly obtained by adding several nematodes of the species normally found in the wrack beds to the split Laminaria stipes in the culture jars set up for this Coelopid. The nematodes reproduced very quickly and their activities soon softened the top two or three millimetres of the cut surface of the stipes. If the flies were newly emerged they were placed with the Laminaria fresh from the wrack beds - the eggs in the female ripened whilst the surface layers of the weed were being softened. In the wild the larvae pupate in compressed wrack material and in the laboratory it was found that a layer of tightly-packed, moist cellulose wool placed in the bottom of the jar after all excess water had been removed was a suitable substitute.

Isolated pairs of flies in the culture jars mated frequently and at all times of the day. The flies were together for up to fifteen minutes, the female walking round the jar with the male in the copulatory position, but actual union lasted only three or four minutes. Males often tried to mate with etherised and immobile females.

The first eggs of each female were laid one to five days after copulation, this variation being probably due to the varying state of decomposition of the Laminaria provided. The frequent matings of the females, it seems, are not necessary for the production of fertile eggs, as four of six bred females, which were allowed to mate only once, laid fertile eggs; the other two dying without laying eggs after only a short life.

Up to about 180 eggs were laid by each female (nine bred flies laid 41, 63, 83, 89, 96, 113, 151, 178 and 179 eggs respectively) within twelve hours. Each egg was embedded in the soft tissue of the cut surface of the Laminaria stipes with its two long filaments either projecting into the air or lying along the wrack surface. A few eggs were sometimes laid amongst the wet cellulose wool but none was ever found laid on the surface of hard Laminaria stipes. The eggs were laid two to three millimetres apart, only their filaments occasionally touching. The filaments have a respiratory function and not just a mechanical one of preventing the egg from sinking into the soft wrack tissue, as eggs the filaments of which had been gently pushed just below the surface of the wrack or eggs in which the filaments had been severed at their base failed to hatch.

The eggs hatched in one to two days.

After hatching, the first instar larvae buried themselves in the soft wrack tissue, only their posterior spiracles with their circlet of hairs remaining in view. The second instar larvae sometimes fed in this position but more usually on the surface of the wrack. The third instar larvae fed on the surface of the wrack and were the only ones found away from the Laminaria stipes, on the lid or side of the jar.

In June at room temperature both the first and second instar stages each lasted 2 to 3 days. Great variation was found in the length of the third instar stage, however, some larvae feeding up quickly and pupating in ten days, others being still found on the wrack or wandering round the jar up to six weeks later. This was most likely due to the larvae not finding suitable places in which to pupate. At room temperature in winter the larvae were very lethargic and the stages lasted much longer, six to eight days for each of the first and second instar stages and ten to twelve weeks for that of the third instar.

The larvae pupated singly in either the moist, tightly-packed cellulose wool placed at the bottom of the jar for this purpose or inside pieces of moist wrack material. Pupae were never found lying either on or under the cellulose wool or in wet weed. Due to the larvae contracting after entering the pieces of wrack material etc., a small chamber was formed, the puparia remaining in contact with the wrack on their ventral surface only.

The pupal stage lasted from eight to thirteen days at room temperature in May, but larvae that pupated on 13th and 14th November, 1956, did not give adults until 20th-26th March, 1957, i.e. nineteen weeks later. This fits in with the diapause that is observed at this time in the life-history in the field.

Oedoparea buccata.

As will be shown later in this account, larvae of Oe. buccata did not survive well in wet conditions and since the larvae normally pupated under material at the bottom of the jar, the jar had to be well drained. For this purpose wand was found more suitable than cellulose wool; more could easily be added if that at the bottom of the jar got too wet, it was the natural pupating medium, and pupae in it could easily be removed. All excess water and semifluid lying on the sand was removed with a pipette.

Coition of isolated pairs of flies occurred frequently and at all times of the day. The male jumped on to the female from behind and gripped her round the abdomen with his metathoracic legs. The genital complex of the male was extended and union effected. The females were often walking round the jar with the male in the copulatory position for periods up to half an hour, but actual union seemed to last less than two minutes.

Eggs were laid one to three days after the first act of copulation of a pair had been observed. Over the next few days up to two hundred eggs were laid singly or in small groups of up to about fifteen, the eggs often just touching but never overlapping. Most were laid with the dorsal convex surface uppermost but occasionally they were laid on their side or with the ventral surface uppermost.

The state of the Laminaria stipes undoubtedly affects oviposition greatly, Oe. buccata being a much more selective fly than C. frigida with regard to egg-laying sites. Of 1,532 eggs laid by seventeen females of Oe. buccata, 1,481 were found on the outside surface of the split Laminaria stipes amongst various brandèd epiphytes etc. that grew on it or near the margins of the cut surface (i.e. on the assimilating layer), and only 51 were found on the more central tissue of the cut surface. They were always found on moist areas of the stipes but not where a film of water was present. Eggs of Oe. buccata were never laid anywhere other than on the Laminaria stipes provided. Females of C. frigida, however, have laid their eggs on Laminaria in all states of decomposition and on a few occasions on damp corks and on moist parts of the side of the jar.

The shell of the eggs of Oe. buccata were very sticky when damp and they were difficult to dislodge after the moisture round them had dried.

The first instar larvae either fed on the outside of the Laminaria stipes or buried themselves in the soft tissue leaving only their posterior spiracles in direct contact with the air. The older larvae usually fed on the outside of the weed, making inroads into the more central tissue or on the harder parts of the cut surface.

The first instar stage lasted three to four days and that of the second instar four to five days when the cultures were kept at room temperature, but great variation was found in the length of the third instar stage. The third instar larvae fed well and were active for about four weeks, but they then became very lethargic, remaining in small groups under the sand or under weed lying on it, and ate very little. This continued for five to six weeks when they eventually pupated. From the hatching of the egg until the resulting larvae pupated took about ten weeks at room temperature and six weeks at 24°C.

The larvae pupated in the sand at the bottom of the jar provided it was only damp and not waterlogged, in which case, the larvae wandered round the jar for several days, sometimes weeks, and usually died, although a small number sometimes managed to pupate on the drier parts of the Laminaria stipes or on the side of the jar. At the time for pupation the larvae were found together and often pupated in contact with one another, but they never formed masses of adhering pupae as in C. frigida. Most larvae of the same age pupated within a day or two of each other, but there were usually some in each culture which did not pupate until up to fifteen days later. It took two to three days for the puparia after first being formed to reach their dark-red to dark-brown coloration. At room temperature the pupal stage lasted eight weeks and at 24°C lasted three to four weeks.

The adults lived between two to three weeks at room temperature in jars containing moist cotton wool.

When conditions in the culture jar were too wet the young stages did not survive well and few adults resulted. The following four cultures show what occurred when the Laminaria stipes were soft and decomposing rapidly and the sand at the bottom of the jar became waterlogged because the excess water was not removed from the jar.

(1) Twenty eggs were laid. Of only seven larvae which matured and moved into the sand to pupate, four eventually did so and the other three died. Two adults emerged, the other two pupae died. Within two days of emerging both adults were dead, being found with their wings sticking to the wet side of the jar.

(2) Thirty-one eggs laid. Seven larvae reached their third instar. Six of these formed poorly-shaped puparia, one died. No adults emerged.

(3) Eighty-five eggs were laid. Seventy-two living first instar larvae were found on and in the soft weed and even more may actually have been present. Thirteen eventually became third instar larvae. The dead larvae were found in a layer of water covering the sand at the bottom of the jar, on the wet inside of the jar, and on the surface of the pulpy Laminaria tissue. Six of the thirteen larvae pupated on the side of the jar, level with the surface of the water and covered with a thin film of it. They remained light-brown or white in colour and no flies emerged from them. Three pupated on the side of the jar higher up and three adults emerged from them. The other four larvae were found dead in the water. The adults died within three days, two were found stuck to the side of the jar and one was in the water at the bottom of the jar.

(4) Fifty-three eggs were laid. Of eleven larvae that survived, seven pupated on top of the waterlogged sand but remained light-brown in colour. No flies emerged from them. The other four pupated near the top of the Laminaria stipes and eventually produced adults. Two of the adults died within six hours of emergence, another one died two days after emergence and the last one four days after emergence.

It will be seen that the wet conditions deleteriously affected all stages except possibly the egg, all or nearly all of which hatched (culture 3). From a total of 189 eggs laid, only 38 third instar larvae were produced. Of these, eight died in that instar, twenty-one died shortly after pupating, and the flies that emerged from the remaining nine all died within four days. As has been mentioned previously, in more normal conditions the larvae move downwards to pupate and do so in or under the sand, and it is interesting to see that whilst twenty-one larvae which went as far as was possible to attaining this situation eventually died, the nine which pupated in abnormal situations all produced adults.

In wet conditions such as these in which O. buccata suffers a great mortality, C. frigida endures with only slight losses, only one or two larvae occasionally being drowned.

Chapter IV.

THE BIOLOGY OF THE SPECIES.

COELOPA FRIGIDA AND C. PILIPES.

All the known species of Coelopidae occur on the sea-shore, the eggs and larvae are found in decomposing wrack-beds and their pupae either among the wrack or under nearby rocks and shingle. The adults are normally closely bound to the wrack-beds and their vicinity.

In the following account of observations made on the species of Coelopidae in the wild, Coelopa frigida and C. pilipes are treated together, and observations made on Orygma luctuosa and on Oedoparea buccata follow (Chapter V). It will become apparent when reading the account that noticeable differences occur in the ecology of the three genera, the significance of which is discussed later (p. 159).

The time and place of occurrence of the adults of C. frigida and C. pilipes.

The large autumn and winter populations of the flies.

At Whitburn the adults of Coelopa frigida and C. pilipes were most numerous during the autumn and winter months of the three years in which they were studied, i.e. after the large masses of wrack, in which their larvae feed, had been cast up on to the shore by the high equinoctial tides of September. It has previously been pointed out (p. 13) that the wrack beds formed at this time are larger than those formed at any other time and this is likely to be true for other European coasts. So these large autumn and winter populations are probably a common feature in the biology of both of the species. Reference by Oldroyd (1954) has already been made to this occurring in C. frigida on the south coast of England.

<u>Even distribution of the two species in the wrack string.</u>

Because of the vast number of each of the two species and their secretive habits, it was impossible to estimate their total population or to observe any absolute change in their state, It was found, however, that the two species occurred together and were evenly distributed along the length of the wrack string and under the adjacent stones. This made it possible to calculate the percentage rate of each of the two flies in the total Coelopa population at any given time.

The flies of both species bred in large wrack banks and, as will be shown later, only a few larvae were found in the wrack string, none being present between September and March, the most important breeding period in the life of the two species. The larvae pupated on the edge of the wrack banks and under stones on its landward side. The adults emerged in large numbers and dispersed along the shore about the high tide level, most moving southwards of the wrack banks. That the chief direction of the dispersion is southwards may be due to some intrinsic reason, but at Whitburn this happens to be the only direction in which they can conveniently move. Any inland dispersion is limited by the cliffs and the north is barred by a prominence. There is often a north wind, too. The wrack string and central regions at Whitburn therefore have a population of C. frigida and C. pilipes adults that had been bred in the wrack banks some few yards away. That the two species were fairly evenly distributed in these regions can be seen from table 3 (p. 64) which shows that the percentage of each species in the total Coelopa population in collections made at different parts of the wrack string differed by only small amounts.

Because of the nearness to the emerging flies, the population in the immediate vicinity of the wrack banks was liable to sudden increases, and the proportion of each of the flies in the total Coelopa population was not so even as that in the wrack string - nevertheless, the difference was within twenty per cent. Similar estimates

Table 3. Collections of C. frigida and C. pilipes adults made from different parts of the wrack string.

a. from the southern half of wrack string.
b. from the northern half of wrack string.

	C. frigida			C. pilipes			Percentage of Coelopa population	
	M.	F.	Total	M.	F.	Total	frigida	pilipes
On 8.xii.55								
a.	69	82	151	6	4	10	93.8	6.2
b.	81	94	175	7	6	13	93.1	6.9
On 30.i.56								
a.	9	8	17	47	50	97	14.9	85.1
b.	16	12	28	85	83	168	14.3	85.7
On 16.ii.56								
a.	13	20	33	111	84	195	14.5	85.5
b.	8	7	15	69	63	132	10.2	89.8
On 15.x.56								
a.	75	38	113	25	23	48	70.2	29.8
b.	41	43	84	23	14	37	69.4	30.6
On 12.xi.56								
a.	28	31	59	2	8	10	85.5	14.5
b.	47	63	110	9	9	18	85.9	14.1
On 15.xi.56								
a.	29	38	67	2	1	3	95.7	4.3
b.	47	72	119	3	9	12	90.8	9.2
On 17.xii.56								
a.	21	47	68	1	7	8	89.5	10.5
b.	10	64	74	4	5	9	89.2	10.8

for the flies actually occurring the wrack banks were not made, as far fewer flies were found there than were found under the nearby stones and in the wrack string at any time; and also because the numerous ways in which the flies could escape made it difficult to catch them.

Variations in the percentage composition of the population.

On several occasions during the periods September 1955, to March 1956, and September 1956, to March 1957, between one hundred and five hundred adults of Coelopa sp. were collected from the wrack string and its immediate vicinity to discover the percentage of the total population each of the two species represented at any given time and to observe any changes in the structure of the population. Because the wrack string and the pebbles under which the flies were found lay on sand and because most of the flies were caught during cold weather when they were lethargic, fairly large numbers could be collected with the aspirator. It should be stated that the two species of Coelopa cannot be distinguished when the flies are walking over wrack and sand with only their dorsal surfaces visible. Females of the two species cannot be separated with the naked eye even when closely examined; large males, however, can. But the quick rate at which the flies were caught (on some occasions large numbers being lifted into jars by a trowel) excludes any chance of one species being selected in favour of the other. The flies caught were killed and each examined under a binocular microscope. The results of the catches for September 1955 - March 1956 appear in table 4 (p. 67) and those for September 1956 - March 1957 in table 5 (p. 68); both sets of figures have been plotted against time in the graph shown on page 69.

The tables and graph show that in October, November and December of 1955 and in November and December of 1956 over 80 per cent of the total Coelopa population was C. frigida, but that during January of each period there was a fairly sudden swing in favour of C. pilipes and that before the end of the month C. pilipes was established at over 80% of the total population. In both periods the Coelopa population became greatly reduced during early March and only a few flies were found after the second week of that month. The figures for October, 1956, show that before C. frigida became the dominant species of the two, the flies occurred in about equal numbers.

The fluctuations in the general trend of the curves may have been caused by mass migration phenomena such as happened on 7th February 1956, 8th October 1956 and particularly on 5th November 1956, when only one species (C. frigida) was migrating at Whitburn, although both were present in large numbers in the wrack beds.

It was decided that it was not necessary to repeat the

Table 4. The proportion of C. frigida and of C. pilipes in the total Coelopa population at Whitburn for October 1955 - March 1956.

Date	C. frigida M.	C. frigida F.	C. frigida Total	C. pilipes M.	C. pilipes F.	C. pilipes Total	Percentage of Coelopa population: frigida	Percentage of Coelopa population: pilipes
18. ix.55	34	45	79	5	4	9	89.8	10.2
28. xi.55	55	75	130	4	4	8	94.2	5.8
8.xii.55	150	176	326	13	10	23	93.4	6.6
22.xii.55	52	87	139	5	10	15	90.3	9.7
12. i.56	40	78	118	12	16	28	80.8	19.2
19. i.56	55	83	138	202	166	368	27.3	72.7
30. i.56	25	20	45	132	133	265	14.5	85.5
*7. ii.56	35	61	96	102	80	182	34.5	65.5
16. ii.56	21	27	48	180	147	327	12.8	87.2
23. ii.56	9	11	20	79	82	161	11.1	89.9
29. ii.56	50	71	121	26	18	44	73.3	26.7
6.iii.56	10	21	31	28	52	80	27.9	72.1
Totals	536	755	1291	788	722	1510		

*Migrating flies caught in flight.

Table 5. The proportion of C. frigida and of C. pilipes in the total Coelopa population at Whitburn for September 1956 - February 1957

Date	C. frigida M.	C. frigida F.	C. frigida Total	C. pilipes M.	C. pilipes F.	C. pilipes Total	Percentage of Coelopa population: frigida	Percentage of Coelopa population: pilipes
24.ix.56	27	27	54	15	18	33	62.1	37.9
8. x.56	a29	56	85	35	67	102	45.5	54.5
15. x.56	116	81	197	48	37	85	69.9	30.1
25. x.56	25	33	58	33	24	57	50.4	49.6
29. x.56	20	21	41	19	18	37	52.6	47.4
1.xi.56	6	6	12	7	9	16	42.9	57.1
5.xi.56	41	67	108	19	36	55	66.3	33.7
*5.xi.56	a128 w 23	190 45	386	a 8 w 0	3 1	12	97.0	3.0
12.xi.56	75	94	169	11	17	28	85.8	14.2
15.xi.56	76	110	186	5	10	15	92.5	7.5
26.xi.56	35	64	99	3	3	6	94.3	5.7
10.xii56	41	35	76	4	1	5	93.8	6.2
17.xii56	31	111	142	5	12	17	89.3	10.7
7. i.57	42	117	159	7	8	15	91.4	8.6
21.i. 57	24	15	39	151	223	374	9.4	90.6
24. i.57	30	67	97	124	166	290	25.1	74.9
31. i.57	11	30	41	92	126	218	15.8	84.2
18.ii.57	4	5	9	35	55	90	9.1	90.9
25.ii.57	2	10	12	43	61	104	10.3	89.7
Total flies caught	786	1184	1970	664	895	1559		

*Migrating flies caught in the air (a) and on wrack (w)

The Structure of the Coelopa Population at Whitburn.

procedure the following year, but enough flies were collected to show that the same phenomena occurred again. (Table 6 and graph 1).

Table 6. The proportion of C. frigida and of C. pilipes in the total Coelopa population at Whitburn for September, 1957 - February 1958

Date	C. frigida M.	C. frigida F.	C. frigida Total	C. pilipes M.	C. pilipes F.	C. pilipes Total	Percentage of Coelopa population C. frigida	Percentage of Coelopa population C. pilipes
24. ix.57	41	77	118	7	8	15	88.7	11.3
16.xii.57	41	81	122	3	8	11	91.7	8.3
19.xii.57	27	43	70	10	4	14	83.3	16.7
20. i.58	7	4	11	72	68	140	7.3	92.7
14. ii.58	11	21	32	64	75	139	18.7	81.3

It would thus seem that at Whitburn at this period of the year a Coelopa population in which C. frigida is dominant for two to three months changes rather quickly to one in which C. pilipes is dominant for the next two months. It is very probable that the same thing takes place in other areas and that it reflects some significant feature of the biology of the larvae of the two species.

The presence of only a small number of flies in spring and summer.

From the decline in the number of flies in March of each year until the great increase in the following October few adults of either species were seen. This was mainly due to far fewer individuals being actually produced and even the small number that were produced were active because of the warmer weather and quickly dispersed. Though C. frigida and C. pilipes were scarce compared with the other species of fly present during March to October, no month of this period passed without a small number, sometimes only one or two of each, being seen.

The places of occurrence of the adults.

At Whitburn during the colder months of the year, the flies of both species were usually found together in large masses under stones near the wrack beds and under wrack in the wrack string. Near St. Mary's Island at this time of the year, besides the large clusters found under stones, many others were found in clefts and crannies in the clay at the base of the cliffs. The clefts could be prised open and pieces of clay broken away to reveal large numbers of the adults.

On warm days in winter the flies crawled out from under the stones and wrack and from the clefts, swarmed over the sand and wrack beds and made short flights in the vicinity. On occasions when this occurred, the disturbance of even only a few Laminaria stipes revealed teeming masses of the flies. At other times when the weather was warm, the flies rested on stones and on the cliff face.

During the warmer months of the year large clusters of flies never occurred and usually only odd flies were seen either under the rocks and wrack or in flight.

Miall (1895) mentions that C. frigida sometimes visits flowers, and although neither this species nor C. pilipes have been observed on flowers near Whitburn, a few of both species have been found among grass nearby. In general, the flies seem to be restricted to the wrack beds and their immediate vicinity, but they occasionally make mass migrations which are described later (Ch. VI).

Field observations on the larvae of the two species.

The larvae of the two species not intermingling.

Before ways of distinguishing between the larvae of Coelopa frigida and those of C. pilipes were found, collections of larvae found together in the wrack beds were allowed to produce flies in the laboratory, and it was observed that in nearly all cases the adults resulting from any particular collection of larvae were all of one species. The only mixed collections found are given in Table 7 (p. 72), which shows that on some occasions a few specimens of C. pilipes larvae were among a large number of those of C. frigida. No case of a few C. frigida larvae occurring among a mass of C. pilipes larvae was found. In trying to obtain adults from the larvae collected, sometimes many larvae died and these could have belonged to one species only of a mixed population, the other species surviving. But collections examined after the larvae could be distinguished showed that this was not so, and that, in general, the larvae of the two species did not occur together in the wrack beds. Of 73 collections of Coelopa larvae removed from the wrack beds, 54 were entirely C. frigida, 6 were chiefly C. frigida with a few C. pilipes, and 13 were entirely C. pilipes.

Table 7. The occurrence of C. frigida and C. pilipes larvae together.

Date	Place	Flies emerging from the larvae collected.			
30.xi.56	Near St.Mary's Is.	C. frigida	78	C. pilipes	1
30.xi.56	Near St.Mary's Is.	C. frigida	75	C. pilipes	1
16. x.57	Whitburn central region	C. frigida	65	C. pilipes	2
24. x.57	Whitburn wrack bank	C. frigida	84	C. pilipes	1
10. i.57	" " "	C. frigida	100	C. pilipes	2
16. i.57	" " "	C. frigida	42	C. pilipes	1

Place of occurrence of the larvae.

The larvae of both species occurred nearly always in wrack banks and were very rarely found in the wrack string.

On the few occasions in which they were present in the string, the string was deep, and was really a small wrack bank. Table 8 (p. 74) gives all the occasions in which larvae of C. frigida were found in the wrack string; C. pilipes larvae were never found there. Coelopa larvae were only rarely found in the wrack banks formed in the central region at Whitburn. These banks became contaminated with sand, which slows down the rate of decomposition of the wrack and reduces the temperature of the wrack bank.

Within a single wrack bank the larvae of each of the two species were not evenly distributed, large masses of larvae being separated by wrack which was devoid of or contained only a few larvae. They never occurred in the drier surface layers of the wrack beds but were found a few inches below in the wetter and more decomposed weed. Larvae found together were usually the same age. When mature third instar larvae were collected they successfully pupated and later produced flies without having to be supplied with more wrack than that in which they had been collected. But when large numbers of younger larvae found together were collected, most of them died unless they were given additional wrack material.

On occasions third instar larvae of C. frigida were found feeding in a horizontal layer, the wrack bed easily breaking away in the plane in which they fed, so that a

Table 8. The occurrence of C. frigida larvae in the wrack string.

Date	Place	Number of larvae found	Remarks
30. x.55	Whitburn central region	Several thousands	A small wrack bank in the wrack string up to 10ins. deep,4yds long. Had been formed for less than 10 days.
25. iv.56	Whitburn wrack string	6	In a 5 inch deep mass of compact wrack with plant debris isolated landward of wrack string. Many larvae of Fucellia maritima present.
30. iv.56	do.	2	Similar to one above,but was part of main string.
3. ix.56	do.	Several hundreds	Found on sand and fresh wet wrack in open position and being fed on by sparrows. Some larvae well below H.T.level. Must have been disturbed at last H.T.
3. ix.56	do.	1	In compact wrack and debris.
17. i.57	do.	1	
18. ii.57	do.	14	An old wrack string with plant debris,a newly formed one being present seaward of it.
16. x.57	do.	237 collected, being about 1/5 of total seen.	In a small wrack bank (2'6" by 1'6") in the wrack string.
24. x.57	do.	A collection of pupae from which emerged 84 C.frigida 1 C.pilipes	Found in an exposed position may have been washed there by the tide.
19.xii.57	do.	7	Found with a large number of Oe. buccata larvae.

sheet of fairly dry wrack, to which only one or two larvae adhered, could be removed exposing a white blanket of larvae on the remaining wrack. Mayhew (1939) also found them in a horizontal zone and believed that it was possibly due to their selecting an optimum temperature of about 30° C.

Vast numbers of larvae of C. frigida together or none at all:

On three occasions when large numbers of C. frigida larvae were present in the wrack banks, four 2-lb. Kilner jars were each filled with larvae and wrack material from the parts of the wrack banks in which the larvae occurred. The number of larvae, which on all three occasions were in their third instar, was found to be over six hundred in each jar. These collections of larvae were only a small fraction of those actually present in the wrack banks and at times the wrack banks at both Whitburn and near St.Mary's Island must have contained some hundreds of thousands of C. frigida larvae. Such vast numbers have already been alluded to by Taylor (1955) who found them on the South Devon coast.

Observations showed that the larvae of both species either occurred in large numbers in the wrack banks or were absent altogether. The females of C. frigida lay batches of usually between 60 and 90 eggs (Thompson) which hatch within a short time of each other, and since the females are likely to choose fairly similar sites, a large number of larvae soon result. Thompson (1951) also found that the larvae of

C. frigida do not survive well if only a few are present together. This is probably due to a slow rate of decomposition of the wrack, caused by only slight larval activity, with the consequence that little Laminaria stipes becomes suitable for feeding purposes. As was mentioned in the section dealing with laboratory observations, Laminaria stalk without larvae withers and dries up, but Laminaria stalk on which larvae are feeding quickly decomposes, becoming very soft and pulp-like, with a brown semi-liquid running from it; so there is little doubt that the activity of the larvae helps greatly in the decomposition of the wrack. Thus the facts that large numbers of eggs are laid and that small groups of larvae do not survive would account for the situation that occurs in the wild, in which if present at all, the larvae were usually present in large numbers. Because wrack strings contain only small masses of loose wrack material, and because they are well drained, they decompose at a much slower rate than the wrack banks and cannot support a large population of Coelopa larvae. Since the alternative to a large population of larvae is apparently the complete absence of larvae, it would account for their absence from the wrack strings. On the few occasions in which only a small number of larvae occurred together (Table 9, p.77), evidence was usually found suggesting that they were

Table 9. The occurrence of only small numbers of C. frigida larvae in or near wrack banks.

Date	Place	Number of larvae	Remarks
27.vii.56	Among pebbles and small pieces of wrack, one yard below wrack bank on rocks at Whitburn	5	Had probably been washed out of the wrack bank (in which there were many larvae) by tide.
24. ix.56	In wet and fresh-looking wrack below H.T. level at Whitburn.	28 were dispersed	The 19 larvae (along with 4 larvae of Fucellia maritima) were found about 15yds below the 28 larvae.
	In wet fragments of wrack 20yds below H.T. level and through which a steady stream of water from higher ground was flowing.	19 dispersed	All had been either washed out of the wrack bed or dragged down the shore by the ebbing tide.
18.iii.57	Wrack bank, Whitburn rocks.	18	The remains of the reduced winter population.
5.iii.58	Wrack bank, Whitburn rocks.	8	The last of the large winter population. The wrack bank though still large (8yds x 1 to 2yds x 9 to 12ins) was devoid of larvae except for these found together at the edge.
10.xii.55	Wrack bank mainland near St. Mary's Island.	11 dispersed	Survivors from a large population; these being found on landward edge, recent tides having almost reached this point.

survivors from a much larger mass of larvae which had been washed out of the wrack bank, or they were on wrack that had been pulled down the shore by an ebbing tide, (both cases giving dispersed larvae) or else they were the remnants of the large winter population (in which case they were still found close together).

Times of occurrence of Coelopa larvae.

The large numbers of larvae of C.ffigida were first found in September of each year and continued to be present until the following February. There was a decrease in their number until early March when no more were found, although the wrack banks were still large at this time. C. pilipes larvae occurred mainly from December to early March. As has been shown (p. 11) the wrack banks are a few degrees warmer than the surrounding air and this allows the two species of Coelopa to breed at this time of the year.

Larvae of C. frigida were found on a few occasions between March and the following September in each year. Times when only a small number of larvae were found appeared in tables 8 and 9 and times when a fairly large number were found have been entered in table 10. These large numbers of larvae were found spasmodically between June and August in wrack banks formed some yards seaward of the 'permanent' wrack beds in either the central region or on the rocks at

Whitburn. The wrack beds formed in these positions remained for only a week to a fortnight and were continually being altered in shape and structure by the tides. Because of the high summer temperature they decomposed very rapidly, the lower layers becoming immersed in a bnown semi-liquid which ran from the layers above.

Table 10. The occurrence of large groups of larvae of C. frigida during March - September.

Date	Place	Remarks
6. vi.56	New wrack bank 4 yds. seaward of 'permanent' one at Whitburn.	Vast number of large larvae which produced adults of the 'eximia' form.
16. vii.56	New wrack bank in central region at Whitburn.	A 2-lb jar sample of wrack contained over 600 third instar larvae.
27. vii.56	Wrack bank on rocks at Whitburn	This wrack bank was 3-4 yds below the 'permanent' wrack bank. Many larvae present.
20.viii.57	New wrack bank formed 20 yds below wrack string in central region.	Large number of larvae present.

Very rarely were larvae of either Coelopa species found in the large 'permanent' wrack bank on the rocks at Whitburn during March to September. During the latter part of this period, however, vast numbers of amphipods (Orchestia gammarella) were found there. Frequently small numbers of amphipods have been found among large groups of Coelopa larvae and vice versa, but on no occasion did large numbers of both amphipods and Coelopa occur together

Thus, in each of the three years in which they were studied at Whitburn, there occurred a large autumn-winter population of C. frigida and C. pilipes larvae, followed by two to three months (mid-March - May) in which very few larvae of C. frigida only occurred, and this in turn was followed by a period lasting until September during which C. frigida bred when the right conditions and opportunities were present giving rise to spasmodic occurrences of fair numbers of larvae. Although no larvae of C. pilipes were found during mid-March to September, there is a possibility that groups of them may have been overlooked.

<u>The production of the large 'eximia' form of C. frigida.</u>

Those larvae collected on 6th June 1956 (see Table 10) pupated the following day and five days later the flies emerged. All (51 males, 72 females) were of the large (9 mm. in male) bristly 'eximia' form, which until Mayhew's thesis had been thought to be a separate species (p. 16).

On 14th June 1956, 16 male and 9 female adults of C. frigida were caught in the same wrack bed from which the larvae had been removed, and all were of the 'eximia' form. At other times when adults of C. frigida have been caught and examined, less than 30% were of this size and structure. Mayhew, although he had no conclusive evidence, believed that temperature had a fairly direct effect on the size of the flies, a lower temperature allowing a longer period of development and consequently giving the larvae more opportunity to feed up. It is difficult to see how this could affect only a certain percentage of larvae living together in winter, and the finding of a 100 per cent 'eximia' population in June suggests that a low temperature is not the cause of their production. A more likely suggestion is that the warmer summer temperature would quickly make available a large quantity of suitably decomposed wrack for feeding the larvae, and since the population was less crowded than the winter ones, a greater supply of food would be available for each individual. The large larvae and consequent production of 'eximia' type flies would then result. In laboratory conditions larvae given a superfluous supply of partially decomposed Laminaria nearly always produced large flies.

The large adults resulting from the wild larvae were allowed to lay eggs and the ensuing larvae were kept in overcrowded conditions with a shortage of food. Small, less bristly flies resulted, a possibility described by Mayhew (1939).

The ecological separation of the two species.

One of the most interesting features in the biology of the Coelopidae concerns their ecology. C. frigida and C. pilipes are very similar ecologically and yet the two species occur together. Usually such closely related species differ in their geographical range, their habitat or their food. Gause (1934) propounded the theory that two species with similar ecology could not live together in the same area and this theory has since been supported by numerous examples (Allee et al.(1949) and Lack (1954) give the most important references). The converse of this theory, that two species occurring together do not have the same ecology is less easy to demonstrate. Lack (1945), however, showed that although their range overlaps, the cormorant Phalacrocorax carbo and the shag P. aristotelis have noticeable differences in their food requirements and in their nesting habitats.

In investigating the biology of C. frigida and C. pilipes, the following differences were found in the adult stages of the two species, Firstly, although the times of occurrence of both species overlapped, C. pilipes were found to be more abundant from mid-January to March, whilst C. frigida were found chiefly from November to mid-January (p. 65). Secondly, C. pilipes were more prone to infection by the phoretic mite Thinoseious fucicola than were C. frigida (p. 188). Thirdly, the two species behaved differently with regard to mass migrations (p. 106) and to other flight activity (p. 106); and fourthly, females of C. frigida readily laid eggs in conditions in which C. pilipes were very reluctant to do so. These four distinctions are enough to suggest that the ecology of the two species is different, but the most significant differences in the biology of the two species should occur in the most competitive stage - the larval stage - yet no such differences were discovered.

Larvae of both species were collected from all levels in the wrack banks, from both the landward and seaward sides, from Fucus only, from Laminaria only, and from mixed wrack, and if there is a factor which separates the larvae of these two species ecologically, it is not an obvious one of food or habitat. It is possible, however, that although the larvae of the two species ingest the same wrack material, they actually digest and absorb different components of it. A chemical analysis of the gut contents and of the excreta of the larvae of both species feeding on the same wrack material would help in solving this problem.

Mayhew (1939) suggested that C. pilipes larvae live in older wrack beds than C. frigida and this seems to be true at Whitburn, where figures given previously show that C. pilipes occurs after C. frigida in winter, although the change in the adult population is far more distinct than the corresponding change in the larval population. The theory would account for the absence of C. pilipes larvae during the spring and summer when only temporary wrack beds of fresh wrack are formed in which C. frigida manages to produce sporadic generations of flies.

Comparison of the anatomy of the two larvae (p. 24) suggests that C. frigida with longer hairs on its posterior spiracles and a greater number of anterior respiratory digits would occur in wetter and softer wrack material than C. pilipes. In fact, C. pilipes larvae, in general, occur in older and therefore more decomposed wrack, which is softer but not necessarily wetter than fresh wrack.

That some other controlling factor operates in the biology of the larvae is evident from the fact that after mid-March no larvae of either species were found in the 'permanent' wrack bank at Whitburn, although at this time it was still large and contained no animals other than the nematodes and oligochaetes which are always present, and adults of Coelopa still occurred though not so numerous as in the previous five months.

Chapter V.

THE BIOLOGY OF THE SPECIES

ORYGMA LUCTUOSA AND OEDOPAREA BUCCATA.

Natural History of Orygma luctuosa.

The occurrence of the adults.

There were two periods in each of the three years occupied in this study when adults of Orygma luctuosa were fairly common, one in the spring, from the end of April to the end of May, and the other in autumn, throughout September. During the rest of the year the flies were scarce or entirely absent. One or two of the spring adults were still to be found in June but none was ever found in July or August, and odd flies from the autumn adults continued to be found until January but none ever occurred in February or March. Orygma luctuosa adults were not as numerous as those of Oedoparea buccata (p. 93) and this, combined with the fact that they were more secretive than Oe. buccata, made their emergence in April and September less noticeable than the emergence of Oedoparea buccata adults in October.

Orygma luctuosa adults were found mainly in the wrack string and in the small wrack banks, but unlike Oe. buccata they were sometimes present in the large wrack banks at Whitburn and near St. Mary's Island. Normally they were never seen on the surface of the wrack string and the wrack had to be turned over to find them. When disturbed, the flies rarely took to flight, and when they did, it was only for a few inches; they preferred to run away and make their escape under the wrack and shingle.

Field life-history.

Eggs were very difficult to find and very few were seen in the large amount of wrack material collected and examined a few days after the emergence of the adults in April and September. Those that were seen had been laid singly, but a number were together in a small area inside soft weed, with their two filaments either lying along its surface or sticking into the air.

The larvae fed on wrack more decomposed than that used by Oe. buccata and they were usually found among a well-compressed mixture of mainly Fucus and Laminaria, with small amounts of other seaweeds. They occurred mainly in small wrack banks in the central region of the Whitburn shore, but odd specimens were found in the wrack string and in the large wrack bank. Only small groups of up to about 25 larvae occurred together, and single ones were often found; no masses of larvae like those occurring in C. pilipes and C. frigida, or even like the much smaller ones occurring in Oe. buccata were found. Most mature larvae were found in May, September and October, but a few were found in November and December.

Orygma luctuosa was the only species of the four Coelopidae studied that always pupated within the wrack bed itself. The larvae worked their way into pieces of tightly compressed wrack for the purpose, and since the larvae contracted in forming the puparia, the latter were usually found free in a small chamber in the wrack material.

The number of flies present.

The adults appeared to be evenly distributed along the length of the wrack string and small wrack banks, so that if the total number of flies occurring in a known fraction of the wrack material was known, the size of the total population present could be estimated. During one of the periods (September, 1956) when the fly was most common, the wrack string and small wrack banks contained about 165 yards of wrack, and in addition there were smaller strings of wrack, inland to the main one, measuring together 40 yards, giving a total of 205 yards of wrack material. In May, 1957, there were 200 yards of wrack material. On seven occasions during these periods an attempt was made to catch with an aspirator all the flies occurring in and under five stretches of wrack each 4 yards long, in order that the total size of the population could be calculated. The decrease in the population in the spring of 1957 was then examined by catching all the Orygma luctuosa flies possible in one hour on seven subsequent occasions. Only a few flies escaped, one or two being lost through their disappearing among the wrack and shingle or by taking to flight. The total number of flies present in the population at any given time (Table 11,p. 89) has been estimated on the assumption that 20% escaped, although fewer were actually seen to do so.

The number of flies caught on four occasions in each of the two populations examined are close enough (20-25 for September 1956; 28-46 for April-May 1957) to show that they are a fair basis for estimating the total population present. Although the size of neither the spring 1956 nor the autumn 1957 populations were calculated, they both were noticeably less than the two populations that were studied. It is probable that the maximum total population of Orygma luctuosa adults that occurred on the Whitburn shore at any one time during the periods of greatest abundance never exceeded seven or eight hundred. This is about one-quarter of that estimated for Oedoparea buccata (p. 93) and agrees well with the impression gained when working among them in the field. From the figures given for the population of spring 1957, it can be seen that within five weeks of the emergence of the flies, the population was reduced to only a few, and since in the laboratory adults live for 2 to 4 weeks at the most, less than twice this number, i.e. fourteen to sixteen hundred, were produced in each of the two seasons of each year.

Table 11. The size of the Orygma luctuosa population at Whitburn.

Date	Number of flies caught M.	F.	Total	Length of wrack string in yards	Fraction examined	Est. total population allowing 20% escape
10.ix.56	10	10	20	205	1/10	250
20.ix.56	17	4	21	205	1/10	260
24.ix.56	16	5	21	205	1/10	260
27.ix.56	20	5	25	205	1/10	310
30.iv.57	13	15	28	200	1/10	350
3. v.57	24	12	36	200	1/10	450
8. v.57	37	9	46	200	1/10 in 1hr.	570
13. v.57	19	12	31		1 hour	390
21. v.57	5	8	13		1 hour	160
28. v.57	4	2	6		1 hour	75
6.vi.57	0	1	1		1 hour	few
11.vi.57	2	1	3		1 hour	few
13.vi.57	0	0	0		1 hour	absent

NATURAL HISTORY OF OEDOPAREA BUCCATA.

The occurrence of the adults.

The adults of Oedoparea buccata began to emerge at Whitburn in the second week of October in each of the three years in which they were studied, and they became very common within a few days. They were continually found in large numbers from then until the second week in December in 1955, and until the third week in January in both 1957 and 1958. Then followed a rapid decrease from their abundancy to either extreme scarcity or complete absence, and this state remained until the emergence of fresh flies in the following October. During this period in 1956, one or two flies were found on occasions until April, but during the same period in 1957, the only flies found were some very small specimens in May. The flies never occurred in June, July or August in either of these years.

The adults were found in the wrack-string only and never occurred in the larger masses of wrack. If the clumps of Laminaria stalks which made up the wrack string were gently turned over, the flies could be seen walking among the weed and over the ground below, and after a few seconds some of them would take to flight settling again a few yards farther along the wrack or on the sand nearby. The adults were rarely seen to fly except when they were disturbed.

During the three to four months in which the adults were about there were two to four generations of the fly.

Field Life-History.

Shortly after the sudden emergence of the adults in October and December of each of the years 1956 and 1957, eggs were found, after assiduous search, on the Laminaria stipes in the wrack string. The Laminaria stipes at this time had been freshly cast up on the shore, were firm and covered in a mucilaginous secretion. The eggs were laid in groups on the surface of the Laminaria stipes, on fronds and among epiphytes growing on them.

The larvae fed on the outside of the wet, but well-drained Laminaria stipes and frond, making inroads into the more central tissue; the Laminaria thus came to have a corrugated appearance sometimes, but due to the weed decomposing, it soon became softer and lost this appearance. Larvae of Oe. buccata were never found in Fucus. Because of the rather exposed position in which the larvae fed and the continual risk of the wrack string drying out, the larvae were found only among the deep stipes of the wrack string which were often partly buried in damp sand. The larvae were found in isolated unevenly distributed groups along the whole length of the wrack string, the groups each containing between thirty and three hundred larvae. What looked like suitable habitats between the groups were devoid of the larvae. The larvae were found in the wrack string only and never in the larger wrack beds at Whitburn, nor did they ever occur near St. Mary's Island where only wrack banks are formed.

Wrack strings being thin, shallow beds of wrack are soon used up as a supply of food, and the Laminaria drying up quickly, soon becomes hard and withered and therefore unsuitable as food for the larvae of Oe. buccata. In 1957 this state was reached in the second week of February, the last larvae of Oe. buccata being found on the eleventh of that month. In 1956 and 1958, however, the wrack string was still suitable until April and larvae continued to be present until mid-March. It would thus seem that the length of the period in which larvae can exist is determined primarily by the availability of food and not by the climate, although, of course, climate is one of the chief factors which determine the size of the wrack string and is constantly affecting it. The short period for the larvae stages in the winter of 1956-57 may in some way account for the production of the very small specimens of Oe. buccata adults which were found in the following May.

The orange-brown puparia of Oe. buccata were found close together, but not touching or adhering as in Coelopa frigida, in the top layers of sand under the wrack string or under adjacent stones on its landward side.

The pupae which resulted from larvae occurring in January to March eventually gave rise to adults in the following October.

<u>The size of the population</u>.

The adults appeared to be evenly distributed along the whole length of the wrack string and the total number of flies occurring there was calculated in the same way as that described for Orygma luctuosa. During the period in which the fly was common, in December 1955, the wrack string contained about 165 yards of wrack, and in addition there were smaller strings of wrack, inland to the main one, measuring together 65 yards, giving a total of 230 yards of wrack material. In November, 1956, there were 220 yards and in December, 1957, 270 yards of wrack material. On seven occasions when the fly was common, five stretches of wrack, each three yards long and separated by about 30 yards, were examined and an attempt made to catch all the Oe. buccata adults occurring in them. The amount of wrack disturbed was thus between one-fourteenth and one-eighteenth of the total amount present in the wrack string. The depth and width of wrack varied so little along the length of the string as not to need consideration.

The results of the investigation appear in table 12.

Table 12. An estimation of the size of the Oe. buccata population when at its maximum.

Date	Number of flies caught M.	F.	total	Length of wrack string in yards	Fraction examined	Est. total population assuming 1/3 escaped
8.xii.55	26	24	50	230	1/15	1100
1. xi.56	64	7	71	220	1/15	1600
12. xi.56	53	28	81	220	1/15	1800
15. xi.56	46	19	65	220	1/15	1500
20. i.57	41	21	62	210	1/14	1300
16.xii.57	24	14	38	270	1/18	1000
19.xii.57	37	7	44	270	1/18	1200

It is difficult to estimate the number of flies that escaped capture - some, of course, were seen to do so, usually by taking flight, and no doubt there were a few not seen to escape. In the last column of the table the size of the population has been calculated assuming that one-third of the flies in the stretches of wrack examined escaped. Since it is certain that not so many as this actually did escape, the figures given represent outside estimates of the number of flies present.

The figures for each of the three seasons do not vary to a great extent so there are probably between one thousand and two thousand flies present at any one time between the emergence in October and their decrease nine to fourteen weeks later. During this time there are two to four generations of the fly, so there are probably not more than eight thousand individuals produced in a season.

Table 13 containing the numbers of flies caught during the decrease in the size of the population, in the two years this was studied, shows that the population falls from its height to zero within about two weeks. Because of the smaller number of flies present, a greater amount of wrack was examined in order that a more accurate estimate could be made.

Table 13. The decrease in the population of Oe. buccata.

Date	Number of flies caught			Length of wrack string in yards	Fraction examined	Est. total population assuming 1/3 escaped
	M.	F.	Total			
8.xii.55	26	24	50	230	1/15	1100
15.xii.55	8	2	10	230	1/15	225
18.xii.55	3	1	4	230	1/10	60
22.xii.55	0	0	0	330	1/4	0
20. i.57	41	21	62	210	1/14	1300
24. i.57	16	12	28	wrack str.	1/14	600
27. i.57	4	3	7	drying out	1/14	150
31. i.57	2	2	4	but length	1/4	25
4. ii.57	0	0	0	about same	1/4	0

Chapter VI.

MASS MIGRATIONAL FLIGHTS OF C.FRIGIDA AND C.PILIPES.

Mass migrational flights are well known to be undertaken by locusts, some butterflies and moths and certain dragonflies, but few observations of this nature have been made concerning flies. Species of Syrphidae have been seen making mass migrations by various students and a number of records have appeared in the literature (e.g.Lack and Lack (1951); Owen (1956); Parmenter (1953)) yet, although species of Coelopidae are known to make such flights, no account of one has been published.

Adults of Coelopa frigida and C. pilipes are normally so bound to the wrack beds and their immediate vicinity that any large scale flight activity is particularly noticeable. Observations at Whitburn showed that concerted flight activity of these species was of two kinds: mass flights in a restricted area and mass migrational flights in a particular direction.

Mass flights in a restricted area.

Usually when a rising tide had almost reached its height and the sea had begun to pervade the wrack banks and their immediate vicinity at Whitburn, the flies left the seaweed and adjacent shingle and walked or flew a yard or so inland where they immediately settled and crawled among the stones and gravel. However, on 28th November 1955, when there was a large number of C. frigida flies in and near the wrack bank, they began leaving their abode while the incoming tide was still about four yards away, and instead of settling a short distance inland they continued flying. Within a few minutes vast numbers of flies were flying up and down about a foot above the wrack and adjacent shingle. Some flies did eventually settle on the stones and gravel inland, but new flies constantly crawled to the surface of the wrack and shingle and commenced to fly.

Nearly all of the flies in the swarm flew backwards and forwards over the wrack and shingle roughly parallel to the shore and not entirely at random. The boundaries of the flight region were the seaward edge of the wrack bank and about three feet beyond the wrack bank on its other three sides.

Twenty minutes later the sea had permeated the wrack bank to a distance of about a foot. Many flies were still flying but a large number were walking among the stones immediately landward of the wrack bank. An hour later when the sea was only at the edge of the wrack bed only a few flies were flying and these rather haphazardly and not in a concerted flight. By this time most of the flies were either walking over the surface of the wrack bank and adjacent shingle or had already disappeared into the clefts and cavities below.

Similar flights were observed in December, 1955, and during October to December, 1956, both at Whitburn and near St. Mary's Island, Northumberland, but none was seen in 1957, probably because the adult population was not as large as in the previous two periods.

During October to December when large numbers of flies were present in the wrack bank and under adjacent stones, mass flights like those described above could be brought about, even when the tide was low, by disturbing the flies, e.g. by walking across the wrack banks. But such a mass flight lasted for only two to three minutes, after which the flies settled down again on or near the wrack bed. These flights could be made to occur over and over again by walking over the wrack bed, and since new flies were continually crawling from the wrack and pebbles, the number of flies taking part increased.

In the more normal flights previously described, it is quite probable that the movements and vibrations caused by the sea as the tide approached the wrack beds acted as a similar and more continuous 'disturbing factor' and so prolonged the duration of the mass flight.

A stick waved over a number of flies settled on a small area of the wrack bank caused them to take to flight immediately and this induced the flies on the rest of the wrack bed and on nearby stones to take to flight within a second or so. The first flies in the air probably acted as a 'disturbing factor' to those still on the wrack bed, and the 'disturbing factor' was possibly a visual one, like the waved stick, rather than the noise made by the buzzing of the flies.

This induced flight activity may be an important agent in the mass migrations now to be discussed.

Mass migrations of flies.

Mass migrations of Coelopa sp. have been observed near Whitburn on four occasions. Each will be described in turn, to be followed by a general discussion of the phenomena.

The first mass migration of Coelopa sp. was seen on 15th December 1955, a warm day after a spell of cold weather. Thousands of flies were flying along the shore in a southerly direction, at varying heights from ground level to 10 feet high. They were travelling roughly parallel to the beach at the high tide level and about 45° down a north-west wind. Flies continued to migrate throughout the time the writer was there - from 1225 to 1430 hours. The tide was low at 1225 hours but by 1430 hours had risen to permeate the wrack banks and was washing Coelopa larvae out of them. On 8th December, before this migration, 326 C. frigida were caught to 23 C. pilipes, i.e. C. frigida was 93% of the total population, and on 22nd December, after the migration, 139 C. frigida were caught to 15 C. pilipes, i.e. C. frigida was 90% of the total population, showing that the mass migration caused no significant alteration in the ratio of the two species.

The second mass migration observed occurred on 7th February 1956, which again was a warm day (temperature 8°C.) after a period of snow and ice. Thousands of flies were seen flying south at heights from 0-10 feet along the high tide level, 45° down a gentle north-west wind. The tide was low. The following migrants were caught with the kite net: C. frigida, 35 males, 61 females, total 96: C.pilipes, 102 males, 80 females, total 182.

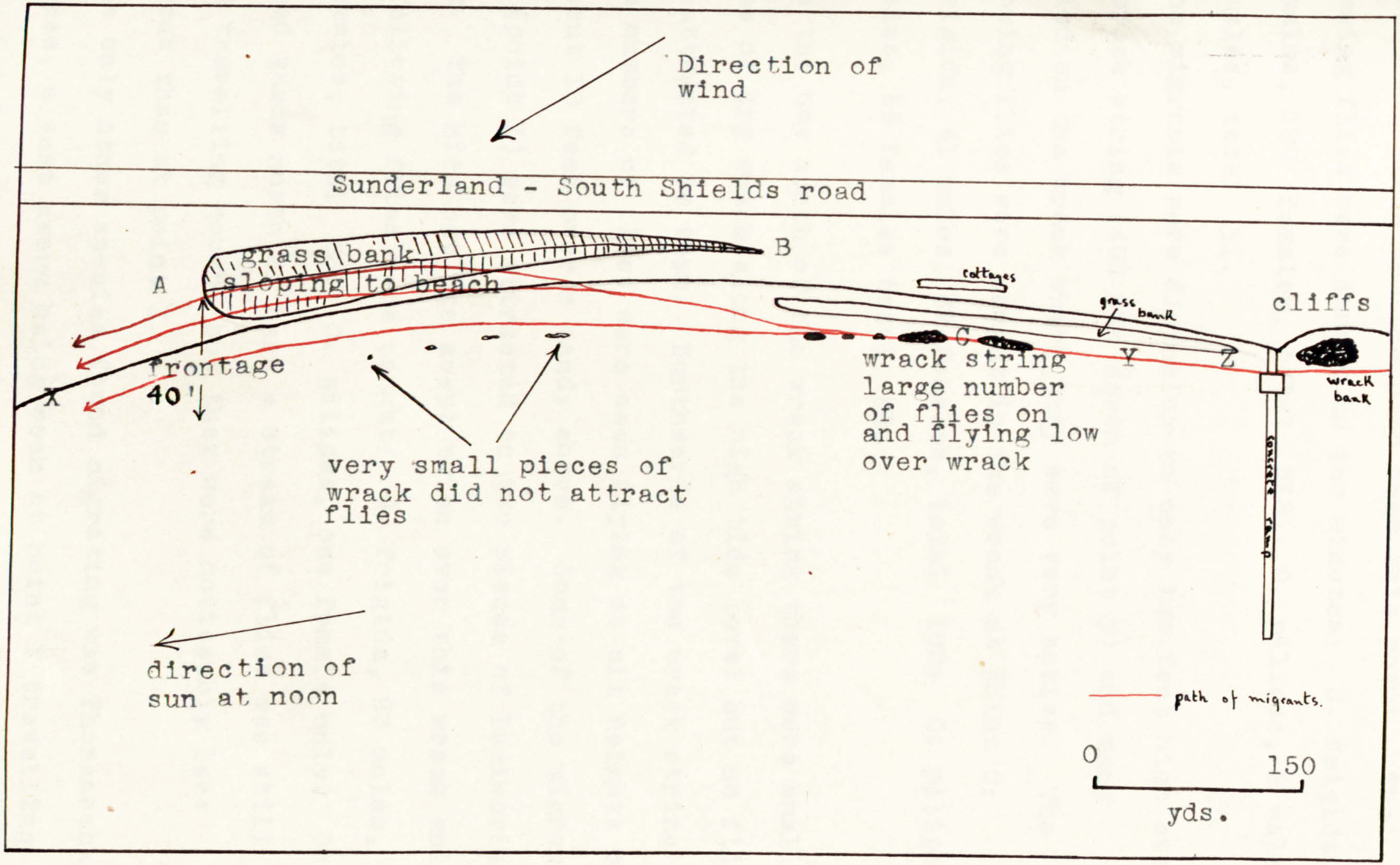
The third mass migration took place on 8th October 1956, which was a warm day (temperature 14.3°C.) although the sky was cloudy and the sun was not visible. The flies were flying roughly south from 0-10 feet high, along the high tide level, downwind to a very gentle northerly breeze. They continued flying all the time the writer was present from 1130 hours to 1300 hours.

A kite net was swept a few times across their path over a stony and sandy part of the beach to avoid disturbing and catching flies from the wrack beds. The following were caught; Coelopa frigida 85 (29 males and 56 females) and C. pilipes 102 (35 males and 67 females). No flies were seen migrating here the following day.

The fourth mass migration occurred on 5th November 56. It was a warm day (13.3°C) with the sun shining. The flies were travelling roughly south but following the coast line very closely. Standing in their path on the beach at point X (fig. on p.102), they appeared to be coming from inland but from point A, which is 15ft high, they were seen to be following the arc of the bay. From the ridge A to B the ground is flat inland, but on its other side slopes quickly to the beach. The flies were travelling on a frontage of about 40 feet, the most landward ones following this ridge and the most seaward ones at about the high tide level. That none went over the ridge may have been due to the north-westerly wind that was blowing across it. Nearly all the flies were flying between ground level and 10 feet, only an odd one being seen above this height. The tide was very low at 1110 hours when the mass migration was first seen.

It was found impossible to estimate the rate at which the flies were passing, as they often came in bursts of twenty to thirty in a small area. The kite net was swept several times across the path of the flies on the beach at point X, care being taken not to disturb flies which had settled on

A mass migrational flight of C. frigida at Whitburn.



the concrete steps and the path near this point. The following flies were caught in ten minutes: C. frigida, 128 males, 190 females, total 318; C. pilipes, 8 males, 3 females, total 11.

The migrants were flying up to only two feet high over the wrack string (400 yds north of point X) and many settled on the wrack where they were very active. The following flies were caught in the wrack at point C: C. frigida, 41 males, 67 females, total 108; C. pilipes, 19 males, 36 females total 55.

In the bay south of the wrack string there were small pieces of dry wrack along the high tide level but no flies were attracted to them. Northwards of the wrack string large numbers of flies were seen flying at all heights up to about 10 feet over a sandy shore. Some of the migrants here (point Z) were attracted to two pieces of Laminaria stalk. The kite net was swept twice over this wrack and the following flies were caught: C. frigida, 23 males, 45 females, total 68; C. pilipes, one female only. One hundred yards north of here a stream of flies was still found travelling south, but they were noticeably less numerous than at point X.

The only other species found migrating was Thoracochaeta zosterae, a vast swarm being seen at point Y travelling south, but it was quite distinct from the Coelopa sp. migration.

No flies were migrating when this stretch of beach was visited the following day.

The main points in the above mass migrations have been entered in Table 14 (p. 105) so that easy reference may be made concerning the subjects now to be discussed.

(1) Time of occurrence of the migrations.

All four mass migrations occurred on warm days during the colder months of the year. This is the only time that large numbers of Coelopa sp. occur at Whitburn and the migration took place two to three weeks after vast numbers of larvae had been found in the wrack beds.

(2) Direction.

The flies in each of the mass migrations were travelling south, parallel to the shore and either directly downwind or about 45° downwind. Probably the southerly direction of the migrations is usual as other species of insects have been observed frequently to migrate in one particular direction (see Williams (1958)). In the third and fourth mass migrations observed the flies were followed southwards until they entered the industrial area round the mouth of the River Wear. Because this area is inaccessible, it was impossible to discover whether the flies reached the mouth of the river or not, and, if they did, whether they continued travelling south over it or whether they followed the coast inland.

Table 14. Mass migrations of Coelopa sp. near Whitburn.

Number of migration	1.	2.	3.	4.
Date	15.xii.55	7.ii.56	8.x.56	5.xi.56
Conditions:				
Temperature	warm	8°C	14°C	13°C
Wind	N.W.wind	gentle N.W.wind	gentle N.wind cloudy, sun not visible	N.W.wind sun visible most of time
Tide	low	low	low	low
Time	1225-1430	1115-1305	1130-1300	1110-1335
	All had started before times given and continued after them.			
Direction of migration	South	South	South	South
Species taking part in migration	(no flies caught but most probably C.frig.)	C.frigida 35m. 61f. C.pilipes 102m.80f.	C.frigida 29m. 56f. C.pilipes 35m. 67f.	C.frigida 128m.190f. C.pilipes 8m. 3f.
Flying height of migrants	Mainly from ground level to 10ft high			
Frontage	(although not measured were similar to 4) 40ft.			
Speed	(similar to 4) Trotting speed of man. 6 m.p.h.			
Other species migrating at same time.	none	none	none	Thoracochaeta zosterae but was not with Coelopa sp.
Species on wrack.				C.frigida 41m. 67f. C.pilipes 19m. 36f.

Oldroyd (1954) thinks that "the resultant movement (of the mass migrations) is a combination of a more or less purposive flight parallel to the beach and an involuntary drift downwind" and these four migrations observed at Whitburn tend to support this idea.

(3) The species taking part.

In the mass migrations of 7th February 1956 and 8th October 1956, both species of Coelopa were well represented. On 5th November 1956, however, only very few (11 caught) C. pilipes were taking part in the mass migration compared with the number of C. frigida (318 caught), though about one third of the Coelopa flies in the wrack beds were of the former species. This difference in the flight activity of C. frigida and C. pilipes was found on one other occasion, though not a mass migration. On 24th September 1956, a mass of flies were flying back and forth over and alighting on some shingle immediately next to a clump of wrack in the wrack string at Whitburn. The kite net was swept a few times through the flying flies and the following were caught: C. frigida, 41 males, 70 females, total 111; C. pilipes, 1 male only. From the wrack the following flies were collected with an aspirator: C. frigida, 27 males, 27 females, total 54; C. pilipes, 15 males, 18 females, total 33.

(4) External conditions for migration.

It has been shown (p. 97) that when large numbers of

Coelopa species are present they can be made to take part in a mass flight if 'disturbed' naturally by the incoming tide or artificially by an observer walking among them, and that a group of flying flies can act as the 'disturbing factor' on other flies on the wrack bed thus causing them to fly. Mass migrations of Coelopa sp. occur at the same time of the year as these swarming flights, and it is possible that they commence after being disturbed in some way but the resulting flight is in one direction. It was found that migrating flies flew near to the surface of wrack beds in their path and this may induce flies in the wrack beds to take part in the migration. In the fourth migration observed at Whitburn there was a noticeably larger stream of flies south of the wrack beds than was approaching them from the north. This would suggest that flies in the Whitburn wrack beds joined in a mass migration that was initiated further up the coast.

When each of the migrations was observed the tide was low, so they differ from the swarming flights that seemed to require a sustained disturbance for their continuance. The lack of a continued tidal disturbance does not, however, preclude the possibility that the mass migrations were started by one in the first place, but it seems very unlikely that this occurred. It could be that the prospective migrants did not require an external initial stimulus and that their own increased activity in warmer weather and in overcrowded conditions was the immediate stimulus for mass migration.

(5) Reproductive state of migrants.

It is likely that the external conditions were only the immediate stimulus to migration and that the flies were in a state of readiness due to some intrinsic reason. A number of female C. frigida flies caught in the fourth migration were dissected and the number and state of the eggs contained were examined. The number of eggs found in each was as follows; 77, 60, 43, 17, 53, 0, 40, 63, 62, 85, 131, 72, 53, 93, 107, 58, 93, 33, 38, 140, 36, 77, 94, 117, 79, 39, 51, 60. Only one fly contained no eggs. The abdomen of nearly all of the flies was large and distended and contained an average of 67 eggs. Although there is much variation in the state of the females in a non-migratory population, on no occasion were so many females found with large abdomens and usually only 10% to 40% contained ripe eggs. The eggs in all were well formed, individual and appeared to be the same as when laid. The abdomen and eggs were, in fact, similar to those of females which had been kept 4 to 5 days in jars containing damp cellulose wool and which had not laid eggs.

Thus the migrating females had large numbers of eggs to lay and few suitable sites available for laying them in the overcrowded conditions present in the wrack beds. It is likely that in some way this would lead the C. frigida to migrate, and the external conditions described being propitious, the migrations took place. The non-migrating flies caught on the wrack beds were not preserved in fixative so unfortunately their reproductive state is not known.

Because nearly all of the flies contained fully developed eggs it means that the flies were at least three days old, as eggs in this state are not normally found until the females have reached that age.

(6) Place of origin of the flies caught.

While it was observed that the mass migration of 5th November, 1956, must have begun somewhere north of Whitburn, the flies caught south of the Whitburn wrack beds at point X ~~which~~ may have been bred either at Whitburn or north of there. Some indication of which of these alternatives is true comes from a study of the mite Thinoseius fucicola which, as shown later (p.188), is phoretic on various insects, particularly on C. frigida and C. pilipes.

All the mites attached to the bodies of a number of the mass migrating flies caught in flight at point X and on all those flies collected from the wrack string were counted. The detailed figures appear in Table 15 on page 190. It can be seen that 156 migrating flies of C. frigida bore a total of only 12 mites, while 108 C. frigida caught in the wrack bore 98 mites, i.e. there were 7 mites per 100 migrating flies compared with 91 mites per 100 flies from the wrack. On dates previous to 5th November, 1956, the number of mites attached to 100 flies was one to two hundred.

The low figure for mites found on these migrating flies could be attributed to either of two causes. Either the flies were fairly freshly emerged and the mites had not yet had time to infect them very heavily or the flies had not bred in the Whitburn wrack beds and had come from a wrack bank in which the mites were not so common. Since it has already been shown that the flies were at least three days old and since migrating flies were actually seen north of and approaching the Whitburn wrack beds, the second of these causes seems the more likely. The flies were, at the most, only temporarily attracted to the wrack string at Whitburn and, possibly because of the great amount of fly activity already present there, had continued the migration.

Although careful watch was kept, no mass migrations of these species were observed at Whitburn in the following autumn and winter, probably because their population were not as high as in the previous two years since less wrack had been cast up on the shore.

From the information given here it would seem that C. frigida and C. pilipes are good species of insects on which to make further observation and study of mass-migrational phenomena, and on which field experiments could be carried out on this important subject. The breeding ground of the flies are clearly visible, restricted and isolated; their life-histories are quick and large numbers of flies are soon produced; with more knowledge it should be possible to predict the time of the mass migrations; and the actual mass migrations in which they take part are conspicuous and easily observed.

PART III.

STUDIES ON OTHER WRACK FEEDING SPECIES.

Chapter VII

HELCOMYZA USTULATA (FAMILY DRYOMYZIDAE)

Helcomyza ustulata Curt. (Actora aestuum Mg.) is a well-known seashore fly belonging to the small acalyptrous family Dryomyzidae. Because of its silvery-grey colour, its fairly large size (up to 11 mms.) and its overt habits, it can easily be distinguished in the field from other wrack-frequenting flies. The larvae of members of the Dryomyzidae develop in decomposing vegetable matter but as far as is known H. ustulata is the only species of the family whose larvae are found in wrack beds.

The Young Stages.

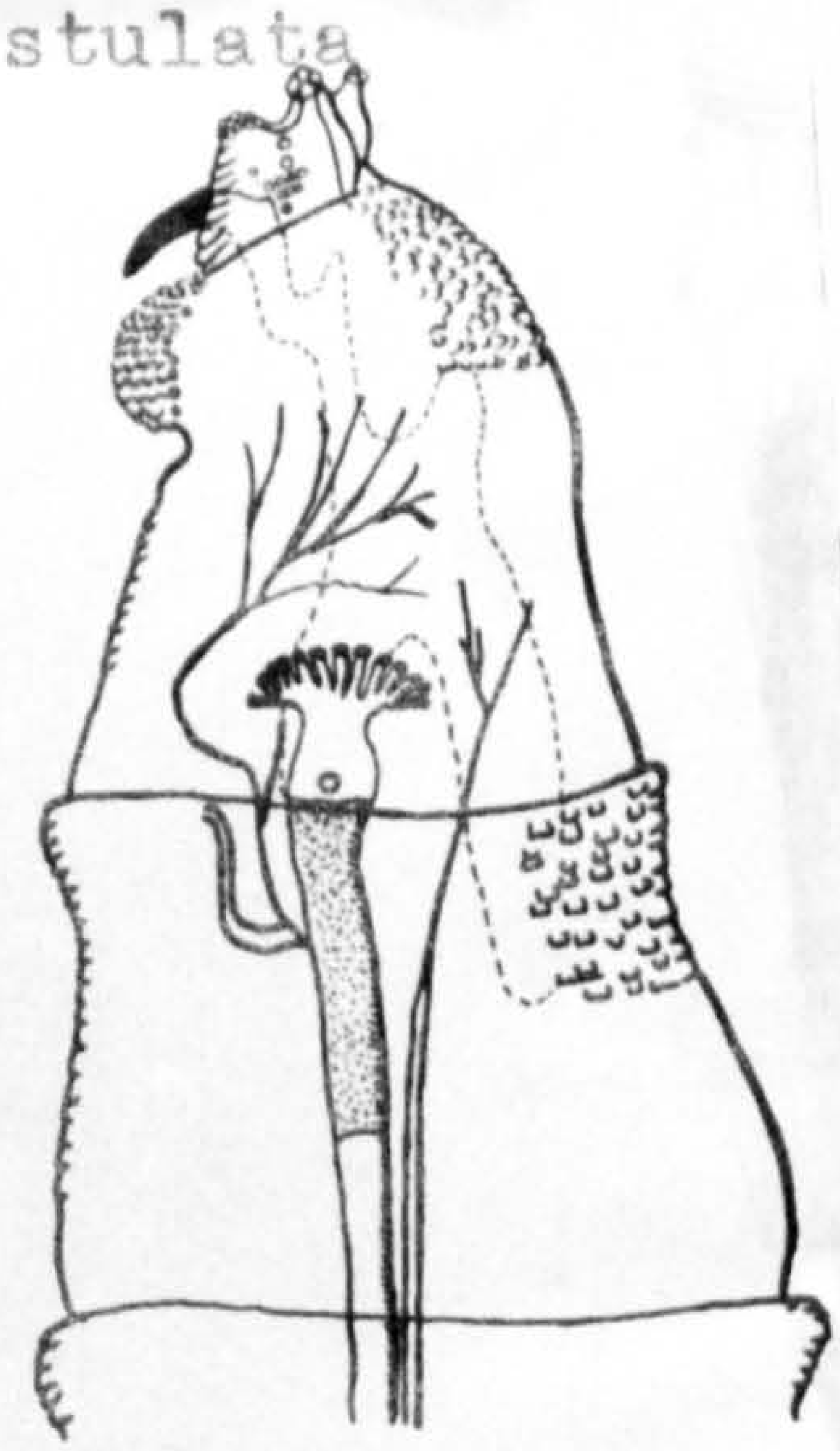
In 1894 Gadeau de Kerville described some larvae he found in muddy sand on the Normandy coast. Although he did not rear adults from these larvae, he considered them to belong to H. ustulata, as adults of this species were present in the locality. Summaries of de Kerville's description and his figures have been frequently given in the literature (e.g. Miall (1903), Czerny (1930), Seguy (1934), Colyer and Hammond (1951)), but the doubt that cannot be overlooked concerning the correct identification of the larvae he found is not mentioned by the last two works quoted above. This is probably due to the fact that in the sixty-four years since de Kerville's description appeared, no evidence has been presented to contradict his attribution of the larvae to H. ustulata.

Larvae differing greatly from those described by de Kerville were found in the wrack beds at Whitburn and the adults which were successfully reared from them proved to be H. ustulata. The true larva and puparium of Helcomyza ustulata can now be described for the first time.

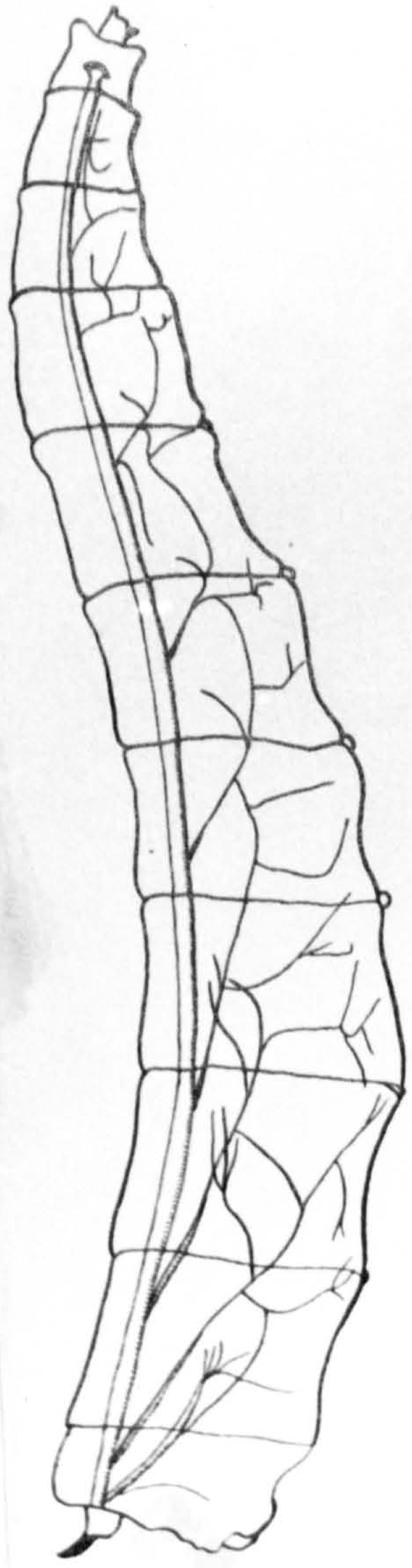
THIRD INSTAR LARVA.

Length mature 16 mms: greatest width (in region of ninth segment) 2.5 mms: greatest depth 2.5 mms. Shape cylindrical, narrowing anteriorly from segment 6, posterior end blunt. Colour white, save for brown sclerotised regions of first segment and posterior spiracles. Body composed of the normal twelve segments; segments 2-4 and 12 subequal in length, segments 5-11 subequal and larger. Segmental divisions clearly indicated ventrally by swellings at anterior margin of segments 5 to 12 and by 'collars' at anterior margin of segments 3 and 4; indicated dorsally by slight depression along each margin. First segment consists of two lobes separated by a median ventral groove at posterior end of

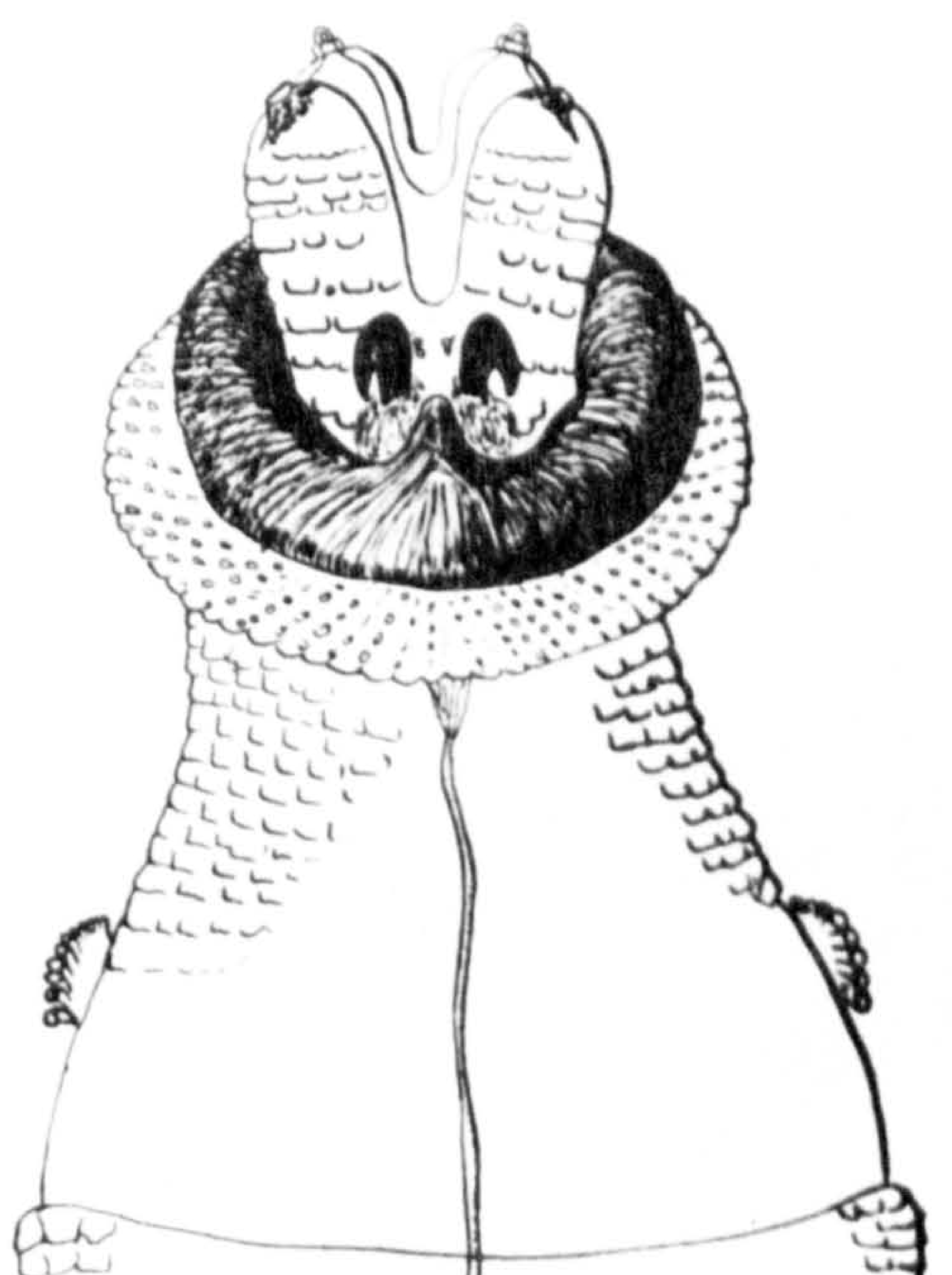
Helcomyza ustulata



Third instar larva
anterior end,
lateral view



Third instar larva
lateral view

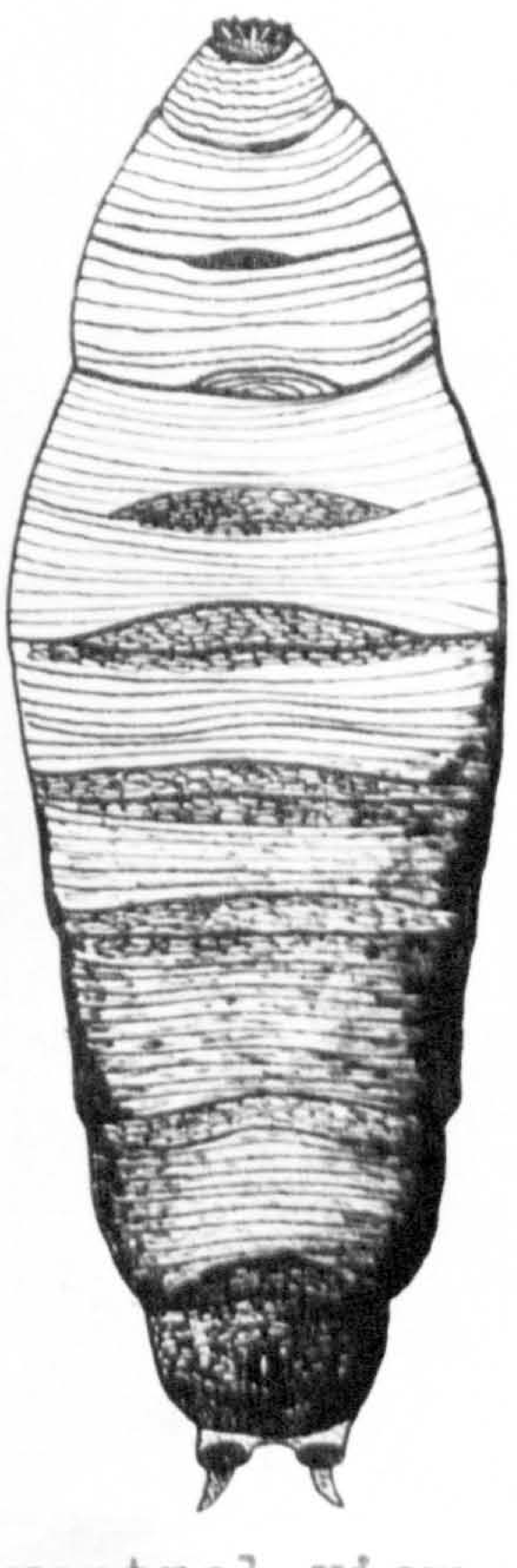


Third instar larva
anterior end, ventral view

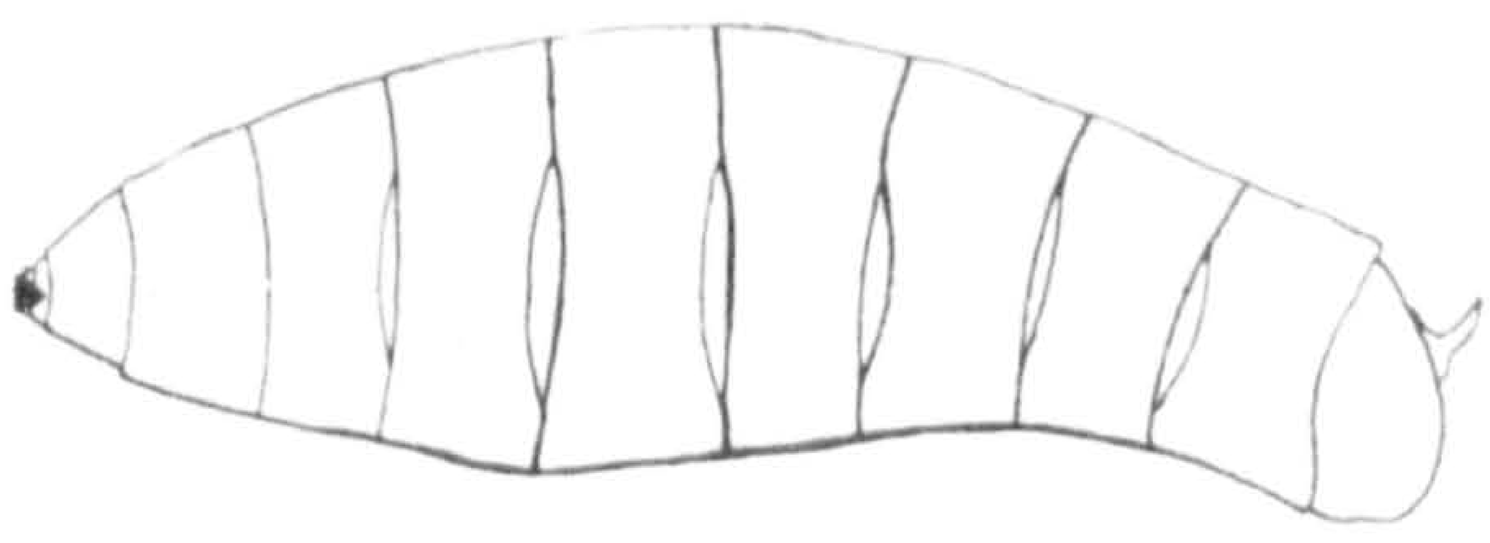
which is mouth. It bears in front, one on a fleshy projection of each lobe, a pair of small, two-segmented forwardly and upwardly-directed antennae; proximal segment cylindrical, the distal one hemispherical and only half diameter of former segment; rims of segments sclerotised. Posterior and ventral to antennae are the pair of 'Maxillary palps'. A third pair of sensory organs, (the smallest and just visible at X100), appear as papillae with round sclerotised bases. They are found, one on each lobe, antero-laterally to the mouth hooks. Each lobe bears a number of rows of sclerotised teeth; there are six or seven main rows of teeth each bearing 2-4 teeth on each of the two lobes, these teeth have brown sclerotised free edges and are of roughly the same size; smaller, less clearly defined teeth are found anterior to these. Anterior spiracles situated laterally near posterior margin of second segment; each composed of 8 to 11 fronto-laterally directed digitate processes. Posterior spiracles borne on backwardly-directed projections from segment 12; peritreme brown and roughly circular in shape; dorsal surface bears a strong, upwardly-directed, heavily sclerotised hook; stigmal plate bears three elongate-oval spiracular openings; no part bears hairs. Spines: there are no spines other than the ones mentioned below, but larva is covered with small backwardly-directed plates, whose

Helcomyza ustulata

Third instar larva
posterior end,
posterior view



ventral view



lateral outline

Puparium

posterior ends are free. Anus opens at approximately middle of ventral surface of last (12th) segment; anterior to anus are two small fleshy ridges, each set at about 45° to mid-ventral line, which join to form an arrow-shaped structure pointing forwards: the sides and posterior end of anus are provided with a small fleshy ridge, the anal (interior) side of which bears small brown spines.

PUPARIUM.

Length 8 mms., greatest width (at middle of segment 7) 3 mms. greatest depth (at segment)7) 2.5 mms. Dark brown, with hooks on (larval) posterior spiracles lighter brown. Outline roughly ovate with elongate posterior portion; tapering anteriorly from middle of segment 7 to less than one-quarter of greatest width, and tapering more gently posteriorly to about half of greatest width. In side view ventral line slopes gently down to end of segment 5, then rises to end of segment 8, then slopes down for rest of its length; dorsal line convex, tapering towards posterior end. Segmentation clearly defined for most part; first segment completely introverted so that larval anterior spiracles are situated at beginning of puparium. Skin in slight ridges which extend right round body, for its whole length. Sides of anus black. Small plates on ventral surface clearly indicated.

Laboratory observations.

On several occasions larvae which were found in the wrack beds at Whitburn were brought back to the laboratory with the wrack material in which they were found, so that observations could be carried out on the life-history of the fly. The larvae, which were in their final instar when found, were kept either at room temperature on the laboratory bench or at 24° C. Those kept at room temperature were very lethargic and were usually found together in a large group at the bottom of the jar. Larvae kept at 24° C. were sometimes seen moving among the wrack material but were often found together motionless. In both cases only about one-quarter, of the larvae pupated successfully and eventually produced adults.

Larvae found in the field in July and kept in the laboratory at room temperature gave adults in September after a pupal stage lasting about four weeks, whilst larvae collected in September and kept at room temperature gave adults in the following April and May after a pupal stage lasting three to four months. This aggees well with the diapause that is found in this species in the field. One group of larvae, however, which were collected on 27th September, 1956, and kept at room temperature did not pupate until the last week in March, 1957, and produced flies in mid-April. As expected, young stages kept at

24°C. produced adults quicker than those kept at room temperature, larvae found in September producing flies in January after a pupal stage lasting 14-20 days.

Some of the reared adults and adults caught in the field were placed in jars containing either wrack material similar to that in which the larvae were found on fresh Laminaria stipes. All told twenty-nine females were placed with males in culture jars and although the flies were seen to mate frequently all the female flies died within a week without laying eggs.

Field Life-history.

The adults of Helcomyza ustulata first occurred at Whitburn in early June of each of the three years in which this species was studied and they continued to be present until the end of that month. They did not appear again until early September when they were present again for a period of about four weeks. None was then found until the following June. Full grown larvae were found in July, August, September and early October. No eggs or younger larvae were ever found although they were searched for in both June and September of 1957.

Bearing in mind the laboratory observations previously described, it would seem that the June flies laid eggs which gave rise to the larvae found in July and August and which developed into the September flies; the latter produced the larvae of September and early October and these, after a diapause, most likely in the pupal stage, gave adults in the following June. Although neither larvae nor pupae were found in the wrack beds or their immediate vicinity during winter and spring, one of these stages must surely have been there.

Both the adults and larvae of H. ustulata were very restricted with regard to their distribution at Whitburn, the larvae being confined to small, fairly dry, wrack beds in the central region there, and to parts of the wrack string near this region; whilst the adults were found on the sand in the vicinity of this wrack material. Neither larvae nor adults were ever found in the wrack banks at Whitburn and the species never occurred near St. Mary's Island where only wrack banks are formed. In August, 1956, adults and larvae were found in a wrack string at Llandudno, Wales, and in September, 1957, adults but no larvae, were found in a wrack string at Bamburgh, Northumberland. The presence of the fly at Bamburgh, which is forty miles north of St. Mary's Island shows that it is not for any geographical reason that the species does not occur at the latter place. In each of the areas in which H. ustulata was found the wrack was fairly dry, in small amounts and lying on sand, which facilitates drainage.

The adults of H. ustulata were the least secretive of all the flies that bred in the wrack beds at Whitburn, and they were usually found exposed on the sand in the central region from the high tide line to about twenty yards down the shore. There were small pieces of dry wrack lying on the sand but the flies did not appear to be attracted to them. When approached the flies flew a yard or two and then alighted on the sand again. This short, quick flight, often repeated several times made the flies difficult to catch. The females seemed less active than the males but were far fewer in number, about ten males being caught to each female.

The larvae were found in small masses of fairly dry wrack in the high tide position and often contaminated with sand and tidal debris. With them have occurred at various times the larvae of Fannia canicularis, of Fucellia maritima and of Thoracochaeta zosterae. On one occasion (27th September, 1956) larvae of all of these four species occurred together along with larvae of Tinea pallescentella (Lepidoptera) and various other insects.

It can be seen that both the larvae and adults of H. ustulata live in fairly dry habitats, indeed, neither are adapted to living in wet wrack beds. The larvae are devoid of 'hairs' on their posterior spiracles and of large spines on their ventral surface, and thus they lack both features shown (p.162) to be most suitable adaptations for those species (Coelopa frigida, C. pilipes, Orygma luctuosa at times, and Thoracochaeta zosterae) that occur in larger and wetter wrack beds, whilst the adults, unlike those of Coelopa sp., easily stick to any wet surface.

Chapter VIII.

FUCELLIA MARITIMA (FAMILY MUSCIDAE).

Species of the genus Fucellia (Muscidae) are well known to be seashore-inhabiting flies; F. Maritima and F. fucorum frequent wrack beds on European shores, F. intermedia, F. pictipennis, F. ariciformis and F. fucorum have all been found in littoral regions of Greenland whilst the last three species have been found on arctic American shores (Madsen (1936)).

Very little appears to be known of the life history and ecology of any of these species. Backlund (1945) reared F. maritima adults from samples of wrack collected on the coast of Sweden, and Madsen (1936) found the larvae of F. ariciformis in clay flats near river mouths and lagoons in Greenland.

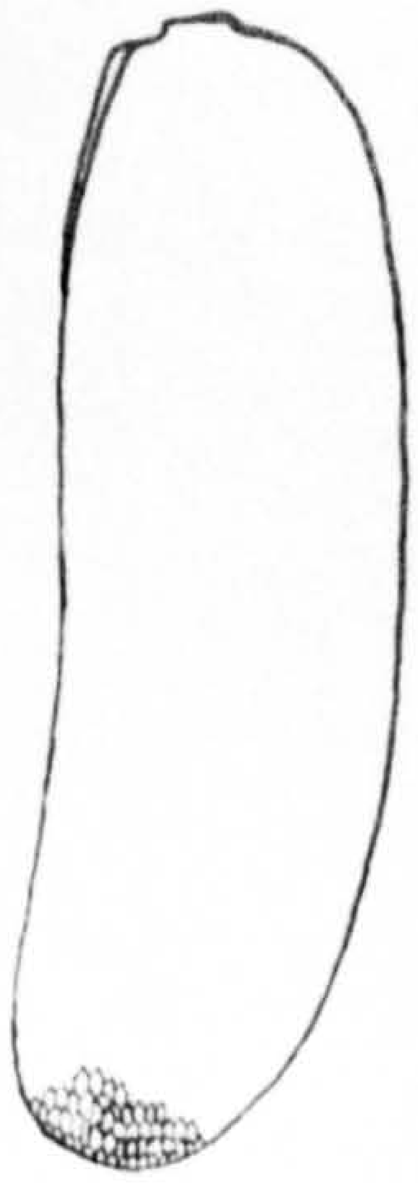
Of the two species, F. fucorum and F. maritima, which are found in Britain only the latter occurred at Whitburn. The young stages of this species are here described for the first time.

EGG

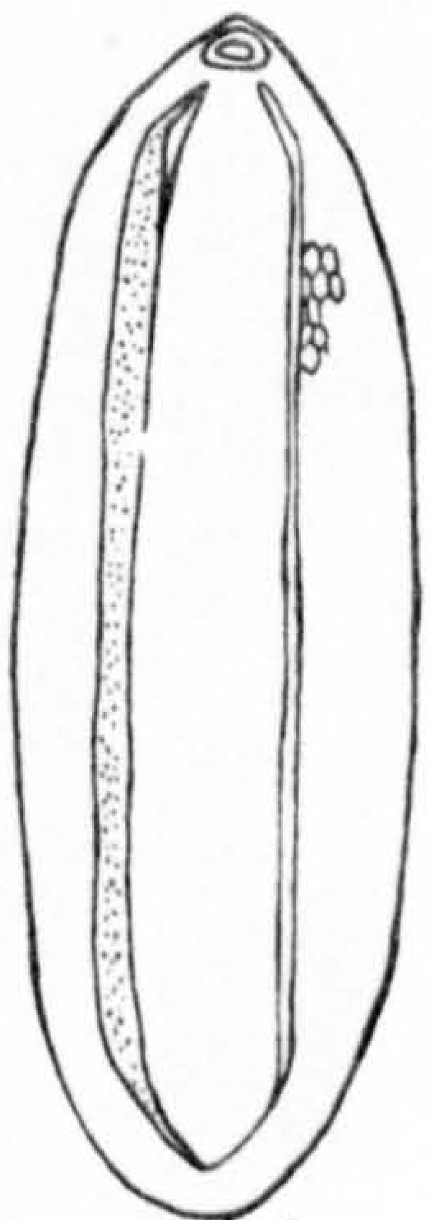
Length 1 mm. In dorsal view outline elongate-oval, Fucellia maritima

Egg

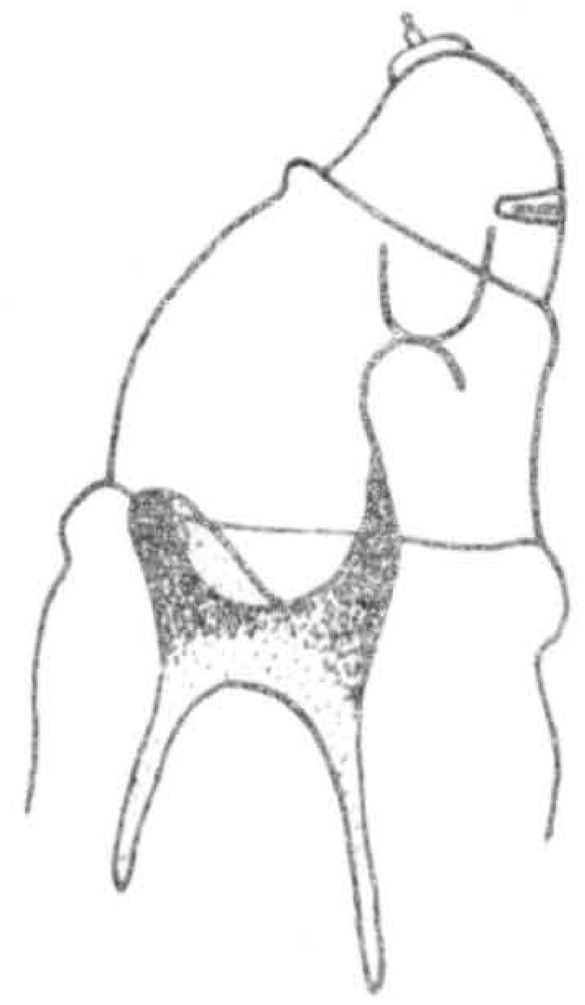
anterior view



lateral view

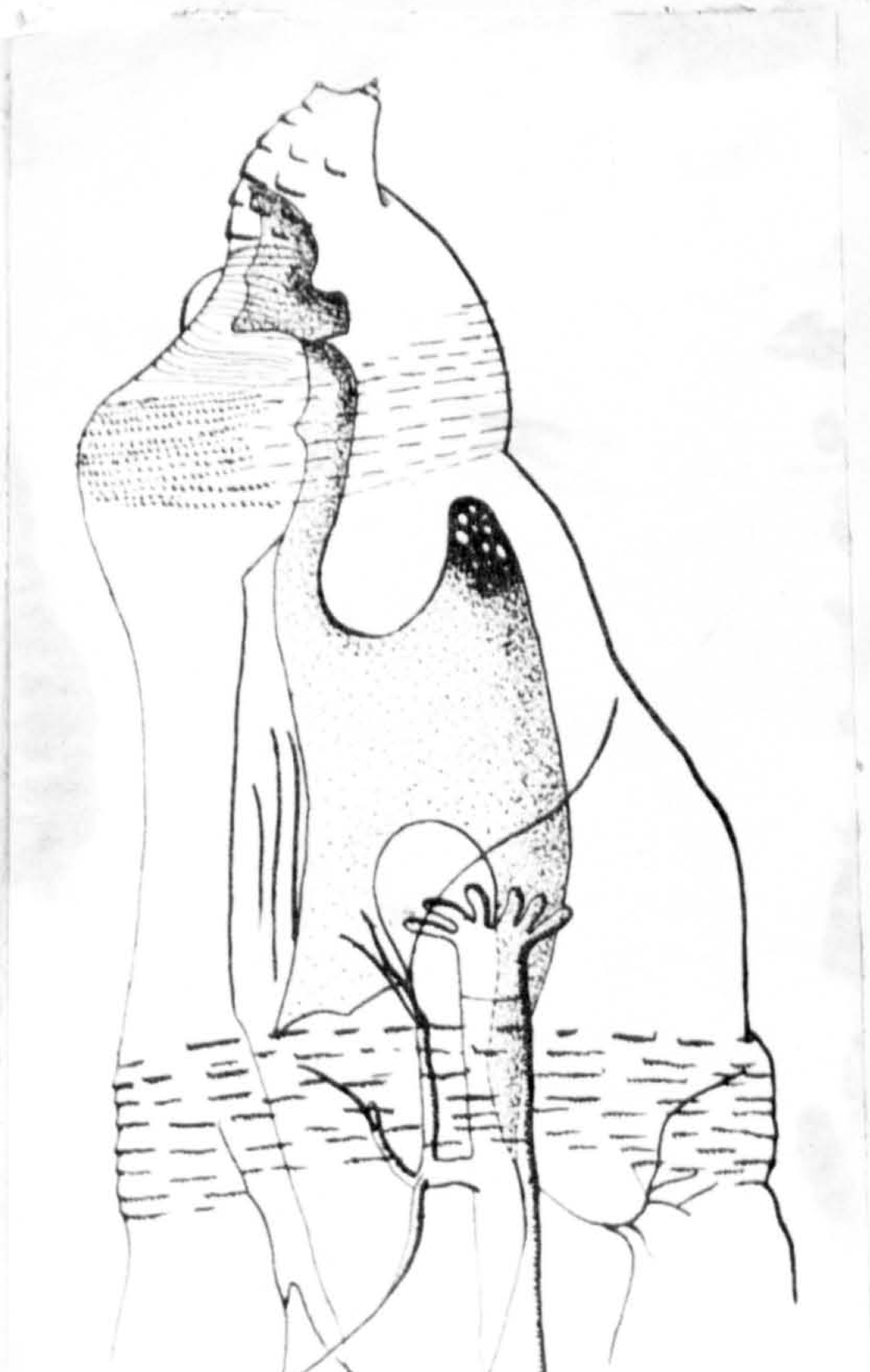


one ridge split

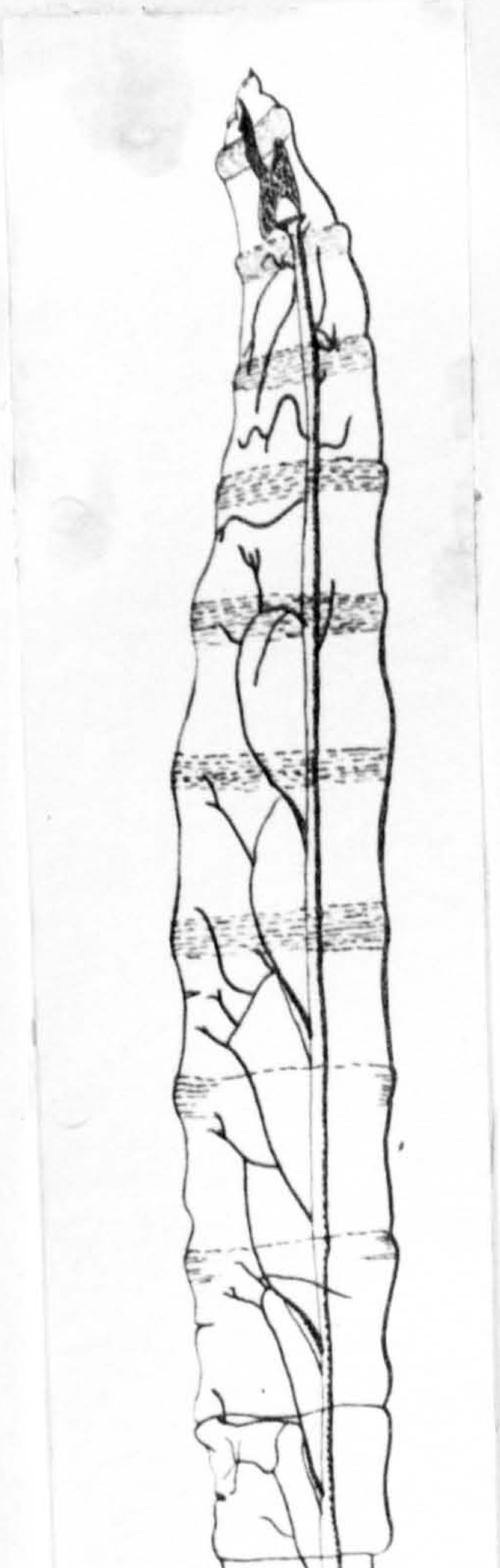


First instar larva

lateral view
anterior end



Third instar larva
anterior end, lateral view



Third instar larva
lateral view

posterior end slightly more rounded than anterior end; in side view longitudinal axis curved. Chorion with two, white, thickened ridges stretching for about seven-eighths length of egg: and parallel for most of their length but approach each other anteriorly and posteriorly; ridges thicker and more obvious at anterior end. In newly laid eggs the ridges are usually close together but as the egg develops the ridges separate, and a split eventually occurs down the middle of one or both of them to allow eclosion of the larva. Whole chorion, except that between ridges, covered with a network of white slightly-raised hexagons. Raised circular thickening of chorion at anterior end with a central depression.

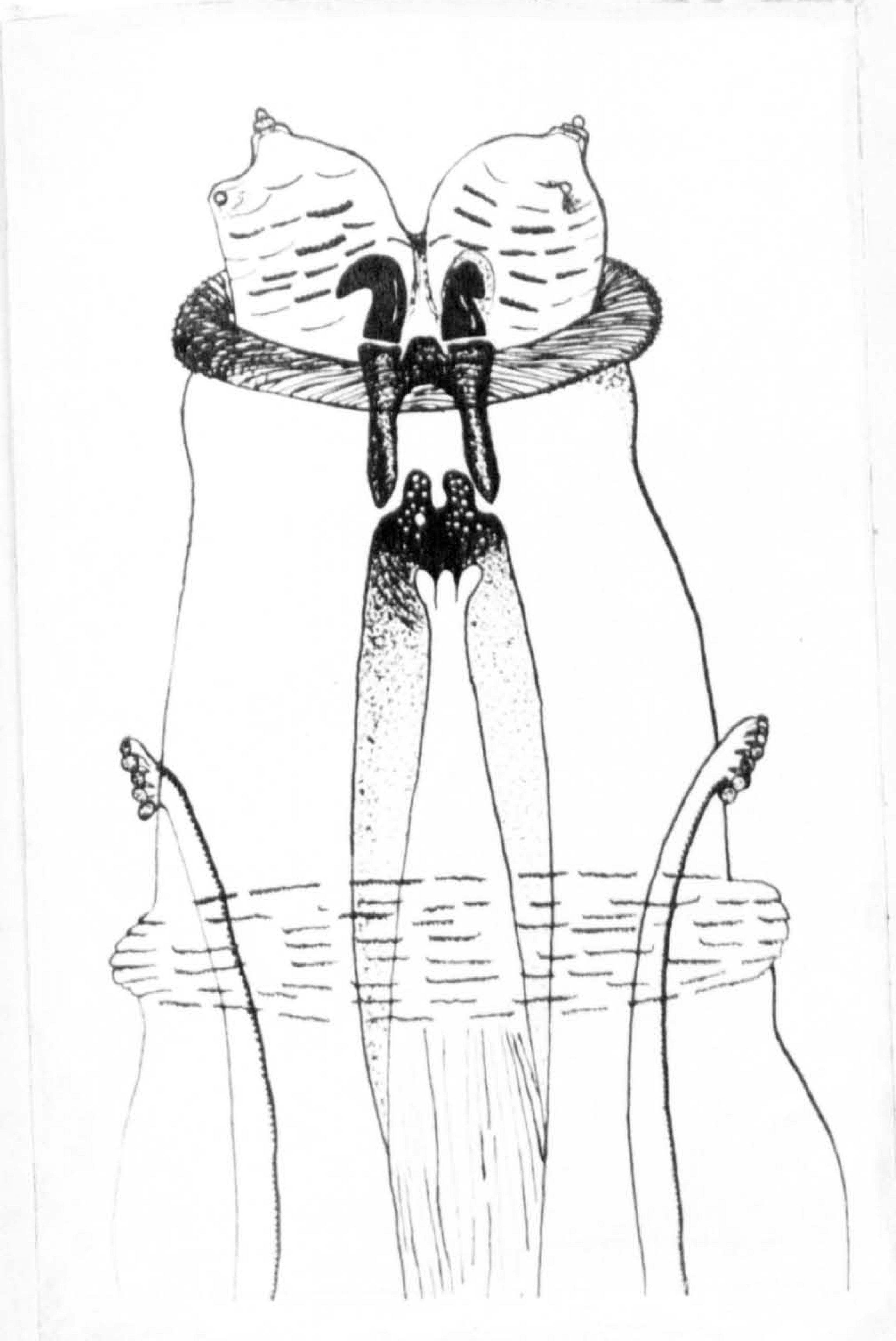
FIRST INSTAR LARVA.

Length 1.2 to 2.2 mms. when extended. First segment bears, in front of mouth, a pair of large comb-like mouth hooks, the teeth of which are curved downwards and backwards. Spines in rough rows extending right round larva in marginal positions of segments 2-12; they are white, very small and directed backwards. Last segment with wart-like swellings similar to third instar larva.

SECOND INSTAR LARVA.

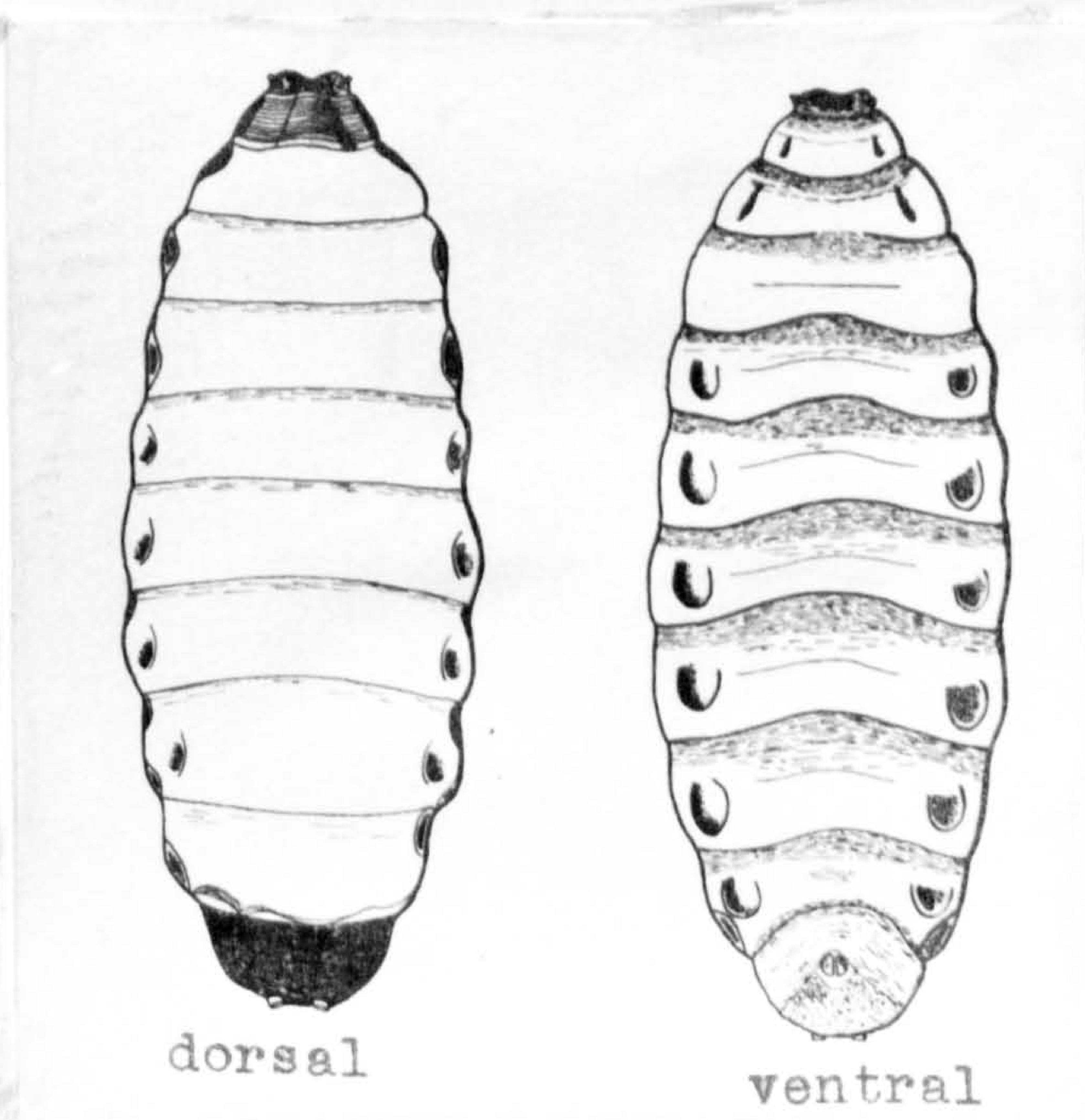
Length 2.4 to 5.3 mms. Anterior spiracles situated laterally towards posterior margin of second segment: each a knob-like projection without digitate processes.

Fucellia maritima



Third instar larva
Cephalo-pharyngeal skeleton

Third instar larva
anterior end, ventral view



Third instar larva
posterior end,
posterior view

Puparium

THIRD INSTAR LARVA.

Length full-grown 9-10 mms., greatest width (segments 8-12) 1.1 mms. Shape cylindrical between segments 8-12, tapers to head anterior to segment 8, posterior end fairly blunt. Colour white except for brown sclerotised regions of posterior spiracles. Body composed of the normal twelve segments; segments 2 to 11 differ little in length, more posterior ones only slightly larger, but segment 12 is noticeably short. Segments clearly distinguished on ventral side by slight swellings at anterior and posterior margins of most segments. First segment consists of two lobes separated by a median ventral groove at posterior end of which is mouth. In front it bears, one on a swelling of each lobe, a pair of small forwardly-directed two-segmented antennae. Proximal segment short and cylindrical, distal one hemispherical. Posterior to antennae on antero-ventral margin of each lobe is a small papilla 'maxillary palp'. There are seven to nine rough rows of sclerotised teeth at the sides of and anterior to the mouth hooks, with 3 to 8 teeth in each row on each lobe. The larger teeth are comb-like. Anterior spiracles situated laterally towards posterior margin of segment; each composed of 6 to 9 fronto-laterally directed digitate processes. Posterior spiracles borne on two backwardly-directed, light-brown sclerotised projections from central part of segment 12. At apex each bears a circular stigmal plate, on which are found three spiracular openings, elongate-oval in shape. No hairs are found on the posterior spiracles. Spines. Very small white to pale yellow spines in groups of 12 to 30; the groups in several rough rows at anterior margins of segments 2-12, and which extend right round larva. Anus opens half-way along segment 12, in a shallow depression at anterior junction of two backwardly-directed swellings. Last (twelfth) segment whose posterior end faces upwards and backwards is provided with a number of swellings of various shapes and prominence which can be seen from the figure given.

Puparium

Length 6-7 mms; greatest width 2 mms. Colour: light-brown to dark-brown. Outline - width of segments 6-10 roughly equal, tapering anteriorly to these to about one-quarter greatest width, and posteriorly to half of greatest width; segment 12 rounded posteriorly; in side view ventral line sinuous, slightly convex anteriorly and slightly concave posteriorly; dorsal line convex tapering gently anteriorly. First segment completely introverted, so that (larval) anterior spiracular processes are situated almost at beginning of puparium. Skin in ridges passing right round body in segments 3-11 but thrown into discontinuous and indistinct folds in segments 2 and 12. There are three or four shallow depressions towards each lateral margin of each segment 3 to 11 - one or two dorsally, one laterally and one ventrally. Puparium splits at almost anterior margin of segment 5 to allow emergence of adult.

Laboratory observations.

Cultures of Fucellia maritima were maintained in the laboratory in conditions similar to those described for species of Coelopidae. Moderately decomposed Laminaria stipes and not fresh wrack had to be supplied to the young larvae of F. maritima otherwise they died.

Adults that had been reared in the laboratory or which had been collected in the field mated freely in the culture jars. The females readily laid eggs on Laminaria and Fucus that was in all states of decomposition, but larvae resulting from eggs laid on fresh wrack died within a few hours if not transferred to partially decomposed wrack. In jars without wrack the females frequently laid eggs on any moist surface. The eggs were laid in small groups and in batches of up to seventy.

At room temperature the eggs hatched 40-60 hours after being laid.

A batch of eggs which was under observation began to hatch at 1445 hours on 28th April, 1956, fifty to fifty-four hours after being laid. Each egg split longitudinally along one or both of the thickened ridges, and after a series of body contractions and expansions the young larva pushed its head through the anterior end of the egg and crawled out of the chorion. Since all of the eggs hatched within a few minutes of each other there was soon a small mass of wriggling larvae present on the wrack. The larvae gradually wandered away from the egg site and burrowed their way into the soft Laminaria tissue where they were seen with only their posterior spiracles projecting above its surface. These first instar larvae and those of the same stage in other cultures of this species were subsequently nearly always found in this position in soft wrack.

At room temperature the first instar larval stage lasted from four to six days.

Both the second and third instar larvae were found either buried in the soft Laminaria tissue with only their posterior ends visible or crawling over the wrack or the side of the jar.

The second instar larval stage lasted 4-6 days and the third instar larval stage 8-10 days when the cultures were kept at room temperature.

With regard to their place of pupation, the mature larvae were not as selective as those of the species of Coelopidae or Helcomyza ustulata. Pupae of F. maritima were found on the sand at the bottom of the jar, on the Laminaria stipes, and on the lid and side of the jar. When, however, there was a solid mass of wrack in the culture jar, they always pupated either in the top layers of the wrack or higher up on the side of the jar.

At room temperature the pupal instar lasted from eighteen to twentyone days.

Field life-history.

At Whitburn, adults of F. maritima first emerged fairly suddenly and in large numbers between the middle and end of March in each of the three years in which they were studied. Adults then remained common until September, when there was a great decrease in their numbers until there was only a few of them about in October and early November, after which they were entirely absent until the following March. On the shore near St. Mary's Island, the flies occurred more casually during the summer and none at all were seen after early October of each year.

These populations of F. maritima at Whitburn although large were never as vast as the autumn and winter populations of Coelopa frigida and C. pilipes. F. maritima adults were, however, far more abundant than the other two species of Coelopidae, Orygma luctuosa and Oedoparea buccata, and after Thoracochaeta zosterae were the commonest wrack-flies at Whitburn throughout the period April to September. Their fairly large numbers, coupled with the fact that the adults were not as secretive as those of other species of flies encountered, made F. maritima, in general, the most noticeable shore-fly at Whitburn.

The adults were found on wrack of any amount and in any state of decomposition. They occurred all along the shore at Whitburn from the beginning of the wrack string to the large wrack bank; they were, however, particularly attracted to the temporary wrack banks of fresh wet Fucus and Laminaria that were frequently formed at various distances below the high-tide level. With Thoracochaeta zosterae they were the only other flies ever present on the most seaward of these wrack beds. At Bamburgh, Northumberland, on 3rd September, 1957, large numbers of F. maritima were found on wet Fucus growing all along the length of a concrete ramp which stretched into the sea. They occurred here even on Fucus that had only just been uncovered by the ebbing tide when this was almost at its lowest level. Adults of F. maritima have also been found on a large area of the Durham coast (from Seaham Harbour to Hartlepool) where no wrack was present at all and Backlund (1945) also found that they occurred in regions devoid of wrack.

The flies were also very much attracted to other kinds of decomposing organic matter, particularly to dead fish and crabs, rotten apples etc., and excrement. Any such material lying on the shore was usually covered with up to several hundreds of the flies. On 19th April, 1956, seventy-seven males and seven females were caught, and on 25th April, 1956, ninety-five males and twenty-three females were caught, each with one sweep of the kite net over dead fish on which the flies abounded. F. maritima is the only species of wrack-breeding fly that is attracted to decomposing organic matter of this nature. The habit, however, is characteristic of the family to which this species belongs.

Many copulating pairs of flies were seen on the wrack and other decomposing organic materials and the females frequently walked with the males attached in the mating position.

Although eggs were often looked for, they were rarely found. Those that were found were scattered singly over the Fucus and Laminaria inside the wrack beds and on only one occasion was a batch of eggs found.

Full grown larvae were first found at Whitburn in late April of each year and continued to be present until October. During this time there were probably three to five generations of the fly. The larvae which pupated in September and October did not produce adults until the following March. This was borne out by observing that larvae which were collected in the field in September and kept at room temperature pupated in early October, but the adults did not emerge until the following February.

At Whitburn the larvae were found mostly in small wrack banks that were formed in the central region there and in parts of the wrack string that were fairly deep. In both places the wrack was compact, contained small amounts of other decomposing vegetable matter and soon got contaminated with sand which helped drainage and slowed down the rate of decomposition. Only on very few occasions were larvae found in the large wrack banks on the rocks at Whitburn.

Larvae of F. maritima, for the same reasons as those given for Helcomyza ustulata, are not adapted to living in large wet wrack banks, and it is interesting to note that at Whitburn the larvae of both species inhabit the same area and same kind of wrack beds and that they were frequently found together. Both species were also found together, in their larval and their adult stages, in a wrack string at Llandudno, Wales, in August, 1956. This wrack string was of similar shape and composition to that at Whitburn. In August, 1957, however, at Furness some larvae which later produced adults of F. maritima were found in a wrack string consisting of clumps of filamentous green seaweed.

The larvae pupated in the drier upper layers of the wrack beds at Whitburn or among nearby shingle, particularly on the landward side.

Chapter IX.

THORACOCHAETA ZOSTERAE (FAMILY SPHAEROCERIDAE).

Many species of Sphaeroceridae (Borboridae) in the adult stage are attracted to various kinds of decomposing organic matter including excrement. Several species of the family have been found among the decomposing seaweed in the wrack beds investigated at Whitburn, but only the very common Thoracochaeta zosterae was found to breed there. The closely similar Th. brachystoma occurred as adults from January to March in 1956 only and its larvae were not found at all.

Richards (1929) described a third British species of the same genus - Th. penteseta - from a female fly he caught on decaying seaweed of a cormorant's nest on the Scilly Isles on 12th July, 1927. No further records of this species appear to have been made and the species is not included in the check list of British insects of Kloet and Hincks (1945). No fly fitting Richards' description was found during the present study of wrack fauna.

Although the two species, Thoracochaeta zosterae and Th. brachystoma, are well-known wrack frequenting flies, very little has been published concerning their young stages and biology. Richards (1930) gives a figure of the puparium of Th. zosterae. Each of the young stages of this species - the egg, three larval instars and the puparium which contains the pupa - are now described here.

EGG.

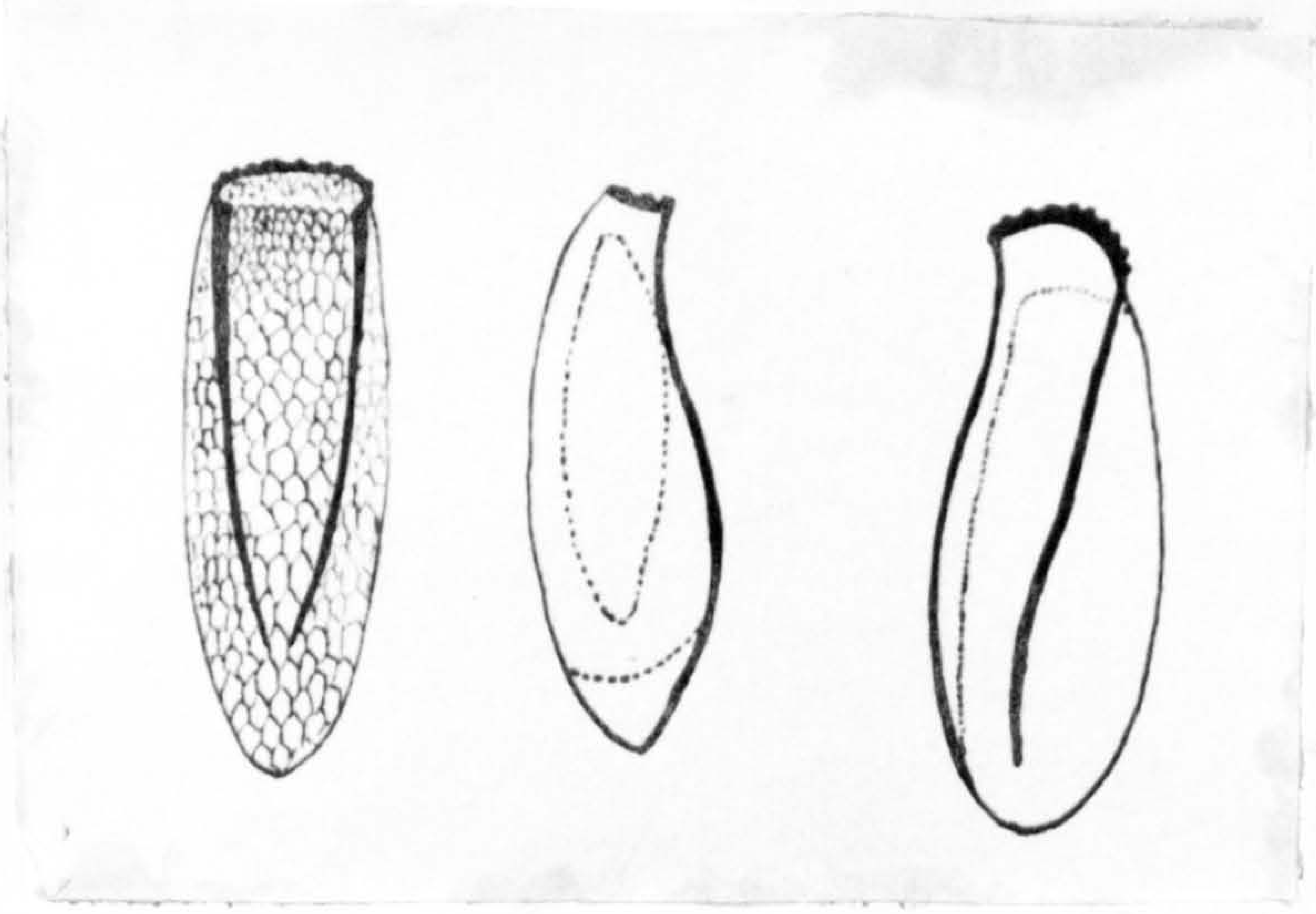
Length 0.6 mm. Colour white. In dorsal view outline elongate-oval with anterior end blunt; in side view dorsal surface convex, ventral surface sinuous, concave anteriorly, convex posteriorly. Anterior margin with a ventro-dorsally curved white, denticulate, thickened ridge; this ridge joined, one at each side, by two longitudinal ridges stretching about three-quarters of length of egg; the two longitudinal ridges widely separated at anterior end and gently approaching each other posteriorly, where eventually they are separated by only a short distance. Whole egg surface covered with white thickened hexagons, these becoming slightly smaller at anterior end.

FIRST INSTAR LARVA.

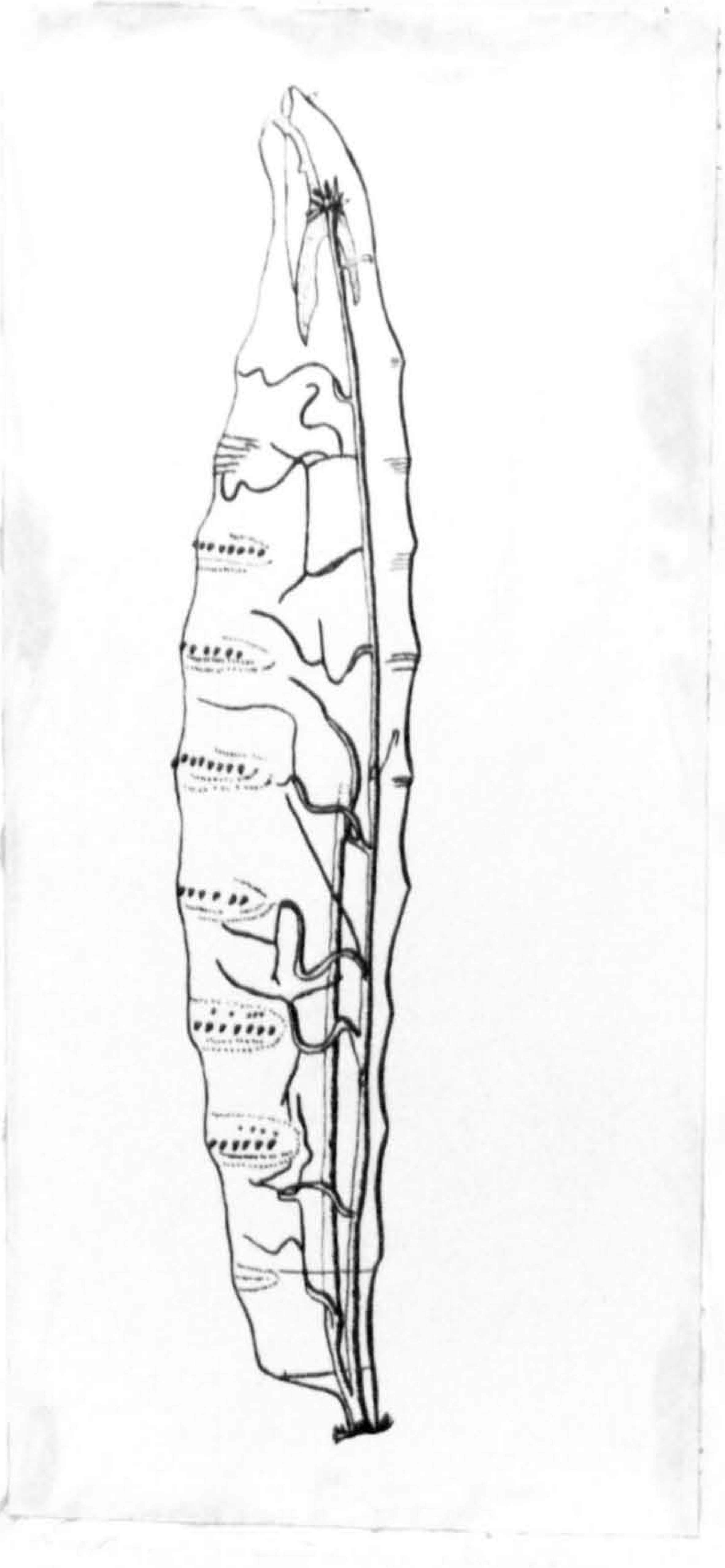
Length 1.0 - 2.0 mm. Posterior spiracles borne on two backwardly-directed processes of last segment; each

Thoracochaeta zosterae

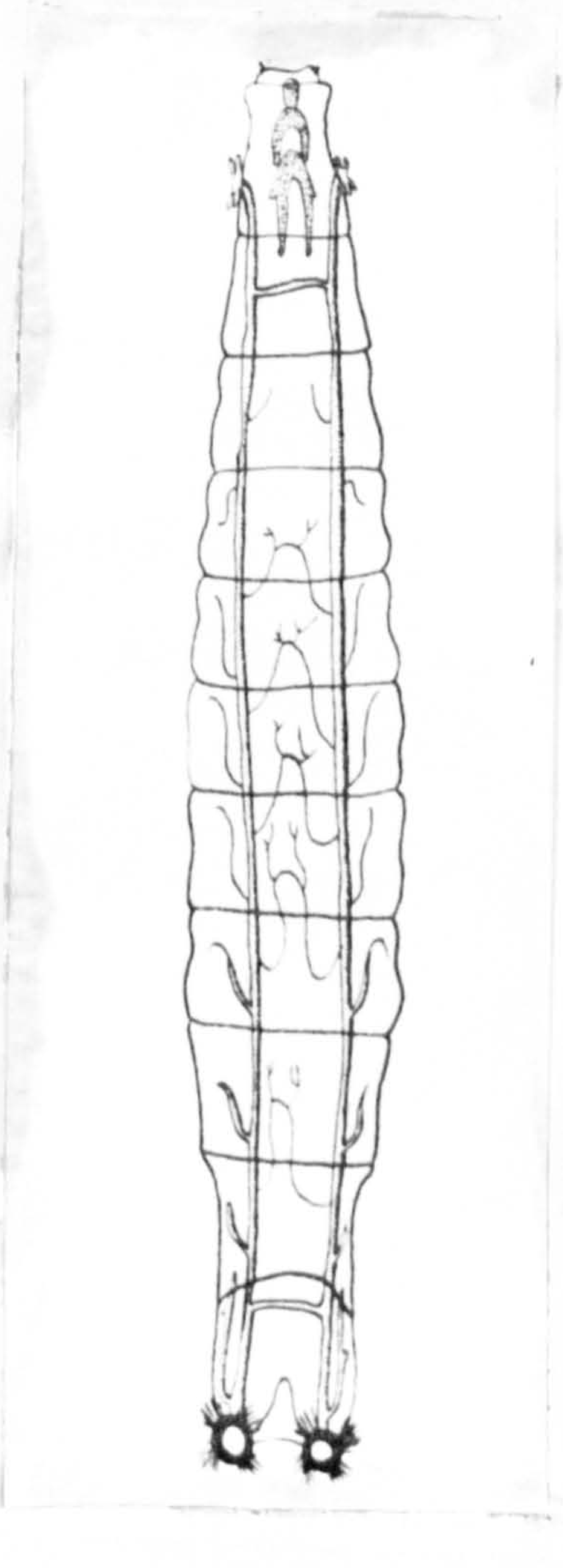
Egg



dorsal lateral dorso-lateral



Third instar larva
lateral view

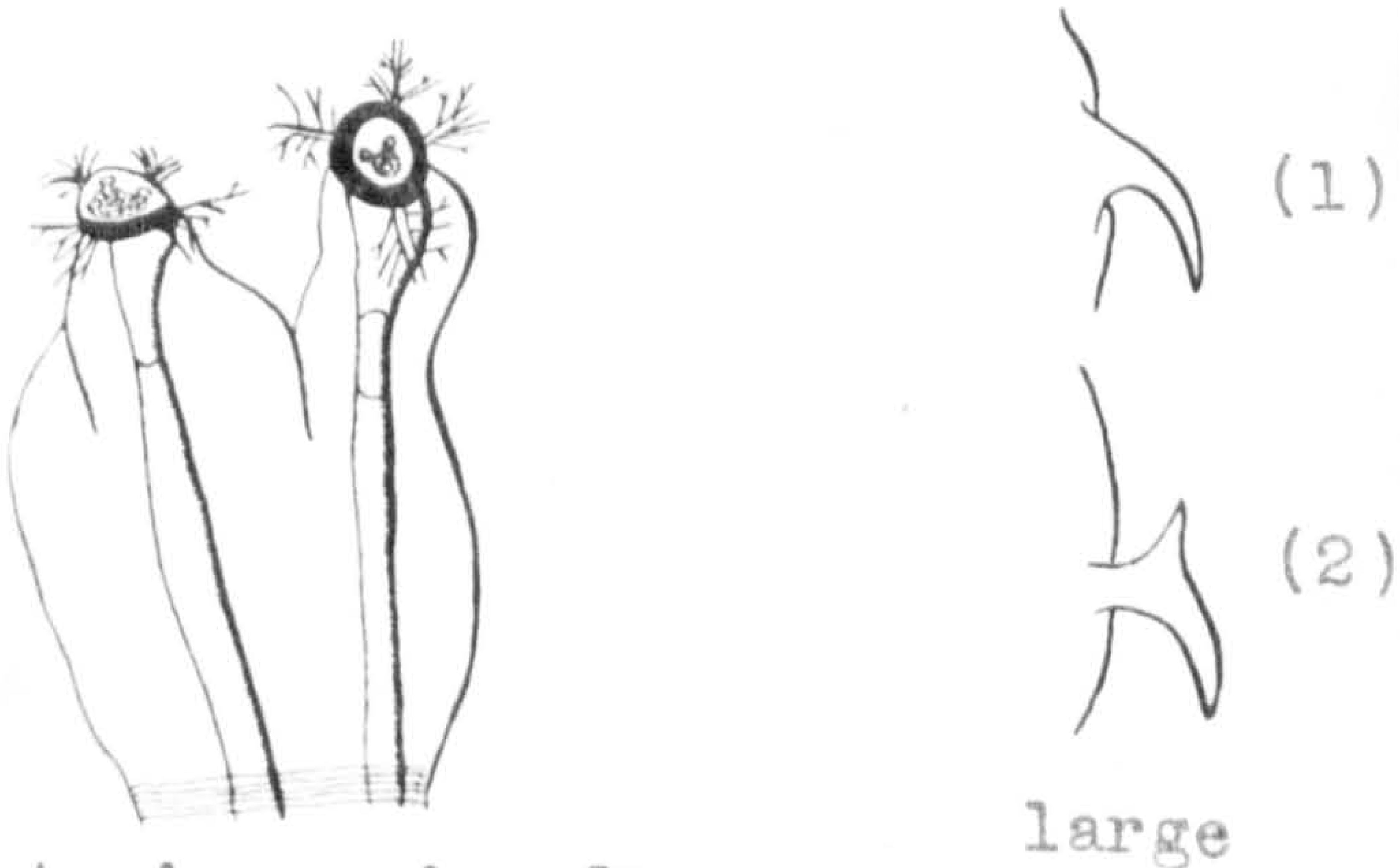


Third instar larva
dorsal view

Thoracochaeta zosterae

Third instar larva
anterior end

ventral   lateral

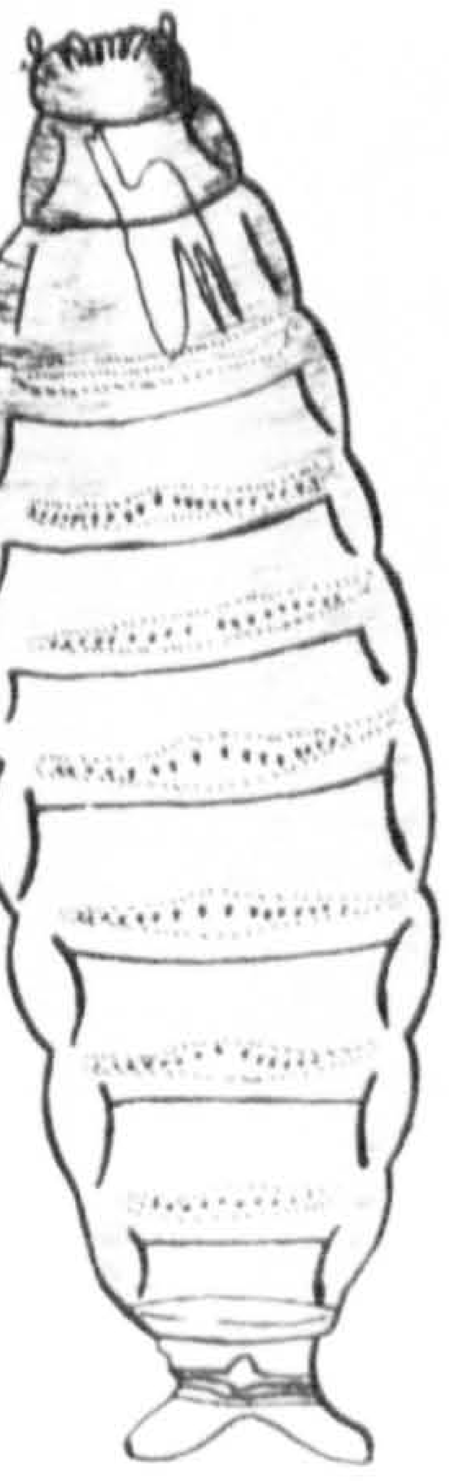


posterior spiracles

large spines

Third instar larva

Puparium
ventral view



surrounded by four tufts of hairs at right angles to each other. Spines found in rows on thickened anterior border of ventral side of segments 4 to 12.

SECOND INSTAR LARVA.

Length 2.0 - 3.8 mm. Anterior spiracles opening on a small papilla at sides of segment 2 near its posterior border.

THIRD INSTAR LARVA.

Length 3.0 - 6.3 mm. Shape almost cylindrical, narrowing slightly towards posterior end, and more so towards anterior end. Colour white save for brown or black sclerotised structures. Body composed of the normal twelve segments; segments 2-12 subequal in length, each segment slightly concave on dorsal surface. First segment bears a pair of two-segment antennae, a pair of 'maxillary palps' and rows of sclerotised teeth. Anterior spiracles situated laterally near posterior margin of second segment; each composed of about nine laterally-directed digitate processes. Posterior spiracles borne on backwardly-directed projections of segment 12; each is surrounded by four tufts of simple and branched hairs, the tufts set at right angles to each other; peritreme black and circular in shape; stigmal plate bears three roughly circular spiracular openings. Spines Anterior margins of segments bear rows of spines on ventral surface. The spines vary in size but may be divided into three main sizes which can be called large, medium and small. The large spines ate of two types - type(1) without a barb and type (2) with a barb. The large spines are in single rows along the middle of the swelling which bears the spines of each segment. The medium sized spines are without barbs and are in single rows placed just anterior to the row of large spines. The small spines are in groups of 10-20, a number of groups forming a row. All of the spines in any one row are about the same size. The arrangement of the spines is as follows: there is slight variation between larvae. Segment 4 bears 7 rows of small spines; segment 5 bears 4 rows of small spines, 1 row of 18 large type (1) spines pointing backwards and 3 rows of small spines; segment 6 bears 5 rows of small spines, 1 row of 20 medium spines pointing forwards, 1 row of 19 large types (1) and (2) spines and 2 rows of small spines; segments 7, 8 and 9 are very similar to segment 6; segment 10 bears 3 rows of small spines, 1 row of 20 medium spines, 1 row of 15 mixed large spines and 2 rows of small spines; segment 11 bears 6 rows of small spines; segment 12 bears 3 short rows of small spines at anterior side of anus.

PUPARIUM.

Length 3.0 - 4.0 mm; greatest width 1.0 - 1.3 mm. Colour light-brown to dark-brown. Outline elongate ovate, but long axis usually bent to one side. Sides compressed dorso-ventrally near edge. Segmentation clearly defined, constrictions being between segments and larval segmental spines obvious. First segment completely introverted so that larval anterior spiracles are situated almost at anterior end. For emergence of adult puparium splits along sides of anterior 3 or 4 segments, and the two flaps so formed are pushed apart.

Laboratory observations.

Cultures of Thoracochaeta zosterae were kept in the laboratory on Fucus in glass containers of various sizes depending on the purpose for which flies and young stages were required.

Stock cultures were kept in 2-lb.size Kilner jars half full of Fucus into which the adults were introduced to commence the culture. The Fucus was kept moist until decomposition began. The larvae did not seem to suffer any losses if water was standing in the jar provided there was enough Fucus projecting above its surface for them to feed on. Since the larvae pupated in the drier, upper parts of the jar such excess water had little effect on the pupal stage. When it became too deep, however, the water was removed with a pipette. Such stock cultures were kept for several months without further addition of Fucus, generation of the fly following generation. With the occasional addition of Fucus, one culture was kept for fourteen months before being discontinued. No doubt similar stock cultures of this species could be kept with but little attention for several years.

Half-pound size jars were found most suitable for rearing all of the progeny of a single female and for observing the duration of the young stages. Pupae were removed from the stock culture and allowed to produce adults in isolation, and pairs of flies were introduced into the small jars containing Fucus.

For examination of the young stages small cultures were kept in a cell formed by two petri-dishes. Pieces of wet Fucus were pressed to the inside surface of each petri-dish and pairs of flies were introduced into the cell. The eggs were laid on the free surface of the Fucus and the young larvae, on hatching, crawled round to the opposite side where they were usually found with their bodies immersed in pockets of water formed between the Fucus and the glass, only their posterior spiracles remaining in contact with the air. In their respective positions both the eggs and the young larvae could easily be observed with the aid of a binocular microscope.

The female flies which mated shortly after emergence, (often when still white in colour) laid eggs about twelve days later. The eggs were laid on the surface of the wet Fucus or were partially embedded in the transparent slime which sometimes covered the decomposing wrack, where they were difficult to dislodge. No eggs were ever found other than on the wrack. Each female laid between thirty and forty-five eggs.

The eggs hatched 6-8 days after laying in cultures kept at room temperature.

The freshly emerged larvae quickly found their way to the wettest parts of the Fucus, particularly to places where a film of water was present either between two pieces of Fucus or between a piece of Fucus and the side of the jar. They were found here with their bodies immersed in the water and only their posterior spiracles projecting into the air. They often entered the water entirely for a few minutes, the hairs of their posterior spiracles forming a cone enclosing a bubble of air. The second instar larvae were also usually found partially immersed in water in a manner similar to those of the first instar.

At room temperature the first instar larval stage lasted

6-9 days and that of the second instar, 5-8 days.

The third instar larvae were not so dependent on such a wet environment as were the younger larvae, and they were found crawling over the surface of the wrack and over the side of the jar. The third instar larvae naturally travelled further and faster and were generally more active than the larvae of the first two instars. This increased activity caused a rapid breakdown of the Fucus, which changed from a firm green frond on the surface of which the younger larvae fed, to a brown, pulpy mass in which the third instar larvae were often found immersed.

At room temperature the third instar larval stage lasted 13 to 15 days.

The larvae usually pupated in the upper drier layers of wrack in the culture jars and on the side and lid of the jars, but a few were found embedded in soft decomposing wrack.

The pupal stage lasted 26-29 days at room temperature.

Adults lived for up to eleven weeks in jars containing wet cellulose wool, but only for a few days in dry jars.

Field life-history.

Thoracochaeta zosterae was the commonest fly at Whitburn at all times during the three years in which the wrack fauna was studied there. Their numbers were so large and the adults so secretive that it would have been very difficult to estimate the size of the total population and to observe any fluctuations during the year. From appearances, however, adults seemed to be equally abundant throughout the year. Although the flies were numerous, they were normally so closely bound to the wrack beds that they were not obvious. Their abundance became apparent only when the surface layers of the wrack beds were raised and the flies beneath were disturbed. Vast numbers then rose to the top of the wrack beds and flew a short distance to another part of the bed.

The wrack banks at Whitburn harboured the greatest number of adults, but large numbers also occurred along the length of the wrack string, each clump of wrack containing at times several hundred flies. Thoracochaeta zosterae adults were found in similar abundance in the wrack banks near St. Mary's Island.

The adults were found in wrack in all states of decompositiom. With Fucellia maritima, Th. zosterae was the only other species found in the temporary wrack banks of fresh wrack formed between successive high tides below the high tide level at Whitburn, but it was not found as far seaward as F. maritima. Even very small pieces of dry, brittle Laminaria or Fucus when disturbed were often found to shelter several adults of Th. zosterae.

The adults of Th. zosterae were rarely found away from the wrack beds except when they emerged from puparia in shingle or sand after the wrack beds had been washed away, or when the flies were mass migrating. On several occasions between July and September many hundred of newly emerged, white adults were found walking over the shore in the central region at the high tide level where there were only some small pieces of dry Laminaria and Fucus. Only one mass migration of the flies was observed and this is described later (p. 147).

The young stages were found in all amounts of wrack, provided it was wet and soft and decomposing. These conditions were most easily obtained in the large wrack banks and it was here that most of the breeding took place.

At Whitburn the eggs and young larvae were found only in the decomposing Laminaria and Fucus in the deeper parts of the wrack banks. In the wrack string they were found chiefly in the middle of soft Laminaria stipes, particularly if several stipes had become entangled, as the Laminaria stipes did not dry out as quickly as the Fucus. The third instar larvae were found at all levels of the wrack beds.

The puparia were found in the fringes and dry surface layers of the wrack banks and among shingle and rocks on their landward side.

In the laboratory puparia covered with a thin film of water failed to produce adults and it is therefore vital that the larvae pupate away from the lower layers of the wrack beds which are liable to become flooded with water. It has previously been mentioned that in the laboratory the larvae usually pupated in the drier parts of the culture jars. In one of his moisture preference experiments, Backlund (1945) found that larvae which occurred in a 100% water-saturated substratum (cork waste) later pupated in substrata varying from dryness to 100% water-saturated.

<u>A mass migration of Thoracochaeta zosterae.</u>

Adults of Thoracochaeta zosterae were normally very closely bound to the wrack beds in which they occurred and they flew only when disturbed. On 5th November, 1956, however, a mass migration of the flies was observed at Whitburn. At this time Coelopa frigida was also migrating, but the two mass flights were entirely separate and distinct; that of C. frigida has previously been described (p. 101).

The Th. zosterae adults were first seen flying south in a dense column which skirted a bank of grass growing on the most landward edge of the shore of the central region at Whitburn (fig. on p.102). The flies were so dense that from a distance of about three yards to their seaward side they gave a shimmering effect to the grass bank behind them. The flies were flying on a frontage of about two feet and from one to three feet high. The kite net was swept once through the column of flies at point Y (fig. on p. 102) and those caught were collected from the net with an aspirator. Many flies were seen to escape through the mesh of the net but, even so, 202 were caught (95 males, 107 females).

The flies emanated from the large wrack banks on the rocks at Whitburn. From there until they reached the grass bank, a distance of forty yards or so, the flies were not as concentrated as they were when they skirted the grass bank where the dense column of them was seen. This column, more obvious in some places than in others, stretched for about twenty yards to some large clumps of fresh wrack lying on the shore in line with the flight. No flies were seen flying south of these clumps, nor were any found flying north of the large wrack banks. Only very few adults of Th. zosterae were found on a wrack string two yards seaward of the large clumps of wrack. The shore over which the migrants flew was devoid of wrack between the wrack banks and the large wrack clumps.

The weather conditions were, of course, the same as those described for the Coelopa frigida migration of the same date (p. 101).

It would seem that what was observed at Whitburn and is described here was a short but complete mass migration of Th. zosterae adults. There was the emigration of large numbers of flies from the wrack banks, their transmigration over terrain devoid of wrack material and their immigration into clumps of fresh wrack some sixty yards from the beginning of the flight.

Other species of Sphaeroceridae found in the Whitburn wrack beds.

Th. brachystoma was fairly common in the wrack string at Whitburn from late January until early March, 1956. This was the only period during which this species was found. Five other species of Sphaeroceridae were found in the wrack string; Copromyza similis was fairly common on one occasion (21st May, 1957), Sphaerocera cropped up now and again in small numbers and the other three species occurred once or twice.

Chapter X.

OTHER SPECIES OF DIPTERA CLOSELY ASSOCIATED WITH THE WRACK BEDS.

The flies previously dealt with - the four species of Coelopidae, and the Helcomyza ustulata, Fucellia maritima and Thoracochaeta zosterae - all bred in the wrack beds at Whitburn with a certain regularity and it is most probable that for this purpose at least they are confined to this type of habitat. Although the young stages of Thoracochaeta brachystoma were not found, it is very likely that this species is similar to Th. zosterae in that they are also confined to wrack beds.

Besides these eight species, there were other flies that were common at some time of the year, either as adults or larvae, and which were more or less closely associated with the wrack beds. They included species of the genus Chersodromia, Sciaria quinquelineta, Fannia canicularis and Scatophaga stereoraria.

Chersodromia species found in wrack beds.

Several species of Chersodromia (Empididae) have been found inhabiting the seashore by various students. Lundbeck (1910) mentions finding Ch. difficilis, arenaria, incana and hirta at seashore localities in Denmark. He found Ch. cursitans with them at times, but this species also occurred at the dide of lakes and rivers. Ch. arenaria and Ch. cursitans were found on the shores of Sweden and Finland by Backlund (1945). In England, Yerbury (1919-22) recorded Ch. hirta and Ch. cursitans found under seaweed at Torcross, Devon.

At Whitburn, the present writer found Ch. hirta and Ch. arenaria; at Llandudno, Ch. hirta, difficilis and incana; and at Bamburgh, Northumberland, Ch. incana.

In the adult stage, species of Chersodromia are, predatory on other insects and this habit is discussed later (p. 181).

Ch. hirta:

Ch. hirta was fairly common at Whitburn from the beginning of June until the end of September. Most were found among the dry seaweed in the wrack string and on the sand down to about six yards below the high tide level, but some were found in the upper, drier layers of the wrack banks. At Llandudno, in August 1956, they were found in the wrack string and on the nearby sand.

The flies ran very quickly over the shore and made darting flights of one or two feet over the sand.

Ch. arenaria:

This species also occurred from June until September at Whitburn and was found in the same parts of the shore as Ch. hirta. Ch. arenaria was not quite as common as Ch. hirta.

Unlike Ch. hirta, Ch. arenaria has only very short wings and was never seen to fly. Lundbeck (1910) believed that the wings are not sufficiently developed for this purpose. The flies, however ran very quickly among the wrack and shingle.

Ch. incana:

Ch. incana did not occur at Whitburn but was found on the Northumberland coast at Bamburgh in September, 1957, and at Llandudno in August, 1956. It is a small light-grey species and tones in well with the dry sand near the wrack strings where it was found in both of these localities. The flies ran very quickly over the sand and wrack and made short flights of a foot or so.

Ch. difficilis:

This species was found only in the wrack string at Llandudno in August, 1956.

These four species of Chersodromia have not been recorded from habitats other than sea-shores and it is very probable that they breed in the wrack beds there. Some larvae which fit Lundbeck's description (1910) of the generalised Empididae larvae were frequently found in the wrack string at Whitburn in July and August. Although some larvae were often brought back to the laboratory along with the wrack in which they were found, the larvae soon died and none ever successfully pupated. Because of their size, 6 mms., however, they are more likely to be those of Ch. hirta (2-3 mms.) and not those of the much smaller Ch. arenaria (1 mm.).

Laboratory observations.

Adults of Chersodromia incana, which were placed in jars containing pieces of wrack with which they had been found, mated frequently. The male first mounted the female and placed the tibiae and tarsi of his first pair of legs along the dorsal surface of the thorax of the female and his other legs round her abdomen. The first pair of legs of the male 'trembled' for a few seconds at a time and moved backwards and forwards jerkingly, the other legs remaining still. The male then moved backwards along the body of the female so that their genitalia could be opposed. The front legs of the male which continued to 'tremble' intermittently, were now over the wings of the female. Actual coition lasted about one minute after which the two flies immediately separated. The whole procedure (throughout which the female remained motionless) from initial mounting of the male to this separation lasted about three minutes.

Although several females mated, no eggs were ever laid. Rearing experiments with Ch. hirta and Ch. arenaria were also unsuccessful although the adults mated frequently.

Sciara quinquelineta.

Another species that may breed in the wrack beds at Whitburn is Sciara quinquelineta (Mycetophilidae, subfamily Sciarinae), although no direct evidence that it did so was discovered.

The fly was fairly common at Whitburn in May and June and in September and October of each of the three years the wrack fauna was studied and it also occurred near St. Mary's Island, though it was rarer there. At Whitburn the flies were found in the wrack string and in the wrack flake which sometimes formed in the central region, the deeper layers of both of which were damp, well-compressed and contained a certain amount of plant debris.

Although much of this wrack material was examined, only one larva that could possibly be ascribed to this species was found. It was 2 mm. long and had the head black, which is typical of larvae of this family. Unfortunately, the larva died in the conditions provided and no proof exists that Sciara quinquelineta breeds in the wrack beds.

The commonness of the flies and their regularity of occurrence, however, suggests that S. quinquelineta is more than just an accidental visitor to the wrack beds at Whitburn. Backlund (1945) frequently found both larvae and adults of Sciarinae in the wrack beds of Sweden and Finland.

Fannia canicularis.

Fannia canicularis (Muscidae) was the only species of fly found breeding in the wrack beds which is not confined to that habitat. The fly is well-known to breed in other kinds of decaying matter and in excrement.

No adults of F. canicularis were ever found in the wrack beds, but larvae were found on Fucus at two places four yards apart in the wrack string at Whitburn on 27th September, 1956. There were between 100 and 200 larvae in various stages at each of the two places. With them were larvae of Fucellia maritima and Helcomyza ustulata. The larvae of Fannia canicularis which were collected continued feeding on Fucus in the laboratory, eventually pupated and later produced adults.

The wrack string was again visited on 10th October, 1956, but in the meanwhile it had been covered with sand. No larvae were found and no further sign of F. canicularis was seen near the wrack beds.

Previous to the finding of these larvae in the field in September, eggs and larvae of F. canicularis were found on 10th May, 1956, on some Laminaria stipes which had been kept in the laboratory for a few days. Adults were often attracted to the wrack material brought back to the laboratory for examination and, in this instance, a female had laid about one hundred eggs at the edge of the most decomposed part of the stipes. The larvae fed on a white slime that exuded through the outer surface of the Laminaria and they later pupated. Adults began to emerge on the 11th June, 1956.

Larvae of F. canicularis are thus capable of living on either Fucus or Laminaria and the species probably crops up now and again in wrack beds when suitable conditions occur. Larvae of F. canicularis have previously been found by Backlund (1945) in wrack beds in Sweden and Finland.

Scatophaga stercoraria.

Scatophaga (Scopeuma) stercoraria (Cordyluridae) was another species of fly which was frequently found in the wrack beds. One or two adults were often found between March and August, while they were fairly common in September, October and November in the wrack string at

Whitburn, where they preyed on other flies present there. This habit is discussed later (p.180).

On 17th September, 1956, an unusually large aggregation of several hundred adults were attracted to a small area (2ft. x 2ft.) of an extensive wrack bank in the central region at Whitburn. Their abundance on this part of the wrack is shown by the fact that fifty males and 28 females were caught with one sweep of the kite net over the assemblage of flies. The area to which the flies were attracted was darker in colour than the rest of the wrack, was fetid and must have decomposed very rapidly. Its deeper layers were immersed in a putrid, brown semi-liquid.

The flies crawled over this part of the wrack bank and returned immediately to it if disturbed. Many pairs of flies were seen mating.

A jar of wrack material was collected from the area to which the flies were attracted and examined in the laboratory, but no eggs were found in it.

A similar aggregation of S. stercoraria adults was seen in the same place on 20th September, 1956. By 24th September, 1956, what had been a large wrack bank 2-3 feet deep was reduced to a wrack flake only about three inches deep and no S. stercoraria flies were seen on it.

Scatophaga stercoraria has not been recorded breeding in wrack beds, but Backlund (1945) found larvae of the closely related Scopeuma litorea and possibly also those of Scopeuma villipes in wrack beds in Sweden and Finland. At one locality (Petsamo) on the northern coast of Finland, he found that S. villipes and Coelopa frigida were the most typical wrack flies.

Chapter XI.

STRUCTURAL ADAPTATIONS OF THE YOUNG STAGES OF FLIES FOR A LIFE IN WRACK BEDS.

The eight species of Diptera which without doubt bred in the wrack beds at Whitburn may be arranged in three groups depending on the size and kind of wrack bed in which their larvae were usually found. The first group includes the flies which bred in the largest (and hence wettest and softest) wrack banks and contains Coelopa frigida, Coelopa pilipes and Thoracochaeta zosterae. The second group contains only Orygma luctuosa which breed chiefly in small, drier wrack banks and is intermediate between groups one and three. Group three includes flies which bred in the smallest wrack banks and wrack strings and contains Fucellia maritima, Helcomyza ustulata, Oedoparea buccata (the most extreme of the group) and also Fannia canicularis.

The same grouping of the flies could be made based on certain adaptational features of the organs of feeding, movement and respiration in the larvae of these species. Some of these features along with adaptations in the egg and pupal stage will now be discussed.

Adaptations in the egg stage.

The most noticeable adaptation in this stage is the two long filaments found on the egg of Orygma luctuosa. These filaments remain in direct contact with the air throughout their length whilst the rest of the egg is buried in soft wrack, and they have already been shown (p. 53) to have a respiratory function. Similar filaments are found on the eggs of a few other species of flies, e.g. Drosophila melanogaster and D. funebrio. The eggs of these two species are laid in soft, or even semi-fluid, decomposing fruit and their filaments probably serve a similar function.

The filaments when lying along the surface of the wrack may prevent the egg from sinking into the soft wrack. In laboratory conditions, however, many eggs were laid with the filaments projecting straight into the air when they could not function in this way. In Fannia canicularis longitudinal projections from the shell of the egg may help in preventing the egg from sinking into the soft materials on which they are laid.

Feeding adaptations.

The mouth hooks and sclerotised teeth of the larvae of the wrack-breeding flies are clearly adapted to the state of decomposition of the wrack on which the larvae feed.

The mouth hooks of Coelopa frigida and Coelopa pilipes (fig. on p. 31) are bifurcate, each being composed distally of two downwardly-curved finger-like processes with rounded edges. Larvae of both of these species feed on very soft wrack. The sclerotised teeth on the head lobes in C. frigida and C. pilipes are broad flattened plates which clearly project from the lobe surface. In feeding, the head of the larva is raised from the wrack surface and extended forwards, it is then lowered on to the wrack surface and retracted, the mouth hooks pulling back the soft wrack.

When the larva is suspended in woft wrack material by the hairs on the posterior spiracles, the head is constantly being extended and retracted, food caught under the mouth hooks and behind the sclerotised teeth presumably being pulled back into the mouth.

In orygma luctuosa larvae, which feed on harder wrack than the larvae of the Coelopa species, the mouth hooks are not bifurcate and are not as rounded as in those species. The mouth hooks of the larvae of Oedoparea buccata are pointed and their edges are sharper than those of the larvae of the other species of Coelopidae. Their sclerotised teeth are also narrower and firmer than in those species and they project only slightly from the head lobes. These features suit Oe. buccata larvae for feeding on the fairly hard Laminaria stipes in wrack strings on which they are found.

The mouth hooks of Fucellia maritima and of Helcomyza ustulata, both of which feed on moderately hard wrack, resemble those of Oe. buccata in being pointed and having a sharp edge.

Adaptations for movement.

Larvae that have to move through or over soft materials need to have larger gripping surfaces (spines and plates etc.) than larvae which move through or over harder material. The larvae of the flies that bred in the various types of wrack beds at Whitburn illustrate this need.

The larvae of Coelopa frigida and Coelopa pilipes and Thoracochaeta zosterae, all of which live in the softest wrack, have numerous black sclerotised spines in transverse rows on the ventral surface. The spines vary in size but those in the same row are usually alike. The larva of Orygma luctuosa has similar transverse rows of spines but the largest of them are smaller than the largest of those of the two Coelopa species; the larvae of the three flies being about the same size.

The larvae of the species that live among harder and drier wrack bear no large spines other than those few normally present in the anal region. Fucellia maritima and Oedoparea buccata larvae each bear numerous rows of very small, white spines. The larva of Helcomyza ustulata has no spines other than the anal ones but it is covered in small backwardly-directed, almost transparent plates.

<u>Adaptations for respiration.</u>

As will have been noticed from the previous accounts of observations carried out in the laboratory and in the field, several species of larvae live buried in the wrack material with only their posterior spiracles remaining in direct contact with the air. Larvae often found in this position were those of Coelopa frigida, and C. pilipes and Thoracochaeta zosterae, and the first and second instar larvae of Orygma luctuosa. Each of these larvae is supplied with groups of 'hairs' on their posterior respiratory spiracles which are splayed over the surface of the wrack.

These groups of 'hairs' have the following three functions.

Firstly, the splayed 'hairs' act normally as a check against the larvae moving too deeply into soft wrack and losing contact with the air.

Secondly, when the larvae of these four species enter soft wrack, the 'hairs' are forced backwards to form a cone over the spiracular plates thus preventing the spiracular openings from becoming blocked. The 'hairs' of Coelopa frigida and C. pilipes are particularly well adapted to forming this cone for this purpose, being broad at the base and tapering distally.

Thirdly, this bending backwards of the 'hairs' causes air to be entrapped within the cone formed (it is visible as a bubble in larvae submerged in water) and allows the larvae to remain entirely immersed in the wrack for a short time.

In addition to these functions the 'hairs' of Orygma luctuosa were found to be very sensitive to touch and this may be true for the other three species. If, when the young larvae of O. luctuosa were buried in the wrack with only their posterior spiracles visible, a few of the 'hairs' were gently touched with a fine needle, the larvae immediately disappeared into the wrack, the soft tissue closing over behind them. The larvae remained entirely buried in the weed for ten to fifty seconds before pushing their posterior spiracles backwards into the air again. If, however, water was dropped onto their posterior spiracles, the larvae instead of disappearing into the wrack jerked themselves backwards until the 'hairs' broke the surface and the larvae once more gained contact with the air. If the water covering the posterior spiracles was too deep and after some backward movements the larvae could not reach the surface, they moved quickly through the wrack and pushed their posterior spiracles into the air elsewhere.

The larvae of Oedoparea buccata, which live among comparatively hard and dry wrack, bear only a small number of hairs on their posterior spiracles. These hairs are too small and too few to perform the functions of the 'hairs' found in the four species mentioned above. It is possible that these small hairs are only the vestiges of a former functional state that was present in larvae that lived in larger and softer wrack beds. Large wrack beds provide a more constant environment than wrack strings and are possibly the simpler habitat in which to live. Hence the ancestors of Oedoparea buccata may quite well have bred in large wrack banks.

The larvae of both Helcomyza ustulata and Fucellia maritima, which live in fairly hard, well-drained wrack, bear no hairs on their posterior spiracles.

Pupal adaptation.

The larvae of species that live in the wrack banks (Coelopa frigida, C. pilipes, and Thoracochaeta zosterae) pupate in its upper layers or among shingle on its landward side. Larvae that live in the well-drained wrack string (Oedoparea buccata, Fucellia maritima and Helcomyza ustulata) pupate among the lower layers of the wrack and in the sand and shingle beneath it.

Orygma luctuosa is the only species that always pupates in the wrack itself and it secretes a white calcareous covering to the puparium.

Chapter XII.

NEMATODES, OLIGOCHAETES, AMPHIPODS AND A LEPIDOPTERAN.

In addition to the larvae of the fly species dealt with, there were usually species of nematodes, oligochaetes and amphipods which fed on the wrack at Whitburn, and on one occasion larvae of a lepidopteran were found feeding on wrack there.

The nematodes (which all seemed to belong to the same small unidentified species) were always present in the wrack beds and were the first animals found in beds that were freshly formed. They were also present in accumulations of wrack found all down the shore to the edge of the sea and were easily the most wide-spread members of the wrack fauna. The wrack at the high tide level always contained very large numbers of the nematode, but the pieces of wrack nearer the sea usually contained only a few specimens and these difficult to find. If these pieces of wrack, however, were kept in the laboratory, the few nematodes reproduced very rapidly and within two or three days there were vast numbers of them.

These nematodes are undoubtedly the most important animals in causing the initial breakdown of the wrack tissues. Their quick reproductive rate and their activity release the water bound up in the wrack tissue, causing the hard, fresh Laminaria stipes to be reduced rapidly to the soft material on which the young larvae of the wrack flies can feed. The softening of the wrack allows the nematodes to move about more quickly and this in turn increases the rate of decomposition of the wrack tissue. The nematodes also prevent the growth of moulds on the wrack. Laminaria stipes in which the nematodes have been killed by immersing the stipes in boiling water for several minutes, instead of decomposing and becoming softer, wither and dry up. Moulds often form on these stipes and an opaque slime exudes through the outer surface. Wrack in this state is unsuitable as food for other wrack animals, particularly the various fly larvae.

Most species of fly larvae found it very difficult (and Fucellia maritima found it impossible) to survive on wrack that had not previously been partially decomposed by the nematodes.

The oligochaetes have a decomposing action on the wrack tissues similar to that of the nematodes, but they are not so widespread in the wrack beds.. The oligochaetes are found only in the wettest regions of the wrack beds and do not enter solid wrack tissue as do the nematodes, they merely move over its surface. Backlund (1945) found the two Enchytraeidae species, Pachydrilus lineatus and Enchytraeus albidus, in large numbers in the wrack beds of Sweden and Finland and it is likely that these are the species that occur at Whitburn.

The amphipods were usually present in the wrack beds throughout the year. Orchestia gammarella was the chief species, although at times large numbers of Gammarus marinus occurred in the wrack beds near St. Mary's Island. All, of course, fed on the wrack itself. They were nearly always. common, and at certain times occurred in very large numbers, usually to the exclusion of the larvae of Coelopa frigida and C. pilipes. When the latter species were present in large numbers there were fewer amphipods.

<u>Tinea pallescentella (Lepidoptera)</u>

Larvae of Tinea pallescentella were found in material brought back to the laboratory from the wrack string at Whitburn on 27th September, 1956. The wrack string at this time was composed of a very dry and brittle surface layer of Laminaria and Fucus covering a moist layer about two inches deep, and it had not been disturbed by high water for several weeks. Also among the wrack material collected there were larvae of the three fly species Fannia canicularis, Fucellia maritima and Helcomyza ustulata.

This was the only occasion in which larvae of T. pallescentella were found and no adults of this species were ever seen in the field. It is interesting to find that larvae of two species of insects (T. pallescentella and Fannia canicularis) which occurred only once in the wrack beds were found in the same wrack at the same time.

The larvae matured and eventually spun silken cocoons of fine interlacing threads, which in places formed a close mesh. On the outside of this was added a covering mainly of sand grains but also of small pieces of wrack, empty fly puparia and pieces of cardboard from the lid of the rearing jar. Each cocoon was attached to either dry wrack or to the lid of the jar by fine threads. The cocoons were about 7 mms. long and 2 mms. wide.

The adults (fourteen) of T. pallescentella emerged in the second week of January, 1957. They were very active when disturbed and ran quickly through the dry wrack in the rearing jar. The empty pupal skins were found almost entirely sticking out from the top of their respective cocoons.

The adults laid eggs from which larvae appeared. Some of these, which were transferred when very young to jars containing Laminaria stipes that had been sterilised by boiling, continued feeding and quickly grew in size. They eventually spun up on the cardboard lid of the jar, pieces of which were used in building the cocoon, and adults emerged later.

The occurrence of the larvae of T. pallescentella in the wrack string at Whitburn appears to be the first record of a lepidopteran from wrack beds. Meyrick (1895) gives grain and dry refuse as its usual food. There is no doubt, however, that this moth can live on wrack only and it probably occurs in wrack beds now and again when the right conditions occur.

PART IV.

PARASITES AND PREDATORS FOUND IN THE WRACK BEDS.

Chapter XIII.

PARASITES.

Collections of larvae and pupae of the four species of Coelopidae and of Helcomyza ustulata, Thoracochaeta zosterae and Fucellia maritima were frequently brought back to the laboratory from the wrack beds at Whitburn so that information could be gained concerning their parasites. The pupae collected and those resulting from the larvae collected were placed in jars containing damp sand. Here they were kept until all flies and parasites had emerged; any puparia still intact were then dissected to examine their contents.

Only two of these seven species of flies were ever found to be parasitised - the Coelopid Orygma luctuosa by the hymenopterans Platymischus dilatatus (Diapriidae) and Nedinoptera subaptera (Cynipoidea), and Thoracochaeta zosterae by Nedinoptera subaptera.

Platymischus dilatatus.

Platymischus dilatatus occurred, normally only one or two at a time, in the wrack strings and wrack banks at Whitburn from July to October. However, on 1st July, 1957, a large number were found together with Nedinoptera subaptera crawling over the dry wrack and stones on top of the 'permanent' wrack bank at Whitburn. In fifteen minutes a collection of the two species was made which contained forty females and three males of P. dilatatus. A similar large number were again found here on the 8th July, 1957, and in fifteen minutes sixty-three females and three males were collected. By 16th July, 1957, the numbers had been greatly reduced, only seven females being collected in one hour on that date. On 1st October, 1956, about thirty P. dilatatus were found walking over some sand under which a wrack string had previously been buried. These were the only occasions on which more than four specimens of this parasite were found at one time in the wild.

In the three years in which the wrack fauna was studied between three hundred and four hundred puparia of Orygma luctuosa were brought back to the laboratory from the field. From only eight of these did P. dilatatus emerge. The particulars are as follows, the date given being that on which the puparia were collected,

(1)	18.x.55	25f. 9m.	(5)	1. xi.56	4f. 6m.
(2)	18.x.55	5f.10m.	(6)	1. xi.56	16f. 9m.
(3)	15.x.56	16f.10m.	(7)	1.vii.57	4f. 7m.
(4)	15.x.56	11f. 7m.	(8)	16.vii.57	6f.11m.

giving 19.5 as an average number of parasites per parasitised pupa. The parasites emerged through three or four small holes they made in each of the puparia.

In his study of the wrack fauna of Finland and Sweden, Backlund (1945) bred ninety-two P. dilatatus from seven pupae of Orygma luctuosa, an average of 13.1 parasites per pupa.

Backlund (op. cit.) pointed out that the hymenoptera emerging from a parasitised pupa did so at a date later than the fly would have done, and that this prolonged stay in the pupal stage helped to keep the balance between host and parasite, since the pupa is the weakest stage with regard to drowning through storms and high water. Seventeen pupae of O. luctuosa which were collected from the wrack beds at Whitburn at various times and which produced neither adults nor parasites within a few weeks were dissected. Five contained withered young pupae, eight contained dead adults and the other four each contained dead P. dilatatus adults and pupae. The exact number of parasites in each puparium could not be counted as many of them were immature and all were brittle and badly damaged. These figures, few as they are, show that there is a higher proportion of parasitism (4 of 17) among pupae that die through drowning than in those that successfully produce adults of some kind (8 of 300-400), which gives support to Backlund's view. In fact about one third of the P. dilatatus die before emerging from the puparia of O. luctuosa.

Nedinoptera subaptera.

Nedinoptera subaptera occurred usually in only small numbers throughout the year, two or three often being found in the wrack string and the wrack banks at Whitburn. On 1st July, 1957, however, large numbers of this species were found with Platymischus dilatatus (see above) walking over dry wrack and stones and the mixed collection of these two species made in fifteen minutes contained one hundred and fifty-five N. subaptera. On 8th July, 1957, large numbers were still present and sixteen were caught in fifteen minutes (along with the 66 P. dilatatus) but on 16th July, 1957, only an odd one or two were seen.

N. subaptera was parasitic on Thoracochaeta zosterae chiefly. One or two usually emerged from groups of puparia of this fly collected at all times of the year. The degree of parasitism was always less than 10%. Only one N. subaptera emerged from each parasitised pupa. On four occasions a single N. subaptera emerged from a pupa of Orygma luctuosa.

Backlund (1945) does not mention N. subaptera and no records of its parasitising these species appear to have been published.

Other hymenopterous parasites that have been bred by other students from wrack breeding flies are Braconidae sp. and Isocyrtus sp. from Orygma luctuosa; Ichneumonidae sp., Gelis sp. and Braconidae sp. from Scopeuma litorea; Trichophria laticeps from Thoracochaeta zosterae; Braconidae sp. from Fucellia sp. (all Backlund) and Aphaereta cephalotes from Orygma luctuosa (Scott 1920).

Parasitic Staphylinidae.

Several species of the genus Aleochara are parasites of various invertebrates. A. algarum is a well-known parasite of some species of Coelopidae, having been bred from puparia of Coelopa frigida and C. pilipes by Scott (1920) and from puparia of Orygma luctuosa by Backlund (1945).

Only four specimens of A. algarum were found in the wrack beds at Whitburn; two in the wrack string on 8th July, 1957, and two on 28th July, 1957. On 24th June, 1957, ten specimens were collected from a wrack bank near St. Mary's Island. Although many hundred of puparia of its hosts were brought back to the laboratory from Whitburn, no A. algarum ever emerged from them. The species is obviously a rare one there. Scott (1920), however, bred about one hundred from a large number of puparia of Coelopa frigida and C. pilipes collected at Swanage, Dorset. Only three of the hundred parasites emerged from puparia of C. frigida, all the others were from C. pilipes.

Both of the two species Aleochara grisea and A. obscurella, which very closely resemble A. algarum structurally, were present in the wrack beds at Whitburn. A. grisea was found throughout the year, but A. obscurella occurred only from April to November. Both occurred chiefly in the wrack string, but only in small numbers. On 8th July, 1957, however, a fairly large number of both species were found on the sand under the wrack string. Altogether 121 specimens of A. grisea and 120 of A. obscurella were collected at Whitburn from October, 1955, to October, 1957. Nothing is known of the life-history of these two species, but it is possible that they, too, are parasites of species of Diptera.

All told, at Whitburn only a small number of fly larvae and pupae were parasitised by either species of Hymenoptera or Staphylinidae. Backlund (1945), however, found that in Sweden and Finland there were often large swarms of hymenopterous insects on the wrack beds and that most dipterous larvae were heavily infected by hymenopterous parasites. It is possible that the wrack beds Backlund studied were more stable than those at Whitburn, allowing the parasites to flourish there. At Whitburn, the wrack beds were constantly being disturbed by storms and high water and the two main hymenopterans (Platymischus dilatatus and Nedinoptera subaptera), both of which are small and easily wetted and have only minute (presumably functionless) wings, are ill-adapted to living in such wet and unstable conditions.

Chapter XIV.

PREDATORS.

The chief predators of the animals living in the wrack beds at Whitburn were sparrows, starlings and rooks. Flocks of at least one of these species were usually present when the wrack beds were not being disturbed. The food of these birds is known to contain a large percentage of invertebrates of various kinds and, presumably, when feeding in the wrack beds they accept whatever they happen to turn up. Pied wagtails, jackdaws, thrushes and various sea birds were also seen now and again on the wrack beds at both Whitburn and near St. Mary's Island. Backlund (1945) lists fifteen species of birds that he has seen on the wrack beds of Finland and Sweden; most, however, being only occasional visitors.

All of the other known predators in the wrack beds at Whitburn were invertebrates and all but one of them (Scatophaga stercoraria) were, more or less, fairly closely bound to the wrack.

Although the wrack beds were visited numerous times and many hours were spent observing their fauna, only on a few occasions were predators actually found with their prey. The species that hunted for their prey on the sand and surface of the wrack beds, e.g. Scatophaga stercoraria, Chersodromia hirta, Ch. arenaria and Erigone arctica, were, of course, the easiest to observe in the field. The species that hid among the wrack (e.g. the Staphylinid beetles and the mites) were difficult to observe and most of the information concerning their prey has come from laboratory observations.

It will be most convenient to treat each of the predatory invertebrates in turn, giving some indication of their abundance at Whitburn and what was discovered concerning their prey.

Scatophaga stercoraria.

The frequency of occurrence of this species at Whitburn has already been mentioned (p. 156). S. stercoraria was the most easily observed predator encountered, being frequently seen preying on Fucellia maritima adults in the wrack string at Whitburn. F. maritima appeared to be its only prey at Whitburn, but on 19th October, 1956, on the shore at Hart, Co.Durham, where F. maritima was absent, S. stercoraria preyed on Dilophis febrilis.

Although it often attempted to catch adults of Oedoparea buccata at Whitburn and at Hart, no successful attempt was seen. Even when the two species were confined together in small jars Oe. buccata always managed to avoid being preyed on by S. stercoraria.

Chersodromia hirta and Ch. arenaria.

The presence of these two species in the wrack beds at Whitburn has already been mentioned (p. 151). Both species run very quickly over the sand and dry wrack and each is provided with a very strong proboscis. On only one occasion was Ch. hirta caught with its prey, which proved to be an adult of Thoracochaeta zosterae. Ch. arenaria was never found with its prey. Thoracochaeta zosterae seems to be the most likely prey for both of these species as it is the only fly about equal to their size. All of the other flies present in the wrack beds are several times larger than the Chersodromia species.

Some idea of the voracity of Ch. hirta can be gathered from the fact that eight flies of this species killed sixty-four Thoracochaeta zosterae with which they had been placed within twenty hours. The Th. zosterae were reduced to empty shells, the contents of the head and thorax having been removed in most cases, and in some the contents of the abdomen had been removed. In the laboratory Ch. hirta attacked dead flies of various kinds probing them with their proboscis. They frequently attacked each other but they were never seen to actually kill and prey on their own species.

Usually there was a scuffle between the two flies after which they quickly separated.

Erigone arctica and other spiders and a harvestman.

In the laboratory, Erigone arctica fed on oligochaetes brought back from the wrack beds, on various fly larvae and on adults of Thoracochaeta zosterae and Fucellia maritima. No other kinds of food were offered. When feeding on the oligochaetes, the abdomen of the spiders became dark green, which was similar in colour to that of spiders found on the wrack banks at Whitburn. This suggests that the natural prey of the spiders there are these oligochaetes. Spiders that lived and fed in the wrack string, where there are far fewer oligochaetes since it is dry, had black abdomens and presumably preyed on some other animals.

In the laboratory, E. arctica spun cocoons on the damp sand and weed and made rough 'webs' in which they occasionally caught an adult of Thoracochaeta zosterae or Fucellia maritima. The 'webs' were not strong enough to hold any of the Coelopidae.

E. arctica was the only spider that occurred frequently and regularly in the wrack beds at Whitburn. Several other species of spiders were found, once or twice, and presumably they were only accidental visitors.

On 30th April, 1957, eight immature specimens of

Opilio parietinus were found in the wrack string at Whitburn and two in the wrack bank there. One or two were found on other occasions in May and June of the same year. Their prey in the wrack beds is unknown.

Cafius xantholoma and other staphylinid beetles.

Cafius xantholoma is the commonest beetle occurring in the wrack beds at Whitburn and the largest species of Staphylinidae regularly found there.

On only one occasion was C. xantholoma actually found feeding. This was on 1st July, 1957, when one was found in the wrack string with a third instar larva of a Coelopa sp. between its mandibles. The beetle and prey were lifted into a glass tube where the beetle continued feeding. Within twenty-five minutes the prey had been entirely devoured.

Individuals and small groups of C. xantholoma were often found partly buried in the sand under stones with only their mandibles projecting. They were found in similar positions in the laboratory when they were placed in jars containing sand. On a few occasions fairly large numbers (40-100) of C. xantholoma adults were found together under stones. On 31st January, 1957, a large stone at the edge of the wrack string in the central region at Whitburn was moved to reveal about twenty beetles. Most were on the surface of the sand but some were in burrows in it. Near the entrance to the burrows there were several small piles of dead flies and their remains. All of these piles were collected with a small trowel and examined in the laboratory. The material collected consisted of portions of the hard parts of at least eleven Coelopa frigida adults (2m. 5f. 4 sex indet.) and six C. pilipes adults (3m 1f. 2 sex indet.), along with thirty complete or almost complete legs of these two species, twenty-one wings, either separated or attached to small pieces of thoracic exoskeleton, odd tarsi, claws, tibiae etc. The flies had almost certainly been killed and partially eaten by C. xantholoma. Nearly all of the bare edges of the various parts were jagged and marked in a way similar to the exoskeleton of Coelopa sp. when these flies were preyed on by C. xantholoma in the laboratory. The combination of the parts remaining, e.g. a wing or leg attached to a small piece of thorax (i.e. hard parts being held together by softer parts) were not the normal ones expected if the flies were merely decomposing after a natural death. Some adults of C. xantholoma were fed in the laboratory on Coelopa sp. adults. All parts of the flies were eaten except for the wings and legs, as seemed to be true for these remains found in the field.

Backlund (1945) found that Cafius xantholoma kept in the laboratory ate a great variety of invertebrates both living and dead and it is likely that in the wild it eats any prey it can catch. Possibly the full-grown larva of this species eats similar food to the adult.

No observations were made in the field on the food of Omalium rivulare nor of the species of Aleochara. In the laboratory O. rivulare fed on small oligochaetes brought back from the wrack beds. Aleochara obscurella and A. grisea attacked similar small oligochaetes but neither were seen actually to feed on them.

Nine other species of Staphylinidae were found in the wrack beds at Whitburn. Not more than half-a-dozen of each were seen in three years and, if any were predators, they presumably affected the wrack fauna only slightly.

Broscus cephalotes.

Broscus cephalotes is well-known to be a voracious shore-frequenting species of Carabidae. At Whitburn both the larvae and adults of this species were found under wrack and stones in the wrack string. Sometimes the larvae were found in burrows in the sand with only their mandibles projecting and at other times they were seen walking over damp sand under wrack with their mandibles apart.

In the laboratory, adults and larvae fed on all kinds of food offered - adult flies of various species, larvae of Coelopa sp. and of Oe. buccata. All parts of the flies were eaten except the wings and legs. Both the larvae and adults of B. cephalotes were very active and they snapped their jaws at anything that moved, even at flies that were flying just above them.

Nothing is known of the feeding habits of the other six species of Carabidae, none of which occurred, however, more than twice in the wrack beds.

Cercyon litoralis.

Larvae of Cercyon litoralis bear well-formed jaws but no larvae were ever found with their prey and they proved difficult to keep in the laboratory. Backlund (1945) states that in the laboratory they feed on more or less soft-skinned animals such as Pachydrilus sp., Enchytraeus albidus and fly larvae.

Mites.

Five species of mites occurred in the wrack beds at Whitburn. Two of these, Thinoseuis fucicola and Parasitus kempersi, were nearly always found in fairly large numbers in both the wrack strings and banks there. Macrocheles superbus was sometimes found in large groups of between thirty and fifty individuals, but more often only one or two occurred together. The other two species, Molgus litoralis and a species of Anoetidae, were very rare, only three of the former being found and about ten nymphs of the latter. These Anoetidae nymphs were found on four Thinoseuis fucicola which were attached to the bodies of Coelopa sp. flies.

Thinoseuis fucicola was kept in culture in 6 x 1 inch glass tubes containing only Laminaria and nematodes on which the mites were frequently observed to be feeding. After lifting a nematode from the wrack each mite appeared to arrange it between its mandibles so that it could be taken (possibly sucked) into the mouth longways. The mites were often seen mating in the glass tubes. The females laid ovoid eggs, usually in groups of between ten and thirty, in small cavities in the moist Laminaria stipes, but odd ones were laid on the surface of the wrack and on moist parts of the glass tube. The eggs hatched in three to five days. The nymphs fed, like the adults, on the nematodes present in the wrack. Both adults and larvae were usually found in small groups of five to ten individuals on the wrack and side of the jar. At times, other mites joined these groups whilst those in the group sometimes left. For the most part the mites in each group remained stationary with their first pair of legs raised in the air pointing forwards. The mites within a group often 'tapped' each other with their first pair of legs and new mites entering a group always 'tapped' one or two of those already present before becoming stationary. This tactile activity of the mites obviously played an important part in their behaviour and may be connected, in some way, with their phoretic habits which are described below.

Parasitus kempersi is a very quick-running mite and in the laboratory has been seen preying on the mite nymphs of either Thinoseuis fucicola or its own species.

Macrocheles superbus, on the other hand, is a fairly slow moving and large mite and most likely feeds on oligochaetes and nematodes. It never fed in laboratory conditions and always died within a day or two.

No observations were made on the three specimens of Molgus litoralis found. King (1914) saw it feeding on Thoracochaeta zosterae and quotes the occurrence of it feeding on Collembola.

The phoretic habit of Thinoseuis fucicola.

The mite Thinoseuis fucicola, besides living freely in the wrack beds at Whitburn, was found in the adult stage attached to the bodies of various insects, particularly Coelopa frigida and C. pilipes.

This phoretic habit of T. fucicola was investigated from 8th October, 1956, to 31st January, 1957. Most of the Coelopa sp. flies that were caught during this period were examined for the mite. The species and sex of each fly was noted and the number of mites on it counted. The percentage of the flies infected and the number of mites per one hundred flies were calculated. The results appear in table 15 (p. 190) and are summarised in table 16 (p. 192).

It can be seen that it occurred fairly consistently that Coelopa pilipes was more infected with mites than was C. frigida. The actual percentage of flies infected was higher and the degree of infection was higher, with the result that there were more than twice as many mites per 100 flies in C. pilipes (215 compared with 103). The males of each of the species bore more than twice as many mites as their respective females.

The difference in the number of mites found on the two sexes could be due to anatomical differences between them. The males of both species being larger than the females could be expected to bear more mites. The difference in the degree of infection of the species, however, can hardly be attributed to anatomical causes since the females of the two species are very much alike, yet they differ greatly in the number of mites found on them. Some difference in the behaviour or in the length of life of the two species probably accounts for this difference in the number of mites they each bear.

Seventy-seven per cent of the infected C. frigida flies

DATE	8.X.56 Migrating flies						15.X.56						25.X.56						29.X.56					
SPECIES	C. frigida			C. pilipes			C. frigida			C. pilipes			C. frigida			C. pilipes			C. frigida			C. pilipes		
SEX	M	F	Tot	M	F	Tot	M	F	Tot	M	F	Tot	M	F	Tot	M	F	Tot	M	F	Tot	M	F	Tot
No. of flies examined	29	56	85	35	67	102	116	81	197	48	37	85	25	33	58	33	24	57	20	21	41	19	18	37
No. with mites	11	18	29	5	6	11	74	38	112	30	18	48	17	17	34	24	15	39	17	12	29	18	15	33
No. of mites	22	49	71	18	33	51	289	104	393	114	48	162	40	31	71	80	50	130	80	31	111	198	57	255
% flies infected	38	32	34	14	9	11	64	47	57	63	49	56	68	52	59	73	63	68	85	57	61	95	83	89
Av. No. per infected fly	2	2.7	2.5	3.6	5.5	4.6	3.9	2.7	3.5	3.8	2.7	3.2	2.3	1.8	2.1	3.3	3.3	3.3	4.7	2.6	3.8	11	3.8	7.7
No. mites per 100 flies	76	88	84	51	49	50	249	128	199	238	130	191	160	94	122	242	208	228	400	148	261	1042	317	689

DATE	1.XI.56.						5.XI.56.												12.XI.56.					
							Migrating flies caught in air						Caught on wrack											
No. flies examined	6	6	12	7	9	16	62	94	156				41	67	108	19	36	55	28	31	59	2	8	10
No. with mites	5	3	8	5	8	13	4	5	9				20	17	37	14	30	44	10	3	13	1	5	6
No. of mites	5	11	16	16	32	48	7	5	12				72	26	98	66	72	138	12	3	15	4	16	20
% flies infected			66			81			6						34			80			22			33
Av. No. per infected fly			2			3.7			1.3						2.6			3.1			1.2			1.8
No. of mites per 100 flies			133			300			7						91			251	43	10	25			200

Table 15

DATE	15.XI.56.						26.XI.56.						10.XII.56.						17.XII.56.					
SPECIES	C. frigida			C. pilipes			C. frigida			C. pilipes			C. frigida			C. pilipes			C. frigida			C. pilipes		
SEX	M	F	Tot	M	F	Tot	M	F	Tot	M	F	Tot	M	F	Tot	M	F	Tot	M	F	Tot	M	F	Tot
No. of flies examined	76	110	186	5	10	15	19	28	47	3	3	6	46	49	95	4	1	5	31	111	142	5	12	17
No. with mites	10	5	15	3	1	4	8	5	13	2	3	5	3	1	4	1	0	1	4	4	8	3	10	13
No. of mites	15	6	21	8	1	9	13	6	19	7	4	11	5	1	6	1	0	1	4	5	9	6	25	31
% flies infected			8			27			27			83			4			20			6			77
Av. No. per infected fly			1.4			2.3			1.5			2.2												
No. mites per 100 flies			11			60			40			183			6			20			6			182

DATE	21.I.57.						24.I.57.						31.I.57.					
No. of flies examined	24	15	39	151	223	374	30	67	97	124	166	290	9	30	39	92	126	218
No. with mites	3	1	4	0	2	2	1	3	4	2	2	4	3	3	6	6	4	10
No. of mites	3	1	4	0	2	2	16	9	25	3	2	5	11	4	15	6	7	13
% flies infected			14			0.5			4			1			15			5
No. mites per 100 flies			14			0.5			26			2			38			6

Table 16. COMPARISON OF THE NUMBER OF MITES FOUND ON C. FRIGIDA AND C. PILIPES

Includes flies caught between 8.x.56. and 26.xi.56. except those caught in flight on 5.xi.56.

	C. frigida			C. pilipes		
	M	F	Total	M	F	Total
Flies examined	360	433	793	171	212	383
Infected with mites	172	118	290	102	101	203
% infected	45.6	27.2	36.6	59.1	47.6	53.0
Number of mites	548	267	815	511	313	824
Mites per 100 flies	152	62	103	299	148	215

carried between 1 and 3 mites, 20% carried between 4 and 10 and 3% between 10 and 20; fifty-seven percent of the infected C. pilipes carried between 1 and 3 mites, 37% between 4 and 10, 3% between 10 and 20 and 3% between 20 and 55.

The mites attached themselves to a fly by gripping a fold of one of its membranes between their chelicerae. About half were found gripping the intersegmental membrane of the abdomen, and other favoured regions were the articular membranes between the legs and thorax and between the wings and thorax.

The mites were also frequently found on Oedoparea buccata, Orygma luctuosa, Helcomyza ustulata, Fucellia maritima and Scatophaga stercoraria, and once or twice on the small Thoracochaeta zosterae. On only one occasion were they found in the wild on species of beetles. On 16th July, 1956, two Cafius xantholoma bearing between them one hundred and forty mites were found in a depression in the sand, seaward of the wrack string at Whitburn. Although the mites do not normally appear to harm the insects to which they attach themselves, the movements of these two beetles were obviously hampered by them.

When a fly died, the mites soon left its body. If in the laboratory they were not provided with other flies, they sometimes managed to attach themselves to species on which they were not found in the wild e.g. Cercyon litoralis and Omalium rivulare. However, the phoretic habit does not appear to be an essential element in the life of T. fucicola as the mites bred and thrived in jars containing only wrack and nematodes.

PART V.

SOME EFFECTS OF THE ENVIRONMENT.

Chapter XV

DIFFERENCES DUE TO LOCATION AND SEASON.

The differences found in the faunae of wrack beds are due to various causes, chief of which are the geographical location of the wrack beds, their size and shape, and the position of the wrack beds on the shore. In addition to faunal differences that can be attributed to these factors, there are seasonal changes in each of the wrack beds.

Some of the more prominent and interesting differences are mentioned below.

Some differences due to geographical location.

Madsen (1936) investigated the shore fauna of East Greenland and compared it with the shore fauna of West Greenland and other arctic regions. Since he dealt with the whole shore fauna, animals occurring in the wrack beds are included. The number of species found in the wrack beds in these arctic regions is much less than the number occurring in the wrack beds of Sweden and Finland, and even in the much smaller locality of Whitburn. In his study of the Swedish and Finnish wrack beds, Backlund collected about five hundred different species of invertebrates (excluding mites) in eleven years. The present writer collected 85 different species at Whitburn in three years. Madsen (op.cit.), however, mentions less than twenty wrack species from Greenland. That only a few species occur on these arctic shores must be due to the harder conditions there.

The predominant wrack animals in the arctic are several species of mites and oligochaetes. In addition to these, there are some Collembola, flies of the genus Fucellia, and a few spiders.

Some of the more interesting differences between the wrack fauna of these three areas are now considered.

Collembola:

Collembola are very common in the wrack beds on the arctic shores and in Sweden and Finland. Madsen found six species and Backlund thirty-five, 15 of which occurred fairly regularly. Only a few Collembola were seen in the wrack beds at Whitburn and they were all probably of the same species. This paucity in the Collembola fauna at Whitburn need not necessarily be due to geographical latitude but to some peculiarity of the Whitburn wrack beds.

Diptera:

No species of the family Coelopidae are recorded from the Greenland shores by Madsen, but Coelopa frigida is known to occur, however, 800 miles within the Arctic Circle at Spitsbergen (Summehayes and Elton). The four species that occurred at Whitburn also occur in Sweden and Finland (although C. pilipes is not included in the list of species Backlund collected). Several species of Fucellia (Muscidae) are found on the arctic shores; F. ariciformis, F. pictipennis, F. fucorum, and F. intermedia being recorded from Greenland.

Fucellia maritima, the only species of the genus that occurred in the wrack beds at Whitburn, is apparently not found in Greenland. No species of Fucellia are mentioned by Summerhayes and Elton (1923) as occurring on Spitsbergen or Bear Island.

Coleoptera:

The beetle fauna of wrack beds on arctic shores appears to be very small compared with the beetle fauna found in more southerly wrack beds. Backlund lists 212 species from Sweden and Finland, thirty of which occurred fairly regularly. At Whitburn 27 species of beetles were found, 6 occurring regularly.

The only beetle Madsen mentions as occurring in seaweed on Greenland's shores is Micralymma brevilingue. Species of the genus Micralymma are well-known shore-frequenting beetles; none, however, occurred at Whitburn.

Spiders:

The spider Erigone arctica is recorded from the arctic shores, and from Sweden and Finland; it was found at Whitburn, too. Only one other spider (Micryphantes nigriceps) was found by Madsen in Greenland. At Whitburn, besides E. arctica, there occurred five other species, but they were fairly rare. Backlund lists almost fifty species from the Swedish and Finnish wrack beds, but only three or four of them occurred regularly.

Mites.

The large red mite Molgus littoralis was found in great abundance in Greenland by Madsen and it is common on other arctic shores. Only three specimens were found at Whitburn. Backlund, unfortunately, does not deal with mites in his work.

Differences in the fauna of wrack strings and wrack banks.

There were several obvious differences between the fauna occurring in the extreme types of wrack beds investigated - the large wrack bank on the rocks at Whitburn and the wrack string some 150 yards south of it. Some of these differences have already been discussed when dealing with the biology of the various fly species found. The larvae of Coelopa frigida and C. pilipes were almost confined to the wrack bank, whilst those of Oedoparea buccata and Helcomyza ustulata were found only in the wrack string.

The adaptations of these species to life in these different habitats have already been discussed in Chapter XI.

Of the species of insects that were found only occasionally in the wrack beds at Whitburn, far more were found in the wrack string than in the wrack bank. Of these occasional visitors, 11 species of Diptera and 16 species of Coleoptera were found in the wrack string and only 2 species of Diptera and one species of Coleoptera in the wrack bank. This paucity of the non-breeding fauna in the wrack bank is presumably due to the extreme conditions prevailing in this habitat. The wrack string, on the other hand, has a wider variation in its physical properties and is therefore suitable to a larger number of species. Many of the occasional visitors to the wrack string were actually found on the sand underneath the wrack and probably it is the protective value of the covering of wrack that is important here.

Differences due to the position of the wrack beds on the shore.

On several occasions two or three wrack beds were found on the shore at different levels seawards of the 'permanent' wrack bank on the rocks at Whitburn. Three wrack beds at different levels can be seen in the photographs on page 6.

The most seaward of these wrack banks existed for only a few hours between successive tides. The only animals found in them were nematodes and these only in very small numbers. On several occasions some of the wrack from these wrack banks was placed in clean kilner jars and the lids tightly screwed down to prevent the wrack being contaminated with nematodes from other sources. The few nematodes present in the wrack reproduced quickly and were very obvious within two or three days.

The wrack banks farther up the shore contained amphipods and oligochaetes as well as the nematodes, but only the most landward of the wrack banks contained the various insect species and their larvae.

Seasonal variation in the fly fauna of the Whitburn wrack beds.

Although there were many changes in the fauna of the wrack beds during the year, only the changes in the fly species will be mentioned.

The change from one dominant species of fly to another always occurred fairly quickly, within about ten days, the decline in the number of one species being accompanied by the sudden emergence of large numbers of the other. As has been shown (p.66) C. frigida was present chiefly from October to early January and C. pilipes from early January to March. Adults of Orygma luctuosa were present for about one month (in September) before the large winter Coelopa sp. population and for a month after (in May). The other Coelopid, Oedoparea buccata, was present as adults from October to January but was found only in the wrack string and did not compete with the three previous species. Only on one or two days in October were adults of all four Coelopids found together. At this time O. luctuosa was in its decline and Oe. buccata adults had just emerged.

The chief summer species of fly was Fucellia maritima which was found as adults from the end of March to September, the period in which the Coelopa sp. were comparatively scarce. Helcomyza ustulata was also a summer species, being found as adults in June and September, but it occurred in much smaller numbers than F. maritima.

Chapter XVI.

SOME EFFECTS OF THE WEATHER.

The wrack animals suffered great losses at times when excessive high water either invaded or destroyed the wrack beds. These high tides had their most disastrous effects on the large winter populations of larvae of Coelopa frigida and C. pilipes in the wrack banks near St. Mary's Island. On several occasions, all or large parts of these wrack banks were carried out to sea and the fly larvae and most of the animals they contained were presumably drowned. The species involved, however, quickly re-established themselves in new wrack beds that were formed. On 28th October, 1955, vast numbers of C. frigida larvae were seen in the wrack banks near St. Mary's Island. The sea was very stormy the following day and most of the wrack banks were carried out to sea. The wrack that remained and the nearby shingle was flooded with water. No Coelopa frigida larvae and only five adults were found in two hours' collecting. By 18th November, 1955, however, the population was re-established, thousands of larvae and adults of C. frigida being found in the newly-formed wrack beds. Similar destruction of the wrack beds and the subsequent restoration of the fauna in newly-formed beds occurred on several other occasions near St. Mary's Island.

At Whitburn excessively high tides were not so immediately disastrous as those near St. Mary's Island. At Whitburn the wrack beds were usually pulled down the shore by the ebbing tide. Some fly larvae usually managed to remain attached to the wrack which was cast up beyond the high tide level at the following high tide. Many larvae, however, were washed out of the wrack and left stranded on the sand. In this exposed position they were soon eaten by the various birds present on the beach.

On 15th December, 1955, some C. frigida larvae which had been washed out of the wrack banks at Whitburn were found in very wet wrack near the low tide line and some were found submerged in seawater in a nearby depression in the sand. Although in the laboratory larvae of C. frigida and of Thoracochaeta zosterae can survive being entirely immersed in seawater for at least twenty-four hours, it is difficult to see how larvae washed out of the wrack beds and separated from them by several yards can regain them safely. This ability to survive periods of immersion in seawater would, however, be of great value in cases where the high water floods the wrack beds without destroying them.

During periods of strong wind the sand in the bay at Whitburn was blown along the shore and accumulated round the wrack string. At times the wrack string became buried in sand with only small pieces of wrack showing above the surface. This covering of their habitat with sand did not seem to effect the wrack fauna deleteriously, however, as living adults and larvae of Fucellia maritima, Oedoparea buccata and Orygma luctuosa were at some time found under the sand. The wrack bank on the rocks at Whitburn was occasionally covered with large amounts of shingle that had been washed there by high water, but this did not appear to effect the animals in the wrack bed.

The wrack beds being warmer than the surrounding air allows certain flies to continue breeding during the winter months. Larvae of Coelopa frigida, C. pilipes and Thoracochaeta zosterae have been found active in the wrack banks when the air temperature was 0°C. At this temperature, however, the adults of C. frigida and C. pilipes are lethargic, and although they vibrate their wings they are unable to fly while Th. zosterae makes only very short flights of about 3-6 inches. Oedoparea buccata, although rare during the cold weather, has been seen flying when the air temperature was 1° C. The larvae of this species in the wrack string hardly move at all when the weather is so cold. The only species of wrack animal found hibernating in groups at Whitburn was the beetle Cercyon litoralis.

PART VI.

LIST OF SPECIES FOUND IN THE WRACK BEDS.

LIST OF SPECIES FOUND IN THE WRACK BEDS.

Most of the animals found in the wrack beds were identified. Only the nematodes and oligochaetes and about ten other species of very rare occurrence were not identified. The number in the bracket refers to the number caught on each occasion.

ISOPODA

Ligia oceanica; Whitburn, wrack string, 7.xi.55 (1); 3.ix.56 (1).
A species of woodlouse occurred under stones in the wrack bank at Whitburn, 1.vii.57 (1).

AMPHIPODA

Orchestia gammarella Pallas: Whitburn, in wrack bank chiefly, common throughout the year. St Mary's Island, wrack bank, common. Llandudno, wrack string, 10.viii.56, common. Furness, wrack string, 8.viii.57.

Gammarus marinus: St. Mary's Island, wrack bank.

CHILOPODA

Several specimens found in wrack string at Whitburn in spring.

DERMAPTERA

Forficula auricularia L.: Whitburn, wrack string, 3.ix.56 (3f) each under a large stone; 8.vii.57 (1f); 16.vii.57 (1f).

HEMIPTERA

Two species each occurred once in the wrack string at Whitburn.

TRICHOPTERA

Three species each occurred once on the surface of the wrack beds at Whitburn.

LEPIDOPTERA

Tinea pallescentella Stn.: Whitburn, wrack string, 27.ix.56 (about 15 larvae).

COLEOPTERA

Carabidae

Broscus cephalotes L.: Whitburn, wrack string, 30.iv.57 (1); 15.v.57 (3); 21.v.57 (1): 11.vi.57 (2): 20.vii.57 (1). Larvae, on sand under wrack and stones at Whitburn, October to May.

Bembidion ustulatum L.: Whitburn, wrack string, 1.vi.56 (1).

B. obtusum Serville: Whitburn, wrack string in central region 21.i.57 (1).

Amara spreta Degean: Whitburn, wrack string, 15.x.56 (1).

A. familiaris Duftsch: Llandudno, wrack string, 10.viii.56 (1).

A. apricaria Payk: Whitburn, wrack string, 17.ix.56 (1); 1.vii.57 (1).

A. convexiuscula Mrsh.: Bamburgh, wrack string 3.ix.57 (1).

Agonum dorsalis Pont.: Whitburn, wrack string 14.vi.56 (1).

Loricera pilicornis Fabr.: Whitburn, wrack string, 24.ix.57 (2).

Dytiscidae

Agabus unguicularis Thomson: Whitburn, wrack string, 20.ix.56 (1).

Hydrophilidae

Cercyon littoralis Gyll.: Whitburn, wrack strings and small wrack banks chiefly, common throughout the year. St. Mary's Island, wrack bank. Larvae, from July to October.

Ptilidae

Ptenidium punctatum Gyll.: Whitburn, in a small clump of densely packed wrack from wrack string, 8.vii.57 (14).

Staphylinidae

Omalium rivulare Payk.: Whitburn, common throughout the year in all types of wrack accumulations.

Philonthus cephalotes Grav.: Whitburn, wrack string, 4.x.56 (2); 30.iv.57 (1).

P. tenuicornis M. and R.: Whitburn, wrack string, 20.ix.56 (1).

Creophilus maxillosus L.: Whitburn, wrack string, 15.v.57 (1).

Cafius xantholoma Grav.: Whitburn, wrack strings and wrack banks, common throughout the year, sometimes up to about 100 being found together. Larvae found all the year. St. Mary's Island, common in wrack banks.

Quedius cinctus Payk.: Whitburn, wrack string, 3.ix.56 (1). St. Mary's Island, wrack bank, 4.x.55 (1).

Q. tristis Grav.: Whitburn, wrack string 3.ix.56 (1).

Tachyporus hypnorum Fab.: Whitburn, wrack flake in central region, 1.vi.56 (1); wrack string 17.ix.56 (2) 15.v.57 (1).

Aleochara obscurella Grav.: Whitburn, wrack string chiefly, April to November. Bamburgh, wrack string 3.ix.57 (3).

Aleochara grisea Kr.: Whitburn, wrack strings chiefly, throughout the year. St. Mary's Island, 24.vi.57 (5).

Aleochara algarum Fauv.: Whitburn, wrack string, 8.vii.57 (2); 28.vii.57 (2). St. Mary's Island, wrack bank, 24.vi.57 (10).

Gauropterus linearis Oliv.: Whitburn, wrack string, 17.ix.56 (1); 26.xi.56 (1).

Carpelimus corticinus Grav.: Whitburn, wrack bank, 21.vi.56 (1).

Coccinellidae

Coccinella 7-punctata L.: Whitburn, wrack string, 18.x.55 (2): 14.vi.56 (2).

Adalia 10-punctata (L.) St. Mary's Island, 13.x.55 (1).

HYMENOPTERA

Cynipidae

Nedinoptera subaptera Walk.: Whitburn, a few found in all types of wrack beds throughout the year, was very common in July, 1957. Bamburgh, wrack string, 3.ix.57 (1). A parasite of Thoracochaeta zosterae and Orugma luctuosa.

Diapriidae

Platymischus dilatatus Wast.: Whitburn, wrack string and wrack banks, a few often found from July to October; was very common in July, 1957. Parasitic on Orygma luctuosa.

Ichneumonidae

Alomya debellator Fabr.: Whitburn, wrack string, 3.ix.56 (1f).

Thersilochus sp.: St. Mary's Island 4.x.55 (1f).

DIPTERA

Tipulidae

Tipula czizeki de Jong: Whitburn, wrack string, 8.x.56 (1).

Trichoceridae

Trichocera regelationis L.: Whitburn, small groups of flies performed aerial dances over the wrack beds, December to February.

Bibionidae

Dilophus febrilis L.: Whitburn, wrack bank, 1.vi.56 (2). St. Mary's Island, wrack bank 13.x.55 (3).

Scatopsidae

Scatopse notata L.: Whitburn, wrack string, 1.vi.56 (1).

Mycetophilidae

Sciara quinquelineta: Whitburn, wrack string, May - June and September - October, fairly common. St. Mary's Island, rarer.

Empididae

Tachista arrogans L.: Whitburn, wrack string, 7.vi.57 (1).

Chersodromia hirta Walk: Whitburn, all types of wrack beds, June to September, common. Llandudno, wrack string, 10.viii.56 (14).

Ch. difficilis Lund.: Llandudno, wrack string, 10.viii.56, fairly common.

Ch. arenaria Hal.: Whitburn, all types of wrack beds, June to September, common.

Ch. incana Walk.: Llandudno, wrack string, 10.viii.56, fairly common. Bamburgh, wrack string, 3.ix.57, fairly common.

Lonchopteridae

Lonchoptera lutea Panzer: Whitburn, wrack string, 23.xi.55 (2f); 29.xi.55 (2f); 15.xii.55 (1f); 8.x.56 (1f); 12.xi.56 (1m); 19.xii.57 (1m).

Syrphidae

Eristalis tenax L. St. Mary's Island, wrack banks, 13.x.55 (1f).

Piophilidae

Piophila vulgaris Fallen: Whitburn, wrack string, 20.ix.56 (1m).

Dryomyzidae

Helcomyza ustulata Curt: Whitburn, wrack strings and flakes, June and September, fairly common. Llandudno, wrack string, 10.viii.56, fairly common. Bamburgh, on sand seawards of a wrack string, 3.ix.57 (16). Larvae, Whitburn, wrack string, July to October. Llandudno, wrack string, 8.viii.56.

Coelopidae

Coelopa frigida (Fabr): Whitburn, large numbers from October to January, fewer from then till March, small number March to September. Larvae, Whitburn, chiefly in large wrack banks from September to December. Large numbers of larvae and adults were also found near St. Mary's Island.

C. pilipes Haliday: Whitburn, large numbers frommid-January to March. Larvae Whitburn, chiefly in large wrack banks from December to February. Adults and larvae also present at St. Mary's Island.

Orygma luctuosa Meigen: Whitburn, common in wrack string and small wrack banks April - May and in September; a few about in June and October - January. Larvae, Whitburn, in small wrack banks chiefly in May, September and October.

Oedoparea buccata Fallen: Whitburn, wrack string, chiefly from October - December. Larvae, October - March.

Borboridae

Thoracochaeta zosterae Hal.: Whitburn, wrack beds, commonest fly throughout the year. St. Mary's Island, very common all the year round.

Th. brachystoma Stenh.: Whitburn, wrack string, late January - early March, 1956, fairly common.

Copromyza nigra: Whitburn, wrack string, 21.v.57 (3).

Copromyza similis Collin: Whitburn, wrack string, 26.ii.56;(2); 26.xi.56 (1); 8.v.57 (1); 21.v.57 (fairly common); 6.vi.57 (2).

C. mitida Meigen: Whitburn, wrack string, 16.ii.56 (1); 23.ii.56 (1).

Borborus ater Meigen: Whitburn, wrack string, 29.xi.55 (1).

Sphaerocera subsultans L.: Whitburn, wrack string, 23.ii.55 (7); 12.i.56 (1); 16.ii.56 (1); 21.v.57 (5); 6.vi.57 (1); wrack bank in central region 17.ix.56 (1).

Calliphoridae.

Calliphora erythrocephala R. - D. Whitburn, frequently alights on the wrack beds. St. Mary's Island, 13.x.55 (1). Hart 19.x.56 (1). In wrack bank, Whitburn, 7.ix.57 (2).

Lucilia sericata Meigen: Several were attracted to two dead gulls lying in the wrack string at Llandudno, 10.viii.56. Four females were caught.

Muscidae

Fucellia maritima Haliday: Whitburn, all types of wrack beds, March to September (common), October and November (few). St. Mary's Island, (common) from March to September. Cullercoats, fresh wrack bank, 12.vi.56. Horden shore devoid of wrack, 24.iv.56. Hart 19.x.56. Llandudno, wrack string, 10.viii.56. Larvae, Whitburn, wrack string and small wrack banks, from April to October. Furness coast, in wrack string of filamentous green alga.

Fannia canicularis L.: Larvae, Whitburn wrack string, 27.ix.56 (C.140); 4.x.56 (1).

Cordyluridae

Scatophaga stercoraria L.: Whitburn, wrack string and small wrack banks, September-November(often fairly common); March to April (fewer). A large number attracted to some rapidly decomposing wrack 17.ix.56 and 20.ix.56. Hart, 19.x.56 (11).

ARANEIDA

Erigone arctica (White). Whitburn, wrack strings and wrack banks March to October, two or three often present, sometimes fairly common.

E. dentipalpis (Wider). Whitburn, wrack string, 30.vii.57 (3m 1f).

Lephyphantes tenuis (Blackwall). Whitburn, wrack string 31.x.57 (6f 1m).

Ostearius melanopygius (O. P.-C.). Whitburn, wrack string 8.vii.57 (1f); 24.ix.57 (1m).

Centromerita sp. Whitburn 31.x.57 (2f).

OPILIONES

Opilio parietinus (De Geer). Whitburn, wrack string 30.iv.57 (8) odd ones in May and June 1957.

ACARINA

Thinoseius fucicola (Halbert). Whitburn, in all kinds of wrack beds and phoretically on various fly species, chiefly Coelopidae. Always common.

Parasitus kempersi Oudemans. Whitburn, in all kinds of wrack beds, common all the year.

Macrocheles superbus Hull. Whitburn, wrack string and wrack bank, May-September, a few could usually be found. On occasions large numbers (30-50) occurred close together in the wrack.

Molgus littoralis (L). Whitburn, on rocks in wrack bank 27.vi.56 (1); 1.vii.57 (1); 8.vii.57 (1).

Some anoetidae deutonymphs were found attached to the mite T. fucicola on a few occasions when this species was found on various flies.

ACKNOWLEDGMENTS.

I should like to acknowledge my indebtedness to Dr. E.T.Burtt for suggesting this interesting subject for research and for his kind supervision of my work.

For their help in identifying the groups named, I am grateful to H. Oldroyd (most of the Diptera), P. Freeman (the tipulid and trichocerid), E.B. Britton (Carabidae), J. Balfour-Browne (other Coleoptera), G. J. Kerrich and G.E.J. Nixon (Hymenoptera), J.D. Bradley (the lepidopteran) and K.H. Hyatt (acarina).

REFERENCES

Allee, W.C. et al. 1949, Principles of Animal Ecology.

Backlund, H.O., 1945, Wrack fauna of Sweden and Finland, Ecology and Chorology. Opuscula Entomologica V. suppl.

Backlund, H.O., 1945b, Larvae and Pupae of Heterochila buccata Fall. compared with the supposed Larva of Helcomyza ustulata Curtis. (Dipt. Dryomyzidae). Kungl. Fysiogr. Sallsk. Forh. 15. 6.

Colyer, C.N., and Hammond, C.O. 1951, Flies of the British Isles. Warne.

Czerny, L., in Lindner, E., 1930, Die Fliegen der Palaearktischen Region. 38a. Dryomyzidae. Stuttgart.

Elwes, E.V., 1915, The life history of a Shore Fly (Fucomyia (Coelopa) frigida Fln.) J. Torquay Nat. History. Soc. 2.

Gause, G.F., 1934, Experimental Analysis of Vito Volterra's Mathematical Theory of the Struggle for Existence. Science 79.

Halbert, 1920, The Acarina of the Seashore. Proc. roy.

Irish Acad. 31.

Haliday, A.H., 1833, A catalogue of Diptera occurring about Holywood in Downshire. Entom. Mag.I, 2, Jan.

Hennig, W., in Lindner E. Die Fliegen der Palaearktischen Region. 52. Coelopidae. Stuttgart. 1937.

de Kerville, H.G., 1894, Soc. Entom. de France, Vol.LXIII.

Keys, J.H., 1918, A list of the Maritime, Sub-Maritime and Coast-frequenting Coleoptera of South Devon and South Cornwall. Journ. Marine Biol. Ass. U.K. 11. (N.S.).

King, L.A.L., 1914, Notes on the habits and characteristics of some littoral mites of Millport. Proc. R. Phys. Soc. Edinburgh 19. 6.

Kloet, G.S., and Hincks, W.D., 1945, A check list of British Insects. Stockport.

Lack, D., 1945, The ecology of closely related species with special reference to Cormorant (Phalacrocorax Carbo) and Shag (P. aristotelis) J.Anim. Ecol. 14.

Lack, D., 1954, The Natural Regulation of Animal Numbers. Oxford.

Lack, D. and Lack, E., 1951, Migration of insects and birds through a Pyrenean pass. J. anim. Ecol. 20.

Lindroth, C.H., 1931, Die Insektfauna Islands und ihre Probleme. Zool. Bidr. Upsala. 13.

Lundbeck, W., 1910, Diptera Danica. Vol. III. Wm. Wesley and Son, London.

Madsen, H., 1936, Investigations on the shore Fauna of east Greenland with a survey of the shores of other arctic regions. Medd. om. Gronland 100.8.

Madsen, H., 1940, A study of the littoral Fauna of northwest Greenland. Medd. om. Gronland. 124. 3.

Mayhew, A.W., 1939, Studies on the structure and life-history of the shore-flies of the genus Coelopa. Thesis for M.Sc. (Durham).

Meyrick, E. 1895, A Handbook of the British Lepidoptera.

Miall, L.C., 1903, The Natural History of Aquatic Insects.

Oldroyd, H., 1954, The seaweed fly nuisance. Discovery. May.

Owen, D.F., 1956, A migration of insects at Spurn Point, Yorkshire. Ent. mon. Mag., 92: 43-44.

Parmenter, L., 1953, The Hover-flies (Syrphidae). Ent. Rec., 65:185-190.

Richards, O.W., 1929, Systematic Notes on the Borboridae (Diptera), with descriptions of new species of Leptocera (Limosina). Ent. mon. Mag., 65: 171-6.

Richards, O.W., 1930, The British Species of Sphaeroceridae (Borboridae, Diptera). Proc. Zool. Soc. Lond. 1930: 261-345.

Scott, H., 1920, Notes on (1) the parasitic staphylinid Aleochara algarum Fauvel and its hosts the Phycodromid Flies. Ent. mon. Mag., 56.

Seguy, E., 1934, Faune de France. 28. Muscidae Acalypterae et Scatophagidae. Lechevalier, Paris.

Taylor, E., 1955, Seaweed flies (Dipt., Coelopidae) in South Devon. Ent. mon. Mag. 91: 107.

Thompson, U., 1951. Studies on the genetics and ecology of Coelopa frigida (Fabricius). Thesis for Ph.D. (Durham)

Williams, C.B., 1958, Insect Migration. Collins. London.

Yerbury, J.W., 1919-22., Seashore Diptera. Jour. Marine Biol. Assoc. 12, N.S.