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THE HOST-SPECIFICITY, MICRO-ECOLOGY, ADHESIVE ATTITUDES, AND COMPARATIVE MORPHOLOGY OF SOME TREMATODE GILL PARASITES

By J. Llewellyn

Department of Zoology and Comparative Physiology, University of Birmingham

(Plates I and II, and Text-fig. 1)

In recent years there have been several accounts of the occurrence of diclidophoroidean trematodes parasitic on the gills of fishes, e.g. Price (1943), Sproston (1946), Dawes (1947), Brinkmann (1952), and Chauhan (1953), and these accounts have included descriptions of the morphology of the parasites. The distribution records have revealed a generally high degree of host specificity and, in some species, a preference even for certain gill arches of the particular hosts, while the morphological descriptions have shown that there is a considerable variation in the form of the parasites, extending to various degrees of deviation from bilateral symmetry (Pl. I, figs. 1–11). These morphological variations are present in spite of the fact that the different parasites occupy such broadly similar habitats in the gill chambers of their respective hosts. But, as far as I am aware, this is the first attempt to investigate the distribution and morphology of the parasites in relation to their microhabitats.

Material and Techniques

Most of the material used in the present study was collected at Plymouth during the months of July and August in 1953, 1954 and 1955, but specimens of *Discocotyle sagittata* on *Salmo trutta* were obtained from Breconshire, Carmarthenshire, Monmouthshire and Shropshire. Some material collected previously (Rees & Llewellyn, 1941) from Cardigan Bay, the Irish Atlantic Slope, and the Porcupine Bank has also been used.

The parasites and hosts studied are listed in Table I. The names of the fishes are those used in the *Plymouth Marine Fauna*, 3rd ed. (Marine Biological Association, in Press), and the parasites, with the two exceptions noted below, have been named as in Sproston's synopsis of the Monogenea (1946). The name *Kuhnia scombri* Sproston, 1946, has been shown (Dollfus, 1946; Llewellyn, 1956) to be a synonym of *Octostoma scombri* Kuhn, 1829, and *Cyclocotyla chrysophryi* (van Beneden & Hesse, 1864), Price, 1943, has been used in preference to *Choricotyle chrysophryi* van Beneden & Hesse. The parasite referred to in Table I as 'microcotylid species' awaits precise

identification: over seventy species of *Microcotyle* have so far been reported (Sproston, 1946), and so the possible addition of a new species becomes a considerable taxonomic task. In the present study it is important only that a microcotylid kind of diclidophoroidean has been found to parasitize a host *Trachurus trachurus* already harbouring *Gastrocotyle trachuri* and *Pseudaxine trachuri*.

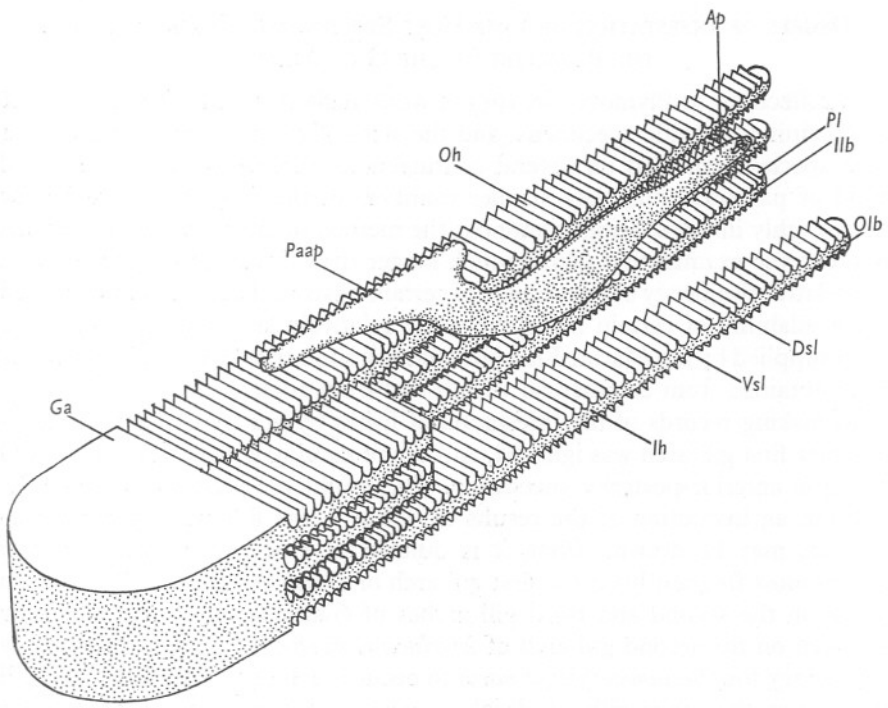
Hosts known from previous records (Baylis & Jones, 1933; Rees & Llewellyn, 1941; Sproston, 1946; Dawes, 1947) to be subject to infection with various diclidophoroideans were examined, as far as was possible, while still alive, the fishes having been brought to the laboratory in baths of sea water. With the parasite of the trout, I have not yet succeeded in examining a living specimen attached to its host: on those occasions when I have taken a microscope to the river bank, my angling friends have not produced a parasitized fish. On other occasions the parasites have died or become detached or have been histologically fixed before examination.

The gills of the fishes were examined by one of two methods, dependent upon previous knowledge of the usual size of the mature parasite. With those fishes, namely *Merluccius merluccius*, *Gadus merlangus* and *G. luscus*, known to be subject to infection with comparatively large parasites, the operculum was lifted and the gills searched while still *in situ*. Sites of infection were then examined carefully with a stereomicroscope. The particular site of infection was noted, i.e. left or right of the fish, serial number of the gill arch, position on the gill arch, inner or outer hemibranch, and dorsal, ventral, or lateral surface of primary lamellae. The importance of a knowledge of all these factors was not realized until the investigation had been in progress for some time, and so early records were incomplete. With hosts likely to harbour smaller parasites, all the gills were removed for microscopic examination. Care was taken so to arrange the excised gill arches that, by inspection, their normal orientation on the fish could be established and so yield records of the precise sites of attachment of the parasites as described above for the larger forms. On only one occasion was a larval trematode observed, but this scarcity could have been due to the loss of larvae after the capture of the hosts, or to insufficiently close observation.

As many as possible of the species of parasites were photographed *in situ* on the gill lamellae, and these have been reproduced in Pl. II. In *Axine belones* the body is bent in two planes, rendering photography very difficult, and a stereogram has been drawn (Text-fig. 1). This figure also illustrates the anatomical terms used for gill structures.

For the preparation of whole mounts for the study of body symmetry, specimens were relaxed either in $7\frac{1}{2}\%$ magnesium chloride solution, or by using menthol, or by simply allowing them to remain in sea water until they were dead. They were then fixed in either Bouin's or Gilson's fluid without the usual pressure of a cover-glass, stained in haemalum, and mounted in

Canada Balsam. Serial paraffin sections were prepared of some specimens of all the parasite species *in situ* on the gills, the sections being stained by Heidenhain's Azan or Masson's trichrome methods.



Text-fig. 1. Stereogram of *Axine belones* on the gills of *Belone belone*. (Very diagrammatic.) *Ap*, anterior end of parasite; *Dsl*, dorsal secondary lamella; *Ga*, gill arch; *Ih*, inner hemibranch; *Ilb*, inner lateral border of primary lamella; *Oh*, outer hemibranch; *Olb*, outer lateral border of primary lamella; *Paap*, posterior adhesive apparatus of parasite; *Pl*, primary lamella; *Vsl*, ventral secondary lamella.

Host Specificity

In the combined earlier investigations of the Irish Sea, the Irish Atlantic Slope, and the Porcupine Bank (Rees & Llewellyn, 1941) and the present Plymouth investigations, 2104 host specimens belonging to seventeen fish species have been examined, and over 900 parasites belonging to eighteen diclidophoroidean species have been collected. Except for *Plectanocotyle gurnardi*, which I have collected from three different species of *Trigla*, namely *T. cuculus*, *T. lineata* and *T. gurnardus*, and *Diclidophora minor* (usually parasitic on *Gadus poutassou*), of which a single specimen was found on a host which I identified as *Gadus merlangus*, all parasite species have been found to be strictly specific to their particular hosts. Only one host has yielded more

than one species of parasite, namely *Trachurus trachurus* often harbouring together both *Gastrocotyle trachuri* and *Pseudaxine trachuri*, and, in addition, on a single occasion one specimen of an unidentified microcotylid species.

Degree of Infestation of some Host Species, and Distribution of the Parasites on the Gill Arches

The collections at Plymouth in 1953–5 were made primarily for the purpose of obtaining parasitic specimens, and the sizes of the samples of the various host species depended on several contingencies. These included the actual yield of parasites, relatively smaller numbers of the hosts found to be the more highly infected being examined; the method of examination of the host, microscopic examination taking much longer than macroscopic (see p. 114); the relative frequency of occurrence of certain hosts in the Plymouth area; and the availability of certain hosts, for while relatively large numbers of fishes were supplied by the Marine Biological Association's trawlers, smaller numbers were obtained from commercial vessels and from anglers.

In making records of the infestation of fishes by gill trematodes the rudimentary first gill arch was ignored, and the remaining arches were numbered 1 to 4 in anterior-posterior succession. The results are included in Table I.

From an inspection of the results in Table I, the following general conclusions may be drawn. First, it is quite clear that *Diclidophora merlangi* occurs most frequently on the first gill arch of *Gadus merlangus*, *Diclidophora luscae* on the second and third gill arches of *Gadus luscus*, and *Anthocotyle merluccii* on the second gill arch of *Merluccius merluccius*. Secondly, there is a tendency for *Plectanocotyle gurnardi* to occur less frequently on the first gill than upon the other gills of *Trigla cuculus*, and similarly a tendency for *Gastrocotyle trachuri* to occur less frequently on the fourth gill than upon the other gills of *Trachurus trachurus*. Thirdly, with *Axine belones* on *Belone belone*, there is a tendency for the first and fourth gills to be less heavily parasitized than the second and third. Insufficient numbers of the remaining species were available for significant comment.

The Morphology and Adhesive Attitudes of the Parasites in Relation to their Hosts

Without exception the parasites were found to be attached with their posterior adhesive organs nearer to the gill arch of the host, and with the anterior end nearer to the distal end of the primary lamellae. In this way the attached ends of the worms lie upstream relative to the gill ventilating current of the host, with the mouth of the parasite downstream.

Beyond this common general adhesive attitude, the parasites exhibited further similarity in that all but two of the species examined were found to attach themselves to the secondary gill lamellae of their hosts (Pl. II, fig. 1).

The exceptional species were *Anthocotyle merluccii* on *Merluccius merluccius* (Pl. II, figs. 5, 6), and *Cyclocotyla chrysophryi* on *Pagellus centrodontus* (Pl. II, fig. 9), where the principal attachment is more directly to primary lamellae. In those parasites which adhere to the secondary lamellae, the opening of each of the attachment organs is directed obliquely postero-ventrally with respect to the parasite, i.e. the plane between the two valves of each attachment organ lies parallel to those which would normally be occupied by the secondary gill lamellae when washed over by the respiratory current of the host (Pl. II, fig. 1).

TABLE I. DEGREE OF INFESTATION OF HOSTS, AND DISTRIBUTION OF PARASITES ON GILL ARCHES, OF FISHES EXAMINED AT PLYMOUTH 1953–55

Category host of sample*	Host	No. of host specimens examined	No. of host specimens infected	Infestation (%)	Parasite	Total numbers of parasites per gill arch 1	2	3	4
A	*Gadus merlangus*	507	44	8·7	*Diclidophora merlangi*	53	8	1	4
	G. luscus	509	108	21·0	*D. luscae*	7	118	91	8
	Merluccius merluccius	500	38	7·6	*Anthocotyle merluccii*	4	28	7	5
B	*Trigla cuculus*	20	19	95·0	*Plectanocotyle gurnardi*	6	22	39	25
	Trachurus trachurus	37	23	62·2	*Gastrocotyle trachuri*	41	56	46	20
			8	21·6	*Pseudaxine trachuri*	8	9	5	2
			1	2·7	Microcotylid species	Not known			
C	*Belone belone*	18	14	77·8	*Axine belones*	19	29	48	22
	Scomber scombrus	8	8	100·0	*Octostoma scombri*	7	15	1	0
D	*Pagellus centrodontus*	47	1	2·1	*Cyclocotyla chrysophryi*	0	0	1	0
	Morone labrax	3	2	66·7	*Microcotyle labracis*	3	0	0	0
	Gadus pollachius	15	1	6·7	*Diclidophora pollachii*	Not known			
	Alosa fallax	2	1	50·0	*Mazocraes alosae*	Not known			

* A, hosts readily available, searched macroscopically; B, hosts readily available, searched microscopically; C, hosts less readily available, searched microscopically; D, hosts less readily available, searched macroscopically.

Beyond the common general features described above, the parasites investigated were found to exhibit considerable variation in their adhesive attitudes. The variable factors include attachment either to one or to more than one primary lamella, attachment to a particular hemibranch, and disposition of the body either between primary lamellae of the same hemibranch or between primary lamellae of different hemibranchs, i.e. between the two hemibranchs of a gill. The pattern of this variation was found to be constant for particular species of parasite and will be described in the following pages, where an attempt is also made to relate the morphology of each of the parasites to its characteristic adhesive attitude.

In *Plectanocotyle gurnardi*, on the gills of *Trigla cuculus* (Pl. II, fig. 2), *Octostoma scombri*, on the gills of *Scomber scombrus*, *Mazocraes alosae*, on the gills of *Alosa fallax*, *Discocotyle sagittata*, on the gills of *Salmo trutta*, and

Microcotyle labracis, on the gills of *Morone labrax*, the posterior adhesive organs are applied either all to the secondary lamellae of the dorsal surface of a primary lamella or all to the secondary lamellae of the ventral surface of a primary lamella, of either an inner or an outer hemibranch, i.e. the trematode is attached to one side or the other of a primary lamella, and never to both sides. In fact the distance between the members of a pair of symmetrical adhesive organs is quite insufficient to span the interval between dorsal and ventral secondary lamellae, i.e. the lateral border, devoid of secondary lamellae, between the dorsal and ventral secondary lamellae.

The longitudinal axis of the parasite, throughout its whole course, always lies parallel to the long axis of the primary lamella, and the whole parasite is bilaterally symmetrical. The attachment organs are all either sessile or borne on very short peduncles. Median ventral posterior hooks (anchors) are present in *Octostoma*, *Mazocraes* and *Plectanocotyle*, but absent in *Discocotyle* and *Microcotyle*.

Further illustrations of the adhesive attitude of the above group of species, as exemplified by *Octostoma scombri*, are given elsewhere (Llewellyn, 1956).

Diclidophora luscae, on the gills of *Gadus luscus* (Pl. II, fig. 3), *D. denticulata*, on the gills of *Gadus virens*, and *D. phycidis*, on the gills of *Urophycis blennoides*, attach themselves to their respective hosts in such a manner that the members of a pair of symmetrical adhesive organs are each applied to opposite sides of the same primary lamella, so that one member of the pair adheres to the secondary lamellae of the dorsal surface and the other to the secondary lamella of the ventral surface. The adhesive organs in these three species of *Diclidophora* are borne on peduncles, the function of which is clearly that of extending the width of the body, and so assisting the parasite to span the distance between the dorsal and ventral surfaces of a primary lamella. As a result of this method of attachment the median longitudinal axis of the worm lies along a lateral border of a primary lamella. The body is bilaterally symmetrical, and no median posterior hooks are present in the adult parasites.

Diclidophora merlangi, on the gills of *Gadus merlangus* (Pl. II, fig. 4), spans both dorsal and ventral surfaces of primary lamellae, as do *Diclidophora denticulata*, *D. luscae*, and *D. phycidis*, but the first-named trematode differs from the other three in that its first and second pairs of adhesive organs are spread over more than one primary lamella, whereas in the other three species all the adhesive organs are applied to the same primary lamella. Characteristically the third and fourth pairs of adhesive organs of *D. merlangi* each grasps the same primary lamella; the second pair grasps the primary lamellae in the same hemibranch immediately on each side of that grasped by the third and fourth pairs; and the first pair of adhesive organs grasps the lamellae that are situated next but one to those grasped by the third and fourth pairs. Occasionally the first pair of adhesive organs may grasp the same lamellae as those grasped by the second pair.

Compatible with this adhesive attitude which involves the spanning of several primary lamellae, the body of *D. merlangi* in the region of the first and second pairs of adhesive organs is relatively wider than the corresponding regions of *D. denticulata* and *D. luscae*, and moreover, the peduncles of the first two pairs of adhesive organs are relatively long. The body is bilaterally symmetrical, and no median posterior hooks are present.

In *Cyclocotyla chrysophryi*, on the gills of *Pagellus centrodontus* (Pl. II, fig. 9), the attachment organs function as suckers and not as clamps (see Llewellyn, 1941), i.e. the adhesive organs do not have opposable jaws for the grasping of pairs of opposite surfaces of primary or secondary lamellae. Instead, each sucker may be applied to any relatively large smooth surface. In the single living specimen that I have had opportunity to examine microscopically, the suckers were applied to the outer lateral borders of primary lamellae, i.e. to regions devoid of secondary lamellae. The four pairs of adhesive organs are borne on relatively long peduncles, and may be spread over two, three, or four adjacent primary lamellae. When forcibly detached from the gill surface, the suckers were able readily to re-establish themselves. When first observed on the living host the parasite was attached to the lateral borders of primary lamellae, but on detachment soon effected new attachment, not only to primary lamellae, but also to the gill arch itself, as shown in Pl. II, fig. 9.

The body is bilaterally symmetrical, and no median posterior hooks are present.

In *Anthocotyle merluccii*, on the gills of *Merluccius merluccius* (Pl. II, figs. 5, 6), the anterior-most of its four pairs of attachment organs is relatively enormously developed so that each of the members of the first pair of organs is itself able to span the distance between the dorsal and ventral surfaces of a primary lamella. The parasite uses this large pair of clamps to grasp the inner border of a primary lamella of an inner hemibranch, the three remaining pairs of small adhesive organs becoming attached to secondary lamellae of the dorsal surface of the same primary lamellae. The body of the parasite passes between primary lamellae of the outer hemibranch and then bends at right angles so that its dorsal surface is in contact with the outer surface of the hemibranch. Were the longitudinal axis of the body to remain in one straight line, the body of the parasite would now lie with its length across the gill ventilating current. However, asymmetrical development has resulted in a bending of the body in the region immediately anterior to the large adhesive organs so that the long axis of the parasite comes to lie more nearly parallel to the direction of the gill ventilating current, and thus the parasite offers less resistance to this current. In a sample of forty-two specimens of *Anthocotyle merluccii* the inclination of the body was found to be towards the animal's right in sixteen (Pl. I, fig. 8, where the animal is seen in ventral view) and to the animal's left in the remaining twenty-six. All twenty-six parasites in which

the inclination of the body was to the left came from gills of the left side of the host fish, and all sixteen with right-inclined bodies came from gills of the right side.

A further feature of asymmetry was found in the relatively greater development of the member of the first pair of adhesive organs which grasps the primary lamella at a position relatively distal to the gill arch (Pl. II, fig. 6). This larger clamp may be on the left or right of the parasite, but is always on the downstream side with respect to the gill-ventilating current of the host, and thus always on the same side towards which the asymmetrical body is inclined. In conformity with the apparently exacting and obligatory requirements of the adhesive attitude of *A. merluccii*, it follows that parasites from the left side of the host fish will be inclined to their left and will have the larger clamp on the left side, and similarly with respect to the right.

Median posterior hooks are present.

In *Axine belones*, on the gills of *Belone belone* (Pl. II, figs. 7, 8A, 8B, and Text-fig. 1), the number of adhesive organs is greatly increased from the more usual six or eight to a number varying between about fifty and seventy. Moreover, in *Axine belones* these posterior adhesive organs, instead of being borne in two symmetrical rows, one on each side of the body, are borne in a single oblique row on what is apparently one margin of the body. This margin is not constantly on the same side of the body in all specimens, at least with respect to the marginal vaginal aperture. This latter organ was found, in a sample of twenty-five specimens, to be without exception on the animal's left. In a sample of 100 specimens of *Axine belones*, the posterior adhesive organs were found on the parasite's right in eighty-seven cases, and on the left in the remaining thirteen cases. Hooks that are presumably homologous with the posterior median hooks of *Octostoma*, *Mazocraes* and *Plectanocotyle* are present approximately mid-way along the row of adhesive organs.

The median longitudinal axis of the body of *Axine* is inclined to the line of the row of adhesive organs at an angle of about 30°.

During attachment to the host, the adhesive organs are applied to secondary lamellae of either the dorsal or the ventral surface of a primary lamella, but always near to the *outer* lateral border of a primary lamella of either the inner or outer hemibranchs. The row of adhesive organs lies parallel to the lateral border of the primary lamella so that the body of the parasite, being inclined to the row of adhesive organs, extends beyond the inner lateral border of the lamella to which it is attached. In the region where the body of the parasite crosses this inner border of the lamella, the body bends at right angles to the plane of the posterior adhesive apparatus so that the greater part of the body of the parasite comes to lie between the two hemibranchs of a gill. As a result of this adhesive attitude the longitudinal axis of the greater part of the body of *Axine*, i.e. the part lying between two hemibranchs of a host gill, lies parallel to the gill-ventilating current of *Belone*. The characteristic disposition of the

body is illustrated in Pl. II, fig. 8, where in fig. 8A the posterior adhesive region is seen in ventral view, and the remainder of the body in lateral view, and where in fig. 8B the body of the same specimen is seen in ventral view.

In *Pseudaxine trachuri*, on the gills of *Trachurus trachurus*, there are about twenty to thirty posterior adhesive organs, all borne in a single row along one margin only of the body. Ventral hooks are present at the extreme posterior end of the row of clamps. The longitudinal axis of the body is inclined to the row of adhesive organs at an angle varying between about 30 and 50°. These adhesive organs are applied near the outer lateral borders of the relatively narrow primary lamellae, and so the body of the parasite soon crosses the inner border of the primary lamella. Here it bends usually through a right angle so that the greater part of the body of the parasite lies between two hemibranchs as in *Axine* (Pl. II, fig. 7; and Text-fig. 1), but more occasionally through 180°, so that the body of the parasite is in contact with the opposite side of the same primary lamella to that to which its adhesive organs are attached.

All twenty-four specimens of *Pseudaxine* that I have collected were found attached near to the distal ends of primary lamellae.

In a sample of sixteen specimens of *P. trachuri*, the adhesive organs were found on the right of eleven animals, and on the left of the remaining 5.

Gastrocotyle trachuri, on the gills of *Trachurus trachurus* (Pl. II, fig. 10), is asymmetrical, the twenty-five to thirty posterior adhesive organs being confined to one side only of the body. The row of adhesive organs lies approximately parallel to the longitudinal axis of the body of the parasite, and ventral hooks are present at the extreme posterior end of the body. In a sample of seventy-eight specimens of *Gastrocotyle trachuri* the adhesive organs were found on the left of thirty-nine animals, and on the right of the other thirty-nine.

The parasite may be attached to any of the secondary gill lamellae, irrespective of whether they be those of the dorsal or ventral surfaces of a primary lamella, or whether the primary lamella belongs to an inner or an outer hemibranch. But invariably the parasite lies with its attachment organs nearer to the outer border of a primary lamella (i.e. the outer border of a hemibranch) so that a (small) part of the body overlaps the inner border of the same primary lamella and comes to lie between two hemibranchs. In the region where it overlaps into the space between the hemibranchs, the body of the parasite is folded ventrally through 90°.

Discussion

The present investigation of the distribution of diclidophoroidean parasites on Plymouth fishes has shown these trematodes to be entirely specific to their particular hosts. My single previous record of *Diclidophora minor* from *Gadus merlangus* very probably involved mis-identification of the fish, for in

an unpublished thesis (1940), in the library of the University of Wales, I referred to this host as '*Gadus merlangus* var. Deep-Sea', probably on account of the trawlermen's name of 'Deep-Sea Whiting' for the fish. Gallien (1937) had previously found *Diclidophora minor* on *Gadus poutassou* in the same locality, and it is almost certain that my specimen of *Diclidophora minor* came from the same host species. It seems distinctly possible also that the record of Baylis & Jones (1933) of *D. denticulata* from *Merluccius merluccius* at Plymouth was also a case of mistaken identity, for the 500 specimens of *M. merluccius* examined in the present study were parasitized only by *Anthocotyle merluccii*. Among the British marine Diclidophoroidea, then, only *Plectanocotyle gurnardi* appears to enjoy the hospitality of more than one host species, and in this case the hosts are closely related. A detailed examination, therefore, should be made of specimens of *Plectanocotyle gurnardi* from *Trigla gurnardus*, *T. lineata*, and *T. cuculus* for signs of incipient speciation.

The descriptions of the adhesive attitudes and of the morphology of the diclidophoroideans studied have shown that there is an exacting topographical relationship between parasite and host, and this is probably an important factor in the mechanism of host specificity.

The present investigation has confirmed Cerfontaine's (1898) observations that the maximum incidence of *Diclidophora merlangi* is on the first gill of *Gadus merlangus*, and that that of *Diclidophora luscae* is upon the second and third gills of *Gadus luscus*. On the other hand, Frankland (1955) found that her observations on a third *Diclidophora* species on a *Gadus* host, namely *Diclidophora denticulata* on *Gadus virens*, gave different results from those of Cerfontaine. The latter author (1898) had found the parasite to be most prevalent on the second and third arches, but Frankland, in a sample of 247 host specimens, found the first and second arches to be the most heavily parasitized. Cerfontaine made no reference to his technique of collecting, and did not record any larval or small forms. Frankland, however, made a microscopic search of the gills, and recorded the presence of larvae. The inference is that there is a change in the maximum incidence of parasite per gill arch with the age of the parasites, the shift, in *Diclidophora denticulata*, being from the first and second arches at initial infestation, to the second and third arches when older. If this is so, it would require either that the parasites are capable of transferring themselves from one gill arch to another, to which there is some contrary evidence (Frankland, 1955), or else that the degree of survival of parasites initially attaching themselves to the second and third gills is greater than for those attaching themselves to the first. In future studies it might be possible to test the latter hypothesis by investigating if there is any correlation between the degree of development of the parasite (size?) and the particular site of infestation.

Cerfontaine thought the explanation of the differential distribution among the gill arches to be in a choice of gill exercised by the parasite at initial

infestation, but in the absence of any evidence that the infective parasite is able to swim well enough to manoeuvre itself in the gill ventilating current, it is difficult to see how any such selective power could operate.

An alternative explanation would be to assume that the infective larvae are swept involuntarily over the gills by the gill-ventilating current. Any variations in the volume of water passing over the different gill arches might then be reflected in the numbers of opportunities for parasites to become attached. However, the greater numbers of larvae brought to those gills receiving the greater ventilation would themselves be committed to a lifelong struggle against the greater current, and the survival rate would be correspondingly lower than on less well-ventilated gills. Those parasites that change their adhesive attitudes during their lifetime, e.g. *D. denticulata* changing from the larval manner of attachment on one side of the primary lamella (Frankland, 1955) to the adult manner of attachment on both sides, appear to be particularly vulnerable at the time of effecting this transfer.

As to the difference in prevalence per gill arch between, on the one hand *D. luscae* and *D. denticulata*, each on the second and third gills of their respective hosts, and on the other hand *D. merlangi*, on the first gill of its host, the most profitable approach for understanding the problem appears to lie in a detailed comparison of the gill ventilating mechanisms of *Gadus luscus*, *G. virens*, and *G. merlangus*.

A common feature of the adhesive attitude found in all the parasites here studied is that the posterior adhesive organs are attached to the gills at a position upstream relative to the gill ventilating current, with the anterior mouth-bearing end downstream. Such an adhesive attitude is obviously well adapted to meet what appear to be the major ecological problems facing these parasites, namely those of clinging to the host in the face of a current, and of feeding, from the highly vascular secondary lamellae, on the blood that forms the main part of their diet (Llewellyn, 1954).

The particular forms of adhesive attitude have been found to vary considerably. The simplest method, e.g. *Octostoma*, *Mazocraes*, *Plectanocotyle*, *Discocotyle* and *Microcotyle*, is for the parasite to apply the whole of its body to the secondary lamellae of one surface of a primary lamella. It thus lies completely between primary lamellae of one hemibranch, and no part of the body is exposed to what presumably are the stronger currents between and outside the hemibranchs.

A variation occurs in *Diclidophora* species. In *D. luscae*, *D. denticulata* and *D. phycidis*, the adhesive organs are applied to both the dorsal and the ventral secondary lamellae of the same primary lamella, and in *D. merlangi* the parasite spans several primary lamellae. This adhesive attitude of *Diclidophora*, however, is achieved at the cost of losing suitable anchorage, in the form of secondary lamellae, for median posterior hooks, which are not found in this genus. The adhesive attitude in *Diclidophora* necessitates a widening of the

span of the pairs of adhesive organs by means of an increase in body width, and in *D. merlangi*, by the development of relatively long peduncles as well.

Cyclocotyla chrysophryi resembles *Diclidophora merlangi* in that it spans several primary lamellae, but differs from it in that instead of using *clamps* to attach itself to secondary lamellae, it uses *suckers* to attach itself to the smooth lateral borders of primary lamellae. The possession of these suckers permits the parasite to wander over other smooth surfaces, and I have observed *Cyclocotyla* to attach itself firmly to the gill arch of a (dead) *Pagellus*. However, the parasite was observed to contain abundant haematin, which has been shown (Llewellyn, 1954) to be evidence of a blood-feeding habit, and it seems probable that the normal habitat of the parasite on the living host is on the gills. Similarly, the numerous previous records of cyclocotylid parasites from the mouth-cavities of their hosts, or even as super-parasites of crustaceans which are themselves parasitic in the mouth-cavity of the host fish (see Sproston, 1946), are probably the result of the wanderings of which these parasites are capable in virtue of their possession of sucker-like adhesive organs and not clamps.

Anthocotyle merluccii is asymmetrical, and the advantage of the asymmetry is obvious since it results in the long axis of the body coming to lie parallel to the gill-ventilating current instead of across it. The need for this asymmetrical adjustment appears to have arisen from the change in the manner of attachment: the adhesive attitude of the ancestral diclidophoroidean probably resembled that of the present-day *Octostoma*, but the adoption of a habit of attachment by means of enlarged anterior clamps applied to the lateral border of a primary lamella necessitated a shift in the orientation of the parasite to a position at right-angles to the gill-ventilating current. A natural consequence would be the development of asymmetry to regain a body disposition offering less resistance to the water current. The reason for the unequal development of the members of the anterior-most pair of clamps is less clear. One would expect the adhesive organ farther upstream to bear the greater burden and so to be the more powerful and presumably the larger. In fact, however, the reverse obtained without exception in a sample of forty-two specimens of *Anthocotyle* observed *in situ* on the gills of *Merluccius*: the clamp nearer to the gill arch was invariably the smaller one of the pair. It has been shown (p. 120) that the side of the parasite on which the larger clamp occurs is directly related to the side of the fish upon which the parasite occurs. Since this appears to be purely a matter of chance, the side of the occurrence of the larger clamp has no taxonomic significance, and Brinkmann's (1952) relegation to synonymy with *Anthocotyle merluccii* of an American species erected on grounds of the side of development of the larger clamp was fully justified.

The asymmetry of *Axine belones*, *Pseudaxine trachuri* and *Gastrocotyle trachuri* fulfils the same function as that in *Anthocotyle*, namely that of bringing the longitudinal axis of the body to lie parallel to the gill-ventilating current,

but the reason why its development should have been necessary is not clear. Presumably it is directly related to the relative disposition of the long axis of the body and the hinge axes of the clamps during early development. This, however, itself presents certain problems, for in a preliminary examination of the orientation of the clamps of *Axine belones*, it was found that the clamps anterior to the hooks, and also those posterior to the hooks, all face in the same direction. The two sets of clamps are thus not mirror images of one another, as would be expected if their disposition were the result simply of the suppression in growth of the longitudinal axis of the posterior adhesive region of the body as has been suggested by Sproston (1946). More complex factors are obviously involved, and await further investigation.

The direction of asymmetry in *Axine belones*, *Pseudaxine trachuri* and *Gastrocotyle trachuri* has been shown to be dependent upon the particular site of infection of the host. In *Gastrocotyle* this is probably a matter of chance (thirty-nine with clamps on the parasite's left, and thirty-nine on the right, in a sample of seventy-eight), but in *Axine* the unequal distribution (eighty-seven with clamps on the parasite's right, and thirteen on the left, in a sample of a hundred) suggests the presence of a dominating factor influencing the position of the parasite along the curved gill arch, or some other variation. On the other hand, Sproston (1946, pp. 453–4) stated that in a sample of at least thirty specimens of *Axine belones* on *Belone belone* at Plymouth, all but one had the adhesive organs on the *left*. It must be pointed out, however, that Sproston (1946, figs. 104*a*, *b*) illustrated a specimen of *Axine belones* in which the vagina was on the animal's right, whereas I found it, without exception, to be on the left in a sample of twenty-five specimens. Lorenz (1878), in a paper on the anatomy of *Axine*, had also found the vagina on the left. Thus further work will be necessary before the precise topographical relationships between *Axine belones* and *Belone belone* can be determined.

Superficially, the three asymmetrical 'microcotylid' species *Axine belones*, *Pseudaxine trachuri* and *Gastrocotyle trachuri* appear to present a series of progressive reduction, in that the adhesive organs which in *Axine* are posterior to the ventral hooks are lost in *Pseudaxine* and *Gastrocotyle*, and that the body itself becomes relatively much smaller in *Gastrocotyle*. However, the morphology of *Axine* itself presents certain problems which should be investigated before worth-while speculations may be made upon evolutionary trends.

I am greatly indebted to the Director and Staff of the Plymouth Laboratory for their valuable assistance. I am also grateful to Dr H. M. T. Frankland for allowing me to read her manuscript on the bionomics and life history of *Diclidophora denticulata* before its publication.

SUMMARY

In a sample of over 2000 fishes belonging to seventeen species, the gills were found to be infested with over 900 parasites belonging to eighteen species of diclidophoroidean trematodes. All the parasites were found to be specific to particular hosts, with the exception of *Plectanocotyle gurnardi*, which may parasitize any one of three species of *Trigla*.

In most cases there was a characteristic differential distribution of the parasite among the gill arches of the host, and it is suggested that this is the result of variations in the flow of water over the different gills rather than of a choice exercised by the parasite.

The parasites were all attached with the posterior adhesive organs upstream relative to the gill-ventilating current and the mouth downstream. Variations in the adhesive attitude, characteristic of species or groups of species, occurred within this common pattern.

Variations in the form of the parasites such as the width of the body, degree of development of the peduncles of the adhesive organs, and asymmetry, could in each case be related to the characteristic adhesive attitude of the species.

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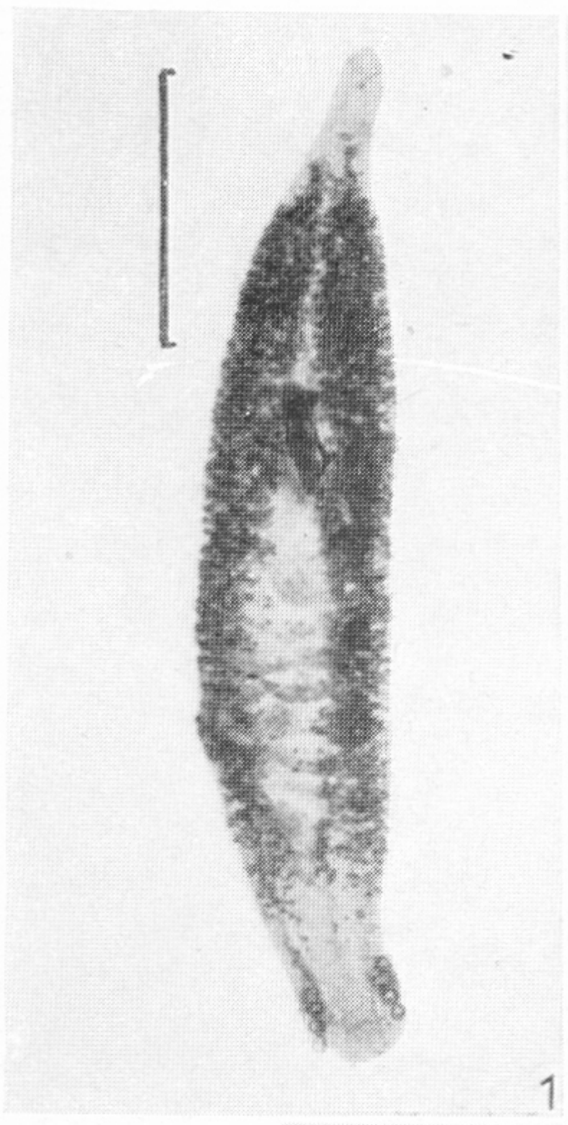
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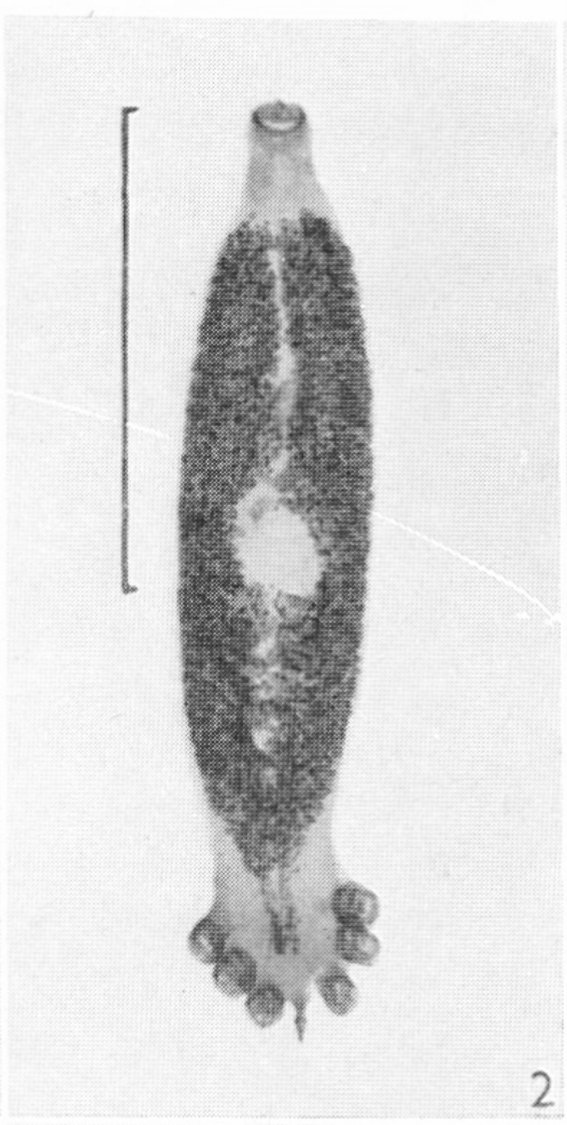
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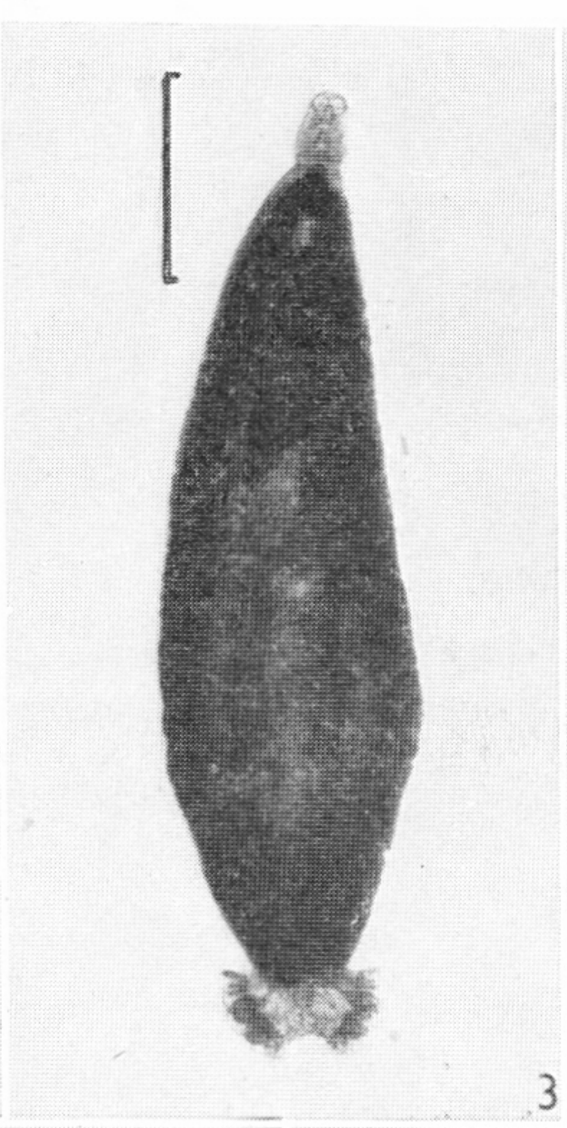
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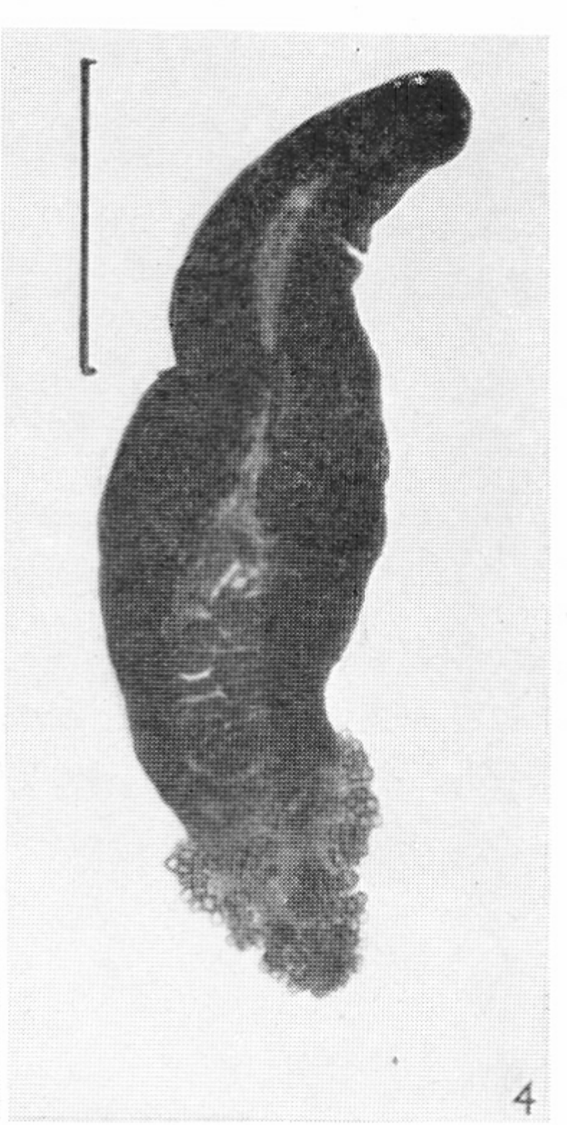
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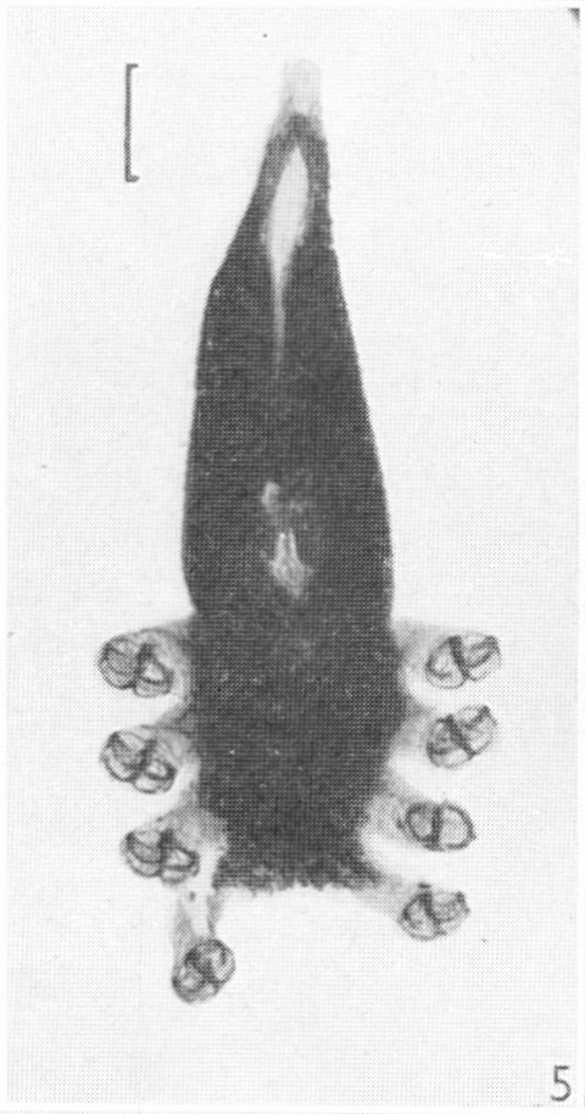
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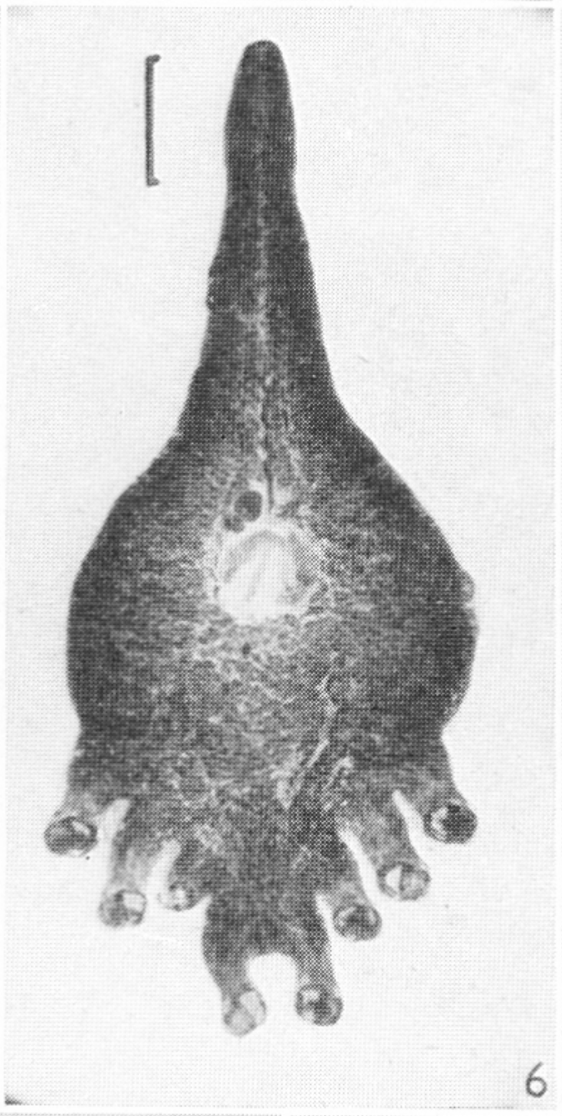
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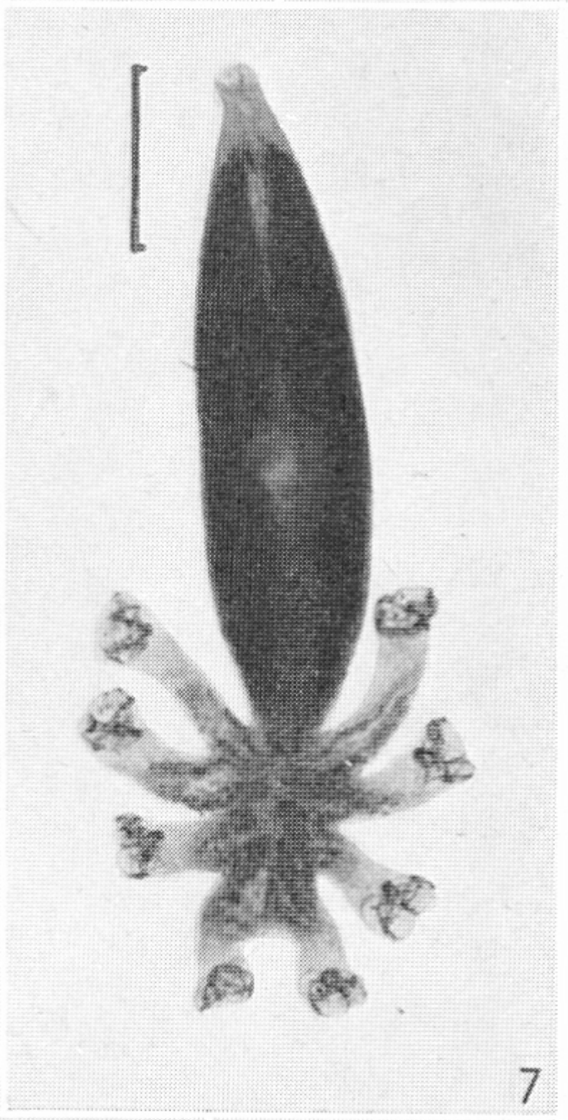
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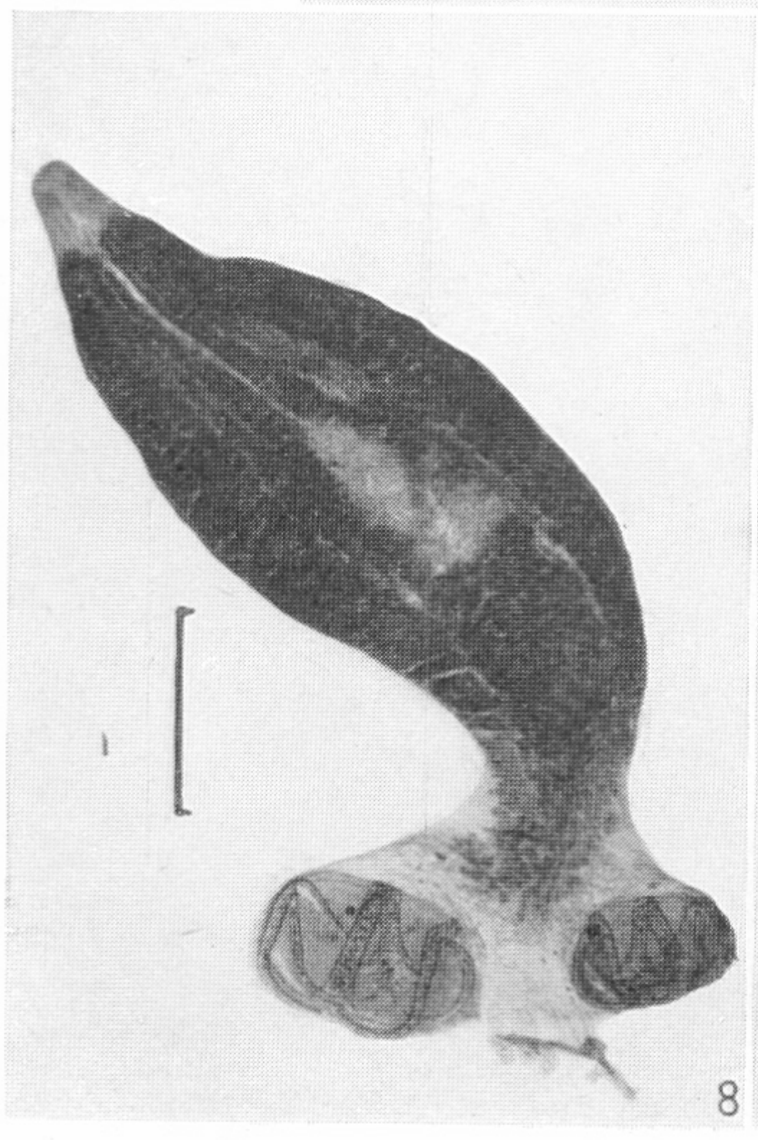
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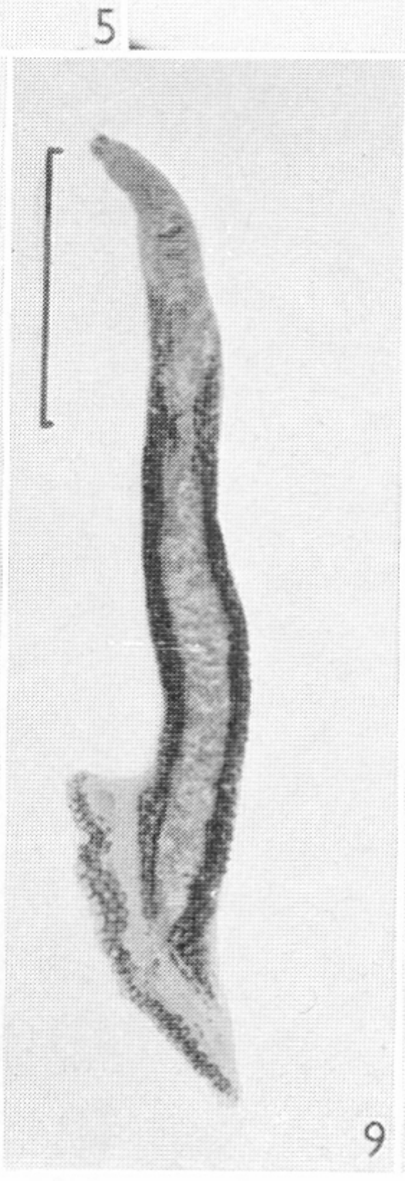
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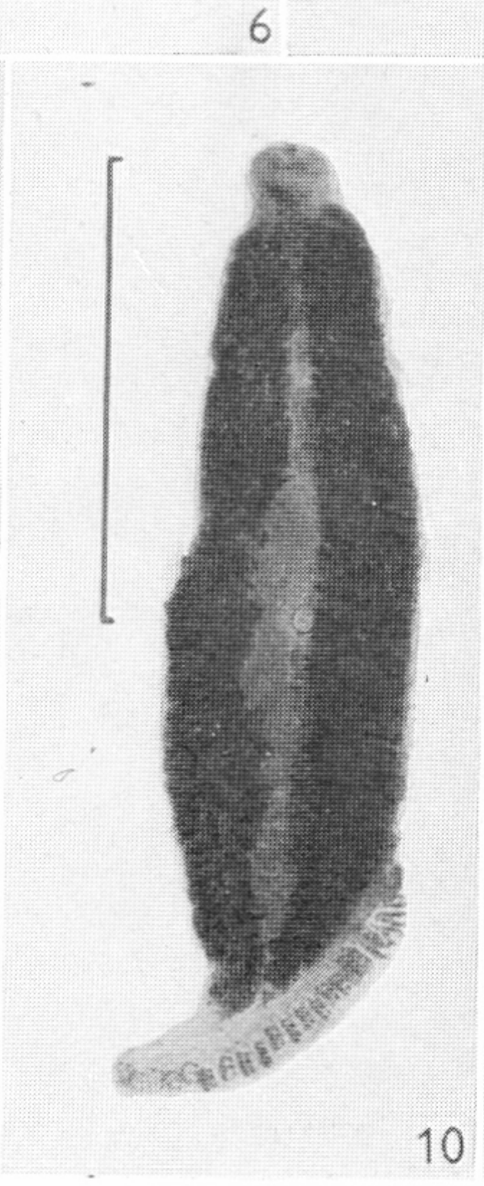
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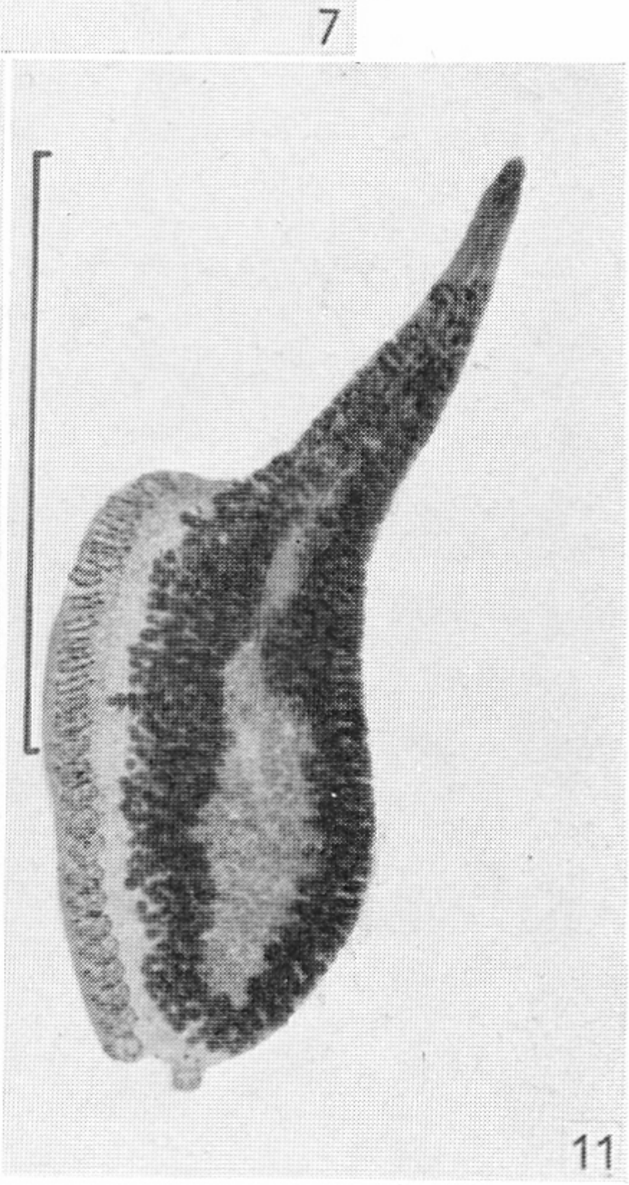
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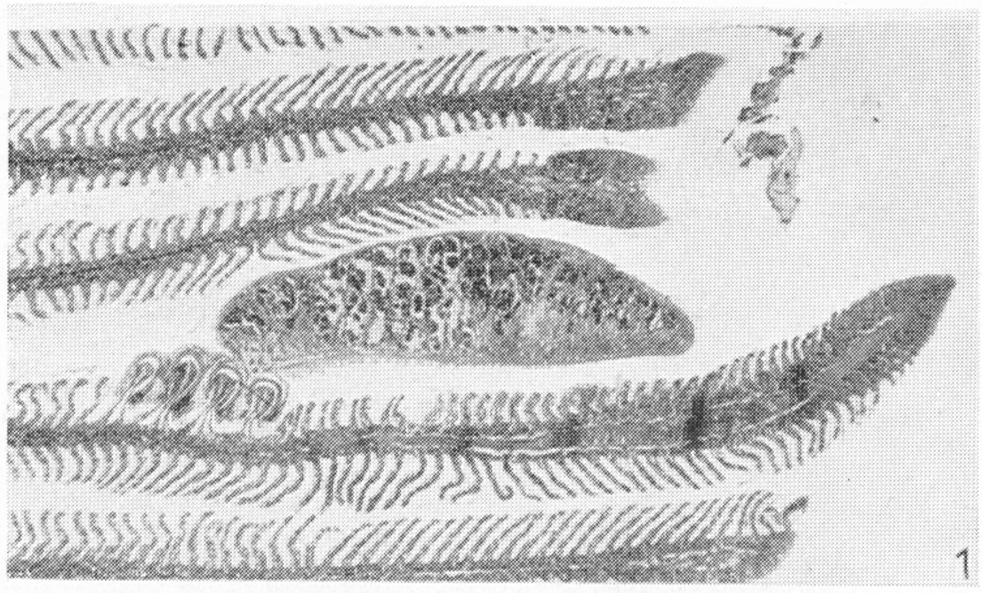
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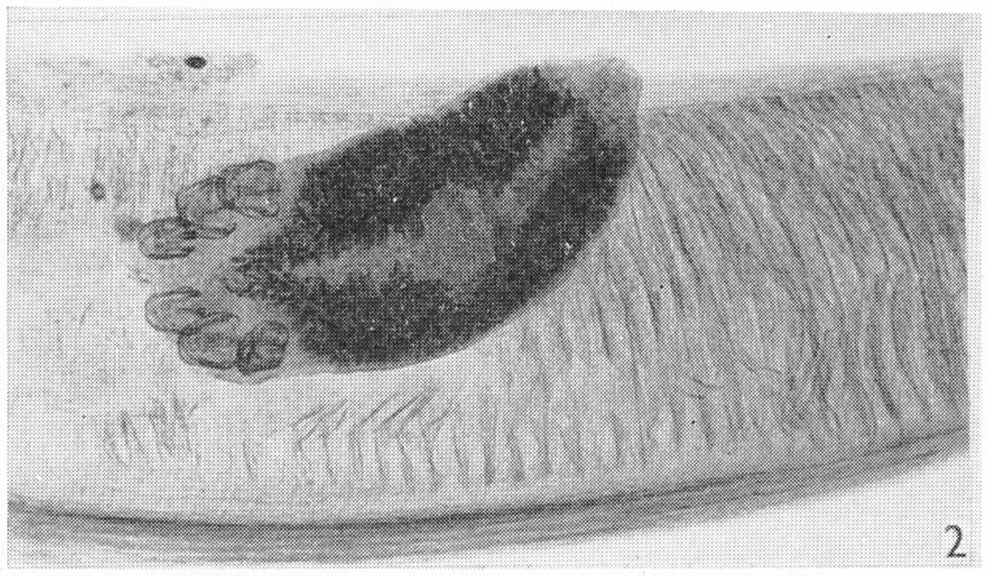
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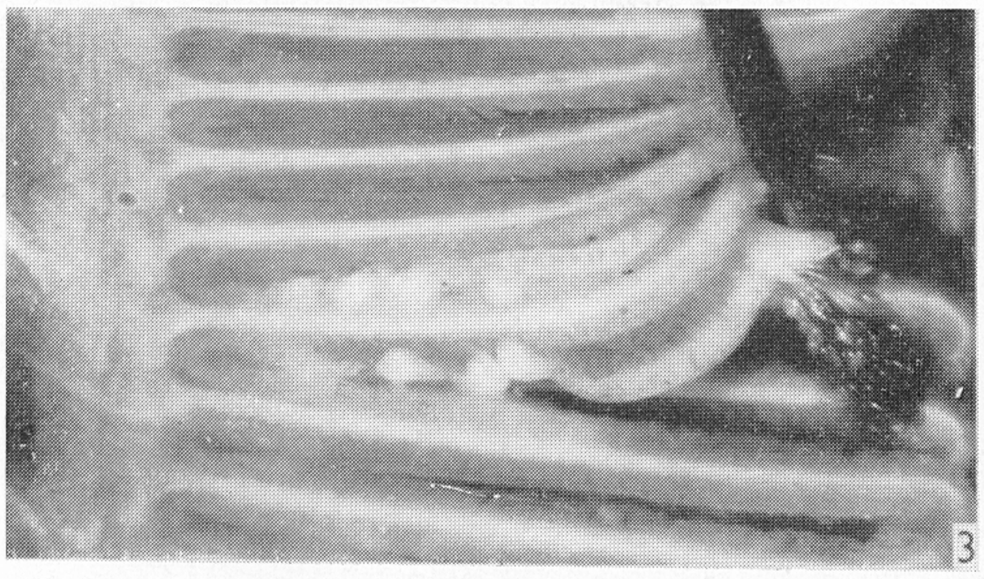
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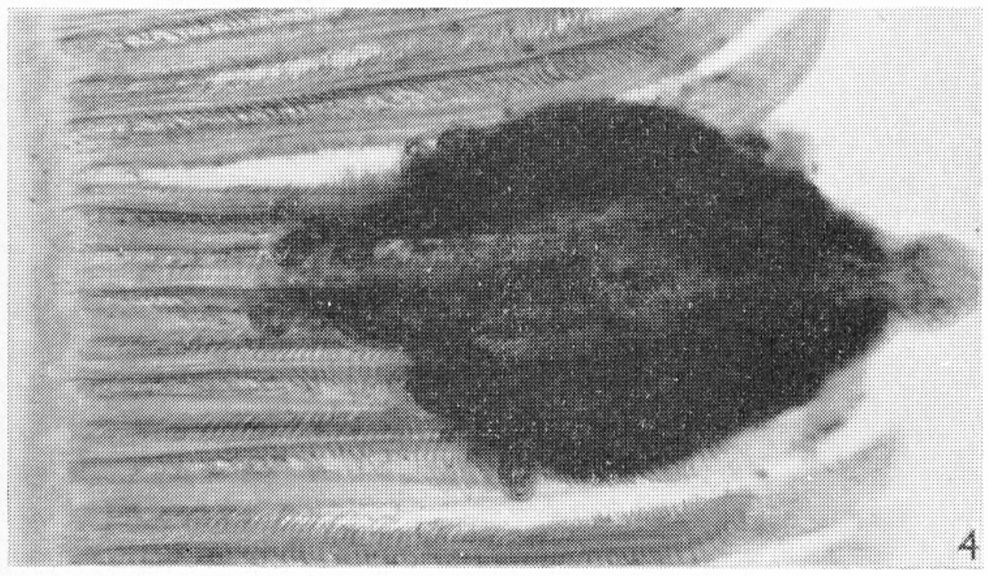
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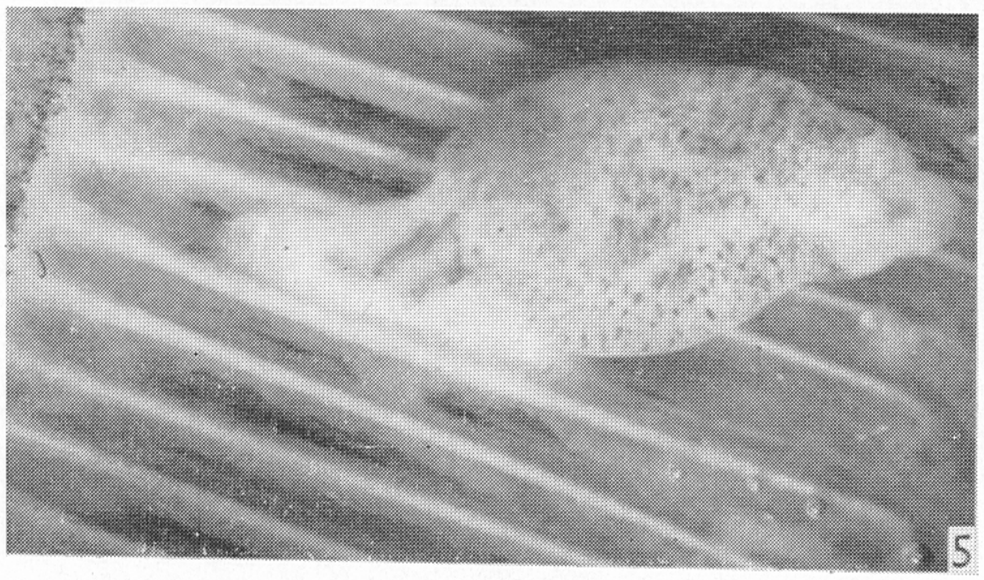
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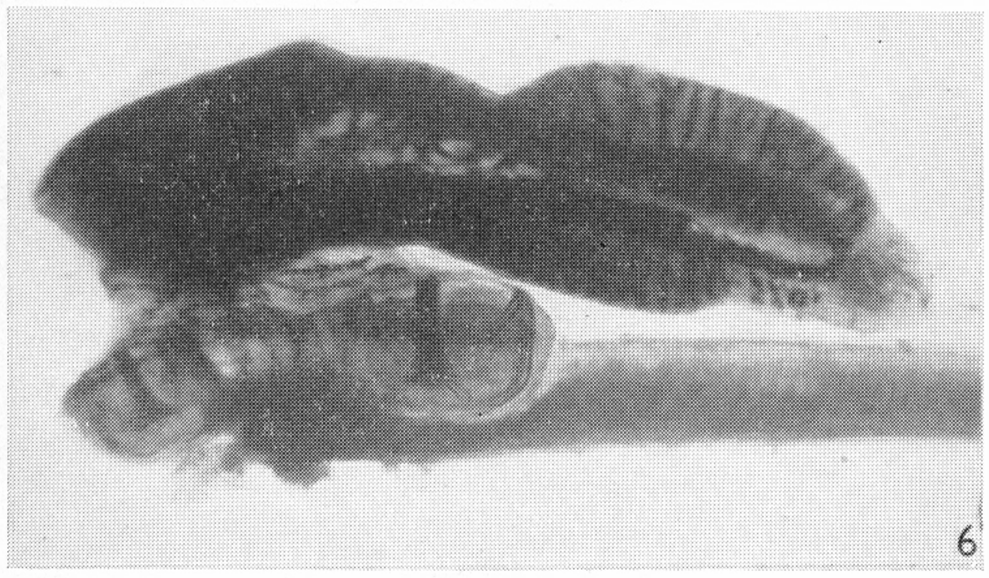
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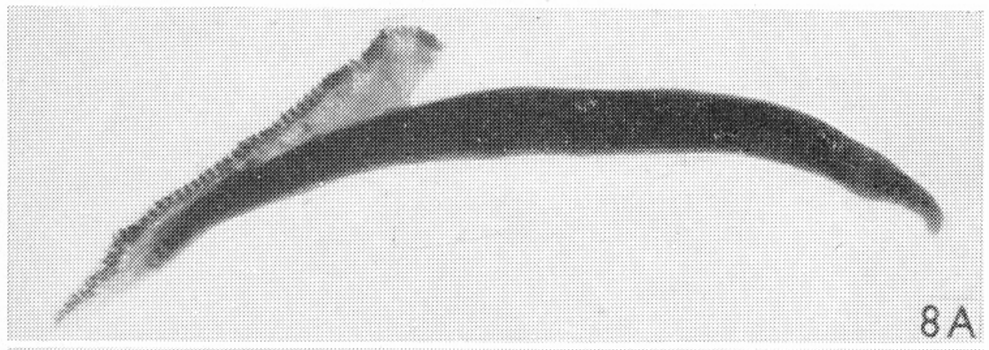
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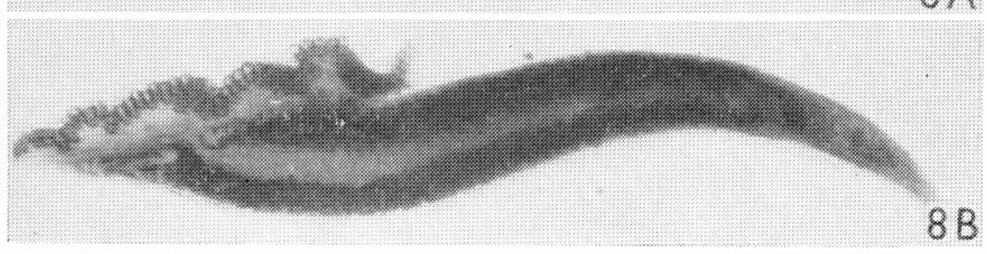
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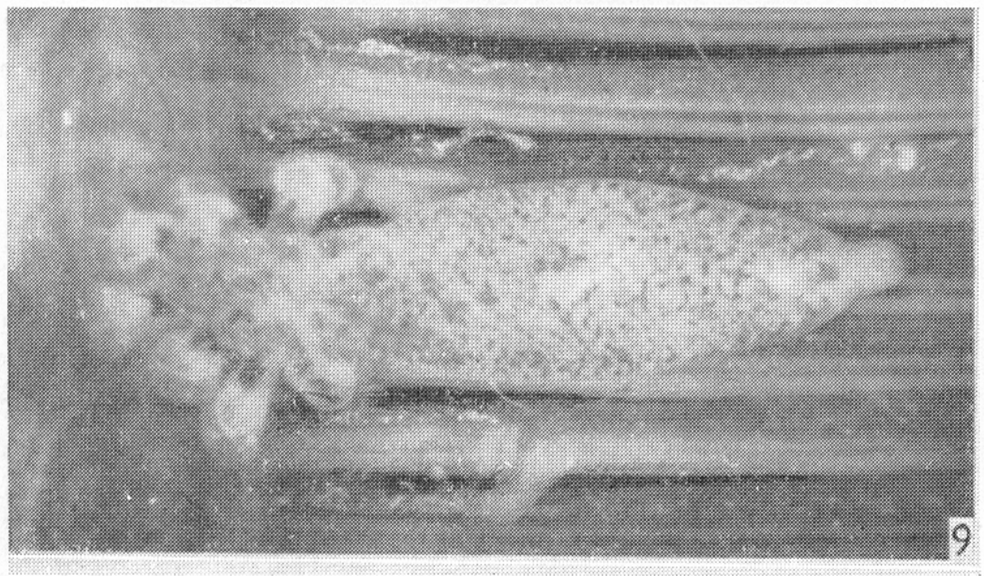
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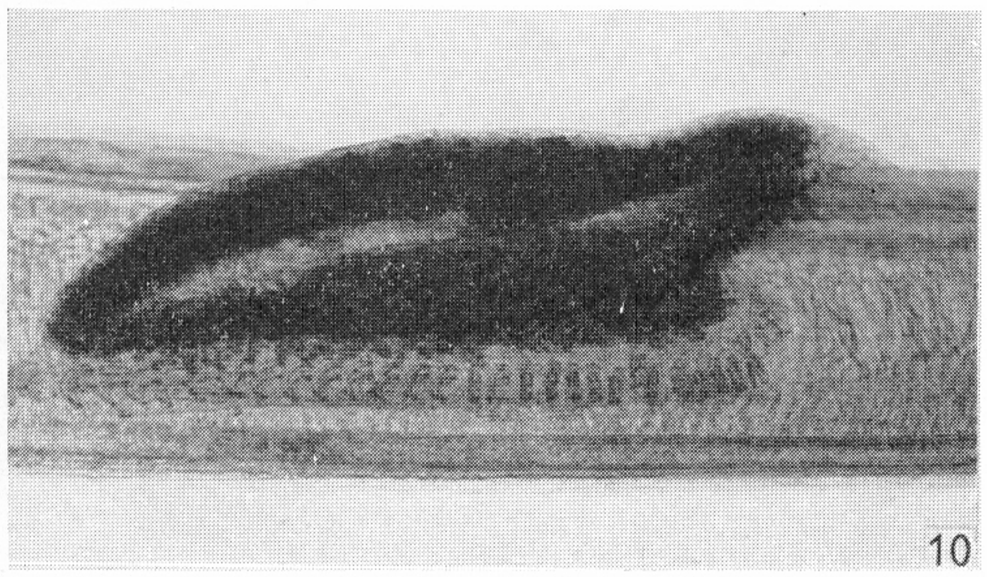
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Direction of gill-ventilating current

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EXPLANATION OF PLATES

PLATE I

The range of form exhibited by representative diclidophoroidean gill trematodes. (Specimens flattened under pressure of cover-glass and mounted in Canada Balsam. Index-line in all figures = 1·0 mm.)

Fig. 1. *Octostoma scombri.*
Fig. 2. *Plectanocotyle gurnardi.*
Fig. 3. *Discocotyle sagittata.*
Fig. 4. *Microcotyle* sp. (from *Serranus cabrilla*).
Fig. 5. *Diclidophora denticulata.*
Fig. 6. *D. merlangi.*
Fig. 7. *Cyclocotyla chrysophryi.*
Fig. 8. *Anthocotyle merluccii.*
Fig. 9. *Axine belones.*
Fig. 10. *Pseudaxine trachuri.*
Fig. 11. *Gastrocotyle trachuri.*

PLATE II

Adhesive attitudes of representative diclidophoroidean gill trematodes. (Figs. 3, 5, 7 and 9: living specimens; Figs. 8A, B: specimens fixed, but not flattened; Figs. 1, 2, 4, 6 and 10: specimens in Canada Balsam.)

Fig. 1. L.S. *Discocotyle sagittata* on *Salmo trutta.*
Fig. 2. *Plectanocotyle gurnardi* on *Trigla cuculus.*
Fig. 3. *Diclidophora luscae* on *Gadus luscus.*
Fig. 4. *D. merlangi* on *G. merlangus.*
Fig. 5. *Anthocotyle merluccii* on *Merluccius merluccius.*
Fig. 6. *A. merluccii* on *Merluccius merluccius.*
Fig. 7. *Axine belones* on *Belone belone.*
Fig. 8A. *A. belones*, body in side view.
Fig. 8B. *A. belones*, body in ventral view (same specimen as 8A).
Fig. 9. *Cyclocotyla chrysophryi* on *Pagellus centrodontus.*
Fig. 10. *Gastrocotyle trachuri* on *Trachurus trachurus.*