The Azygiidae, Hirudinellidae, Ptychogonimidae, Sclerodistomidae and Syncoeliidae (Digenea) of fishes from the northeast Atlantic

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Synopsis

Keys, descriptions (mainly original), full host-records, locality data and comments on some aspects of their biology are presented for all of the species of the hemiuroid families Azygiidae, Hirudinellidae, Ptychogonimidae, Sclerodistomidae and Syncoeliidae recorded from the northeast Atlantic region. The species described are: *Otodistomum veliporum*, *O. cestoides*, *O. plunketi*, *Otodistomum* sp. metacercariae, *Hirudinella ventricosa*, *Botulus microporus*, *Lampritrema miescheri*, *Ptychogonimus megastoma*, *Prosorchiopsis legendrei*, *Copiatestes filiferus* and, in addition, *Distoma gigas* of unknown family. The *Otodistomum veliporum–cestoides* problem is examined and discussed in detail. It is proposed that the family Hirudinellidae is composed of three monotypic genera, *Hirudinella*, *Botulus* and *Lampritrema*. *Distoma microporum* Monticelli and *Lampritrema miescheri* (Zschokke) are considered to be senior synonyms of *Botulus alepidosauri* Guiart and *Lampritrema nipponicum* Yamaguti, respectively. It is considered that the genus *Copiatestes* Crowcroft is distinct from *Syncoelium* Looss, and that *C. filiferus* (Leuckart, in Sars) belongs to this genus. It is suggested that *Distoma gigas* Nardo is a hemiuroid, possibly being related to the sclerodistomids.

Introduction

This is the second in a projected series of papers on the helminth-fauna of fishes from the northeast Atlantic region. The families dealt with, the Azygiidae, Hirudinellidae, Ptychogonimidae, Sclerodistomidae and Syncoeliidae, with the Accacoeliidae which has already been studied (Bray & Gibson, 1977), are all members of the superfamily Hemiuroidea Looss, 1899. This group of families tends to be relatively rare or restricted to certain hosts in the marine environment. They are usually somewhat larger than, and, we believe, more primitive than, the remainder of the hemiuroid families, which we hope to deal with in a future paper. The classification and phylogenetic relationships of the Hemiuroidea will be commented upon in detail elsewhere (Gibson & Bray, in preparation).

Materials and methods

The materials and methods used in this investigation are outlined in the first paper in this series (Bray & Gibson, 1977). In addition to the sources of material mentioned in our previous report, we have now collected material at Split, Yugoslavia, in 1975 (by D. I. G.), aboard the R.V. *Cirolana* in the NE Atlantic in 1976 (by R. A. B.) and at Kristineberg Zoological Station, Sweden, in 1976 (by D. I. G.). We have used the classification of fishes presented by Greenwood *et al.* (1966) and Compagno (1973).

Terminology

Several new anatomical terms used in this paper require explaining, although detailed definitions of these terms will be presented elsewhere (Gibson & Bray, in preparation). A *prostatic sac* is the term used by Gibson (1976) to describe the muscular sac which surrounds the pars prostatica and seminal vesicle of the azygiids. A *rudimentary Juel's organ* is a distal dilation of a blind Laurer's canal which contains disintegrating seminal and vitelline material, and is probably associated with the breakdown and reabsorption of these waste products. A *rudimentary seminal receptacle* is a very small proximal dilation of Laurer's canal, where spent seminal material and excess vitelline material are stored (? and killed), before being passed down Laurer's canal. In a fully developed *Juel's organ* (Gibson & Bray, 1975), which occurs in many of the more advanced hemiuroids, the terminal bulb of Laurer's canal (rudimentary Juel's organ) actually envelops the rudimentary seminal receptacle, forming a distinct oval structure. All of the above arrangements of the proximal female reproductive system occur in the presence of a uterine seminal receptacle.

Systematic section

Family AZYGIIDAE Lühe, 1909

Aphanhysteridae Guiart, 1938.

DIAGNOSTIC FEATURES. Body large or small; usually elongate. Body-surface smooth, without spines or plications. Oral and ventral suckers well developed; latter in middle or anterior half of body. Prepharynx absent. Pharynx well developed. Oesophagus usually short. Gut-caeca terminate blindly close to posterior extremity. Testes two; in tandem, oblique or symmetrical; pre- or post-ovarian; in hindbody. Seminal vesicle tubular, usually short, thin-walled; convoluted in forebody. Pars prostatica tubular. Prostatic sac present surrounding pars prostatica and seminal vesicle. Ejaculatory duct usually long and convoluted, but of variable length. Hermaphroditic duct short; at distal extremity of sinus-organ. Permanent sinus-organ of variable length; usually conical. Sinus-sac absent. Genital pore mid-ventral in forebody. Ovary oval; pre- or post-testicular. Mehlis' gland pre-ovarian. Laurer's canal and uterine seminal receptacle present. Juel's organ and canalicular or blind seminal receptacle* absent. Uterus entirely or almost entirely pre-ovarian;

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* Terminology for modifications of Laurer's canal as used by Gibson & Bray (in preparation). See above: 'Terminology'.

coiled mainly in hindbody. Eggs numerous; small; non-filamented. Vitellarium follicular; usually present laterally in much of hindbody, occasionally extending into forebody. Excretory vesicle Y-shaped, arms uniting in forebody or not. Parasitic in stomach. or occasionally body-cavity, of elasmobranchs and freshwater bony fishes.

Subfamily AZYGIINAE Lühe, 1909

Aphanhysterinae Guiart, 1938.
Gomtiotrematinae Gupta, 1955.
Allogomtiotrematinae Yamaguti, 1958.
Proterometrinae Yamaguti, 1958.

DIAGNOSTIC FEATURES. Body normally relatively large; occasionally small. Testes post-ovarian.

Otodistomum Stafford, 1904

Xenodistomum Stafford, 1904.
Aphanhystera Guiart, 1938.

DIAGNOSTIC FEATURES. Body large; spatulate to elongate. Ventral sucker larger than oral sucker; close to anterior extremity. Testes tandem or slightly oblique. Sinus-organ capable of considerable extension or may contract to form small papilla. Uterine field almost entirely between ovary and ventral sucker. Vitelline follicles extend in lateral fields posteriorly to ventral sucker, reaching back to post-testicular region where fields are, at least to some extent, confluent. Excretory arms usually unite in forebody, but occasionally do not. Parasitic in stomach or body-cavity of elasmo-branchs (sharks, rays and chimaeras).

TYPE-SPECIES. *Otodistomum veliporum* (Creplin, 1837) (by monotypy).

The *Otodistomum veliporum–cestoides* problem

(1) *History*

Over the years there has been a great deal of confusion concerning the problem of whether there are one or two species of the genus *Otodistomum* which parasitize the stomach of elasmobranchs. *Distoma veliporum* is the name first used by Creplin in 1837 for specimens, which he later (1842) described in greater detail, from the stomach of the shark *Hexanchus griseus* in the Mediterranean Sea. Although most of the early records of this species and its synonyms were from sharks, Olsson (1868a, 1868b, 1869, 1876), Lönnberg (1889a, 1889b, 1890, 1891), Linton (1898, 1901), Jägerskiöld (1900), Stafford (1904) and Lebour (1908) all recorded it from rays. The combination *Otodistomum veliporum* was first used by Stafford (1904) when he erected this genus after examining specimens from *Raja laevis* off the eastern coast of Canada.

The name *Distoma cestoides* was first used by van Beneden (1871) for specimens from *Raja batis* off the Belgian coast. After examining specimens and studying the literature, Odhner (1911) came to the conclusion that the form from sharks, which he called *Otodistomum veliporum*, differed from the form from rays, for which he coined the combination *O. cestoides*, since van Beneden's *D. cestoides* was the oldest available name for the ray-parasite. Odhner (1911) distinguished the two species as follows:

O. veliporum [size 50 × 5–6 mm; sucker-ratio 3 : 5; anterior limit of vitellarium behind middle of uterine field and compressed into narrow lateral bands; eggs 86 × 60–63 μm; shell-thickness 6 μm; parasite of sharks.]

O. cestoides [size up to 65 × 3–5 mm; sucker-ratio 3 : 4; anterior limit of vitellarium usually in front of middle of uterine field and not so narrowly compressed into lateral bands; eggs 65–72 × 43 μm; shell-thickness 3μm; parasite of rays.]

Odhner (1911) also noted that the material collected by Lönnberg (1898) from the shark *Chlamydoselachus anguineus* off northern Norway appeared to be *O. cestoides* rather than *O. veliporum*.

This would appear to have simplified the matter a great deal. Manter (1926), however, compared in great detail material from *Raja laevis* off the eastern coast of the U.S.A., which he called *O. cestoides*, with material from *R. binoculata* off the west coast of the U.S.A., which he called *O. veliporum*. Why Manter considered the specimens from *R. binoculata* to be *O. veliporum* is not clear; but he concluded that the only significant difference between the two species was egg-size, an average of $69\cdot4 \times 46\cdot2$ μm for '*O. cestoides*' and an average of $85\cdot5 \times 57\cdot8$ μm for '*O. veliporum*'. Dollfus (1937a), in a very detailed study, considered that Manter's two 'species' were in fact two subspecies, *O. cestoides cestoides* and *O. cestoides pacificum*, and that *O. veliporum*, which he subdivided into three subspecies, occurred only in sharks and torpedoes. Van Cleave & Vaughn (1941), after examining more material from *R. binoculata* and *R. laevis*, indicated that the egg-sizes of the specimens of *Otodistomum* were not significantly different ($60-94 \times 40-70$ μm and $55-90 \times 36-58$ μm, respectively), and, therefore, could not be differentiated even at the sub-specific level. These authors concluded that the American form of *Otodistomum* comprised a single variable species to which the name *O. cestoides* could be applied. Later workers, led by Dawes (1946) who based his conclusions mainly upon Manter's initial assumption that he was in fact dealing with specimens of *O. veliporum*, have considered *O. cestoides* and *O. veliporum* to be synonymous. Dawes concluded his contribution thus: 'Pending further inquiries, which will not provide a very attractive problem, it seems logical to conclude that a single species of the genus *Otodistomum* infects cartilaginous fishes all over the world, and that it should be known not as *O. cestoides* but as *O. veliporum*.' It was not until the work of Kay (1947) that a North American worker examined specimens of *Otodistomum* from a shark, and on this occasion it was described as a new species, *O. plicatum*. As pointed out by Gibson (1976) this species is not only morpho-logically very similar to *O. veliporum* (in the European sense), but was also recorded from the type-host, *Hexanchus griseus*, of the latter species, and thus can probably be regarded as a synonym. Recently, Brinkmann (1975) has followed Dawes (1946) in considering that there is a single worldwide species of *Otodistomum*, but indicates that morphological differences observed in different hosts and in different geographical regions may possibly warrant the recognition of subspecies. He also suggests that larger specimens may produce larger eggs than do the smaller ones and that larger elasmobranchs may entertain larger specimens of '*O. veliporum*'. Finally, Gibson (1976), after studying specimens in the collection of the British Museum (Natural History) from sharks and rays, recognized both *O. veliporum* and *O. cestoides* as valid species. He stated that while variations of 20 μm were found in the length of eggs from the same worm and 40 μm in eggs from the same host-species, the specimens from rays (*O. cestoides*) had an egg-length usually within the limits $60-90$ μm and a shell-thickness of $3-6$ μm, and specimens from sharks (*O. veliporum*) had an egg-length usually within the limits $80-120$ μm and a shell-thickness of $5-8$ μm. Gibson also noted that there was a relationship between the size of the worm and the egg-size and suggested that this might be the result of growth in the oötype. He agreed with Odhner's (1911) comments about the anterior limit of the vitellarium in the two species, and implied that he considered the specimens which he examined from the shark *Centroscyllium fabricii* to be *O. cestoides* rather than *O. veliporum*.

There are, therefore, two schools of thought: one which considers that there is a single species of *Otodistomum* which occurs in the stomach of elasmobranchs and the other which considers that there are two species, *O. veliporum*, occurring in sharks and torpedoes, and *O. cestoides*, occurring mainly in rays but on rare occasions in sharks.

(2) *Criteria*

In an attempt to resolve this problem we decided to investigate the various criteria which have been used by authors, especially Odhner (1911), for distinguishing the two species. With this aim in mind, we examined a great deal of material from the collection of the British Museum (Natural History) in addition to that which we have collected ourselves. This material represents a much wider variety of hosts and larger number of specimens than appears to have been studied by other authors.

Firstly, dealing with the criteria listed by Odhner (1911):

(a) Maximum length

Table 1 shows the maximum length of specimens of *Otodistomum* from the stomach of various species of host. We have included data from the literature in this table to give a more comprehensive range.

Table 1 The maximum length (mm) of specimens of *Otodistomum* recorded from different hosts.

Host	Present work	From the literature
Hexanchus griseus	–	101 (Dollfus, 1937a)
Dalatias licha	92	135 (Bråten, 1964)
Echinorhinus brucus	–	52 (Guiart, 1938)
Centroscymnus coelolepis	35	38 (Guiart, 1938)
Centroscyllium fabricii	31	–
Sharks	–	55 (Mühlschlag, 1914)
Sharks	–	50 (Odhner, 1911)
Torpedo spp.	–	51.8 (Tendeiro & Valdez, 1955)
Raja batis	46	(*c.* 37) (van Beneden, 1871, figure)
Raja binoculata	–	69 (van Cleave & Vaughn, 1941)
Raja jenseni	48	–
Raja laevis	–	65 (Manter, 1926)
Raja nidarosiensis	62	–
Raja radiata	23	52 (Layman & Borovkova, 1926)
Raja richardsoni	75	–
Raja spinicauda	33	–
Raja sp. (? *griseocaudata*)	–	20 (Gibson, 1976)
Raja spp.	–	65 (Odhner, 1911)

These results illustrate the wide variation in size attained in different species of host; but tell us little except that the specimens from *Dalatias licha* and *Hexanchus griseus* appear to be capable of reaching a much greater length than specimens from the remainder of the hosts. A great variation in size was noticeable in material we examined from various species of ray. Although we did not find any specimens from *Raja radiata* or *Raja* sp. (? *griseocaudata*) which reached more than 23 mm in length, both Lebour (1908) and Layman & Borovkova (1926) have reported much larger specimens from the former species. This illustrates the danger of relying upon material from a small number of host-specimens caught at the same time of the year, as we have no data on any relationship between season and size of the parasites. There is evidence that the average and maximum size of these parasites is different in various species of ray, but final proof that this is a host-induced effect must await the results of carefully controlled experiments involving the feeding of uninfested rays of various species with metacercariae from the same species of teleost. In connection with this, it is worthy of note that *Otodistomum* is quite unknown in certain common species of ray, e.g. *R. naevus*.

(b) Sucker-ratio

Sucker-ratio is generally considered to be a relatively good specific criterion. Although there are indications in some groups that allometric growth may occur, our observations and the comprehensive series of measurements of Manter (1926, table 4) indicate that the sucker-ratio is relatively constant, irrespective of the size of the specimen. Our results (Table 2) show that, except for the specimens from *Dalatias licha*, the sucker-ratio of the specimens are very similar, regardless of host. The specimens from *D. licha*, although there might be a slight overlap in extreme cases, almost always have a significantly smaller oral sucker relative to the ventral sucker. This strongly suggests that more than one species is involved. Care should be taken, however, in assessing ratios taken from flattened specimens, as the pressure needed to flatten these large worms cause the more protruded ventral sucker to increase in size relative to the oral sucker. Such specimens have not been included in our results.

(c) Distribution of vitelline follicles

(i) Anterior limit. The results of this investigation (Table 2) indicate that the anterior limit of the vitelline follicles is a very variable feature, in the majority of cases reaching anteriorly to the middle of the uterine field. Admittedly, in the specimens from *Dalatias licha* the follicles tend not to reach quite as far forward as in the specimens from the other hosts; but it does not appear that this is significant. These results, therefore, suggest that, although in specimens from some hosts the follicles tend to reach well anteriorly to the middle of the uterine field, this feature is far too variable and the differences too small for this to be a reliable criterion. There is also some evidence that the follicles reach further anteriorly in small specimens: this would account for the high percentage given for specimens from *R. radiata* and *R.* sp. (? *griseocaudata*), the latter being 70–80%.

Table 2   The sucker-ratio and anterior limit of the vitellarium of specimens of *Otodistomum* from various hosts.

Host	Sucker-ratio		Anterior limit of vitellarium	
	Range	Mean	Range	Mean
Dalatias licha	1·5–2·1	1·8	33–60	50
Centroscymnus coelolepis	1·25–1·5	1·4	60–78	68
Centroscyllium fabricii	1·3–1·6	1·45	44–77	65
Raja batis	1·25–1·55	1·4	42–73	55
Raja jenseni	1·3–1·4	1·35	55–70	62
Raja radiata	1·2–1·6	1·4	59–80	72
Raja richardsoni	1·25–1·6	1·4	40–68	55
Raja spinicauda	1·3–1·5	1·4	56–85	70

The sucker-ratio is represented as the width of the ventral sucker when the width of the oral sucker equals 1. The anterior limit of the vitellarium, when measured from the ovary, is represented as a percentage of the uterine field (the distance between the ovary and the ventral sucker).

(ii) Posterior limit. One feature which was very noticeable was that in specimens from *Dalatias licha* the posterior limit of the vitellarium normally extended only a short distance into the posterior half of the worm and did not extend into the posterior third. In contrast, in the specimens from other hosts the posterior limit of the vitellarium normally occurred within the posterior third of the body. Within these limits this feature is very variable, in the specimens from rays, for example, the posterior limit of the follicles ranges from just within the posterior third of the body almost to the posterior extremity. There is evidence that the follicles tend to reach further posteriorly in the smaller specimens.

(iii) The degree of lateral banding of the vitelline follicles. Odhner (1911) noted that in the specimens from sharks the follicles, presumably in the post-testicular region, tended to occur in lateral bands which were more distinct than those in the forms from rays. This banding can be clearly seen in our specimens from *Dalatias licha*; but as it also occurs in some specimens from *Raja batis* and *R. richardsoni*, we do not consider it to be a reliable feature.
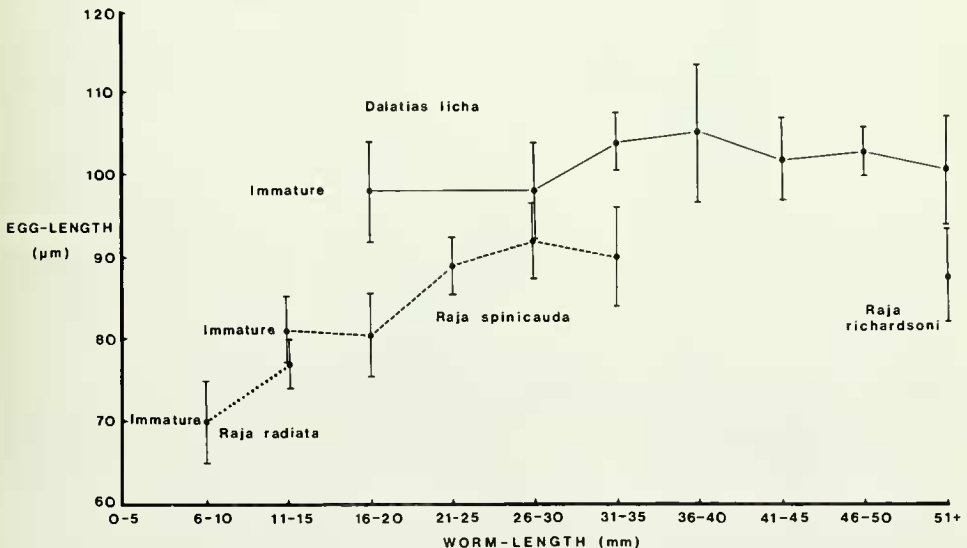
(d) Egg-length

Egg-length is generally regarded as being a good specific criterion. A great deal of care must be taken when measuring eggs, as they rarely lie absolutely horizontal *in situ*. In the majority of cases in this work eggs were removed from the anterior extremity of the uterus and measured in isolation. It is important that eggs from the distal region of the uterus are examined, as those from the proximal region often have thin shells and are very susceptible to changes in shape and size caused by differences in the osmolarity of the reagents with which the worm has been treated. Even so variations of up to 20 μm were obtained for eggs from a single worm and up to 40 μm in specimens from the same host-species. This is a much greater variation than normally occurs in digeneans, but similarly large variation also occurs in other azygiids.

Results based on 40–120 eggs from each host-species (8 per worm) are presented in Table 3. These indicate that the specimens from *D. licha* have a mean egg-length which is distinctly greater

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Table 3 The length and shell-thickness of eggs occurring in the distal uterus of specimens of *Otodistomum* from various hosts.

Host	Egg-length (μm)		Shell-thickness (μm)	
	Range	Mean and standard deviation	Range	Usual thickness
Dalatias licha	80–120	101 ± 7·5	4–10	6–8
Centroscymnus coelolepis	72–97	83 ± 7·5	3–4	3–4
Centroscyllium fabricii	74–102	87 ± 6	3–6·5	3–5
Raja batis	67–87	76·5 ± 5	3–7	3–4
Raja jenseni	58–94	78 ± 8	3–6	3–4
Raja radiata	59–95	72·5 ± 5	2·5–5	3–4
Raja richardsoni	68–100	83·5 ± 7·5	3·5–5	*c.* 4
Raja spinicauda	72–100	85·5 ± 7	3–6	3–5

than those from other host-species. This is not a function of the larger size of the worms, for, as illustrated in Fig. 1, although there is an initial relationship between the size of the worm and the size of the eggs in smaller specimens, after the worm reaches a certain size (about 25–30 mm) the mean egg-length tends to be relatively constant irrespective of the size of the worm. The relationship between egg-length and worm-length in the smaller specimens probably explains the apparently significant differences in the mean egg-lengths given in Table 3, particularly those from *Raja radiata* and *Centroscyllium fabricii*. Layman & Borovkova (1926), who record much larger specimens from *R. radiata*, give the egg-length as 82–98·5 μm (see Table 8). Although the standard deviation of the mean egg-length in the specimens from *D. licha* does not overlap those from the other host, the fact that their overall ranges do overlap reduces the value of this criterion. If eggs from several specimens can be measured then the mean egg-length may be a useful feature. In addition it should be noted that eggs of more than 100 μm were rarely found except in specimens from *D. licha*.

Fig. 1 Mean egg-length and standard deviation vs length of worm in different hosts.

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(e) Egg-shell thickness

This feature is used by several authors to distinguish *O. veliporum* and *O. cestoides*. Egg-shell thickness is undoubtedly related to egg-size, larger eggs tending to have thicker shells. Nevertheless, the results presented in Table 3 show that, although the ranges do overlap, the specimens from *D. licha* tend to have distinctly thicker shells than those from other hosts, this difference being somewhat greater than would be expected if it was related to egg-size only. Eggs from specimens from the other hosts have a relatively constant thickness. Although this feature does appear to be useful, it should not be used in isolation.

In addition to the above features, we have noticed the following differences:

(i) Pre-oral lobe. In specimens from rays the well-developed pre-oral lobe can be seen to be filled with gland-cells, when viewed in sections. They can also be seen in some whole-mount preparations. In the single sectioned specimen from *D. licha* this concentration is not present, nor does it appear to occur in the whole-mounts. We also sectioned a specimen from *Centroscymnus coelolepis*, where the gland-cells were present, but in not nearly the same concentration as in the material from rays. We feel that this observation is worth noting, although further material from other hosts must be examined before this feature can be given any credence.

(ii) The extent of the uterine field. Superficial examination of the material and figures from the literature suggests that the uterus in specimens from rays is much larger and takes up a greater proportion of the total body-length than that of the specimens from sharks. We have therefore measured our specimens and calculated the length of the uterine field, i.e. the distance between the ovary and the ventral sucker, as a percentage of the total body-length.

Table 4 presents the results from mature specimens only (i.e. those containing eggs), as the uterine field of immature specimens is noticeably shorter. This latter feature is illustrated by Fig. 2,

Table 4 The length of the uterine field (the distance between the ovary and the ventral sucker) as a percentage of the total length of mature specimens of *Otodistomum* from various hosts.

Host	Range	Mean and standard deviation
Dalatias licha	11–15	$13 \cdot 5 \pm 1 \cdot 5$
Centroscymnus coelolepis	17–21	$19 \cdot 5 \pm 1 \cdot 5$
Centroscyllium fabricii	18–40	$28 \pm 7 \cdot 5$
Raja batis	17–28	23 ± 5
Raja jenseni	$12 \cdot 5$–37	$23 \cdot 5 \pm 6 \cdot 5$
Raja radiata	18–36	26 ± 7
Raja richardsoni	19–37	26 ± 5
Raja spinicauda	16–33	$23 \pm 4 \cdot 5$

which we have prepared from the measurements given by Manter (1926). It shows that in immature specimens the ratio of uterine field to body-length increases with body-length, but that in mature specimens the ratio is nearly constant.

Our results indicate that the uterine field : body-length ratio in mature specimens from *D. licha* is significantly smaller than those from the rest of the hosts. As the uterine field in mature specimens does not appear to show any allometric relationship to body-length, this criterion may be a sound one. Taking into account the literature and other material which we have examined, it would appear that these differences may not be so distinct (see Tables 7 and 9). Nevertheless, mature specimens resembling those from *D. licha* in other morphological features appear to have a uterine field which is less than 20% and usually less than 16%, whereas specimens from rays and some small sharks which are morphologically similar to those from *R. batis* have a uterine field which is almost always greater than 16% and usually greater than 20%.

(iii) The level of the bifurcation of the excretory vesicle. This feature, although not visible in many whole-mounts, may be of some assistance in distinguishing the two species. In specimens

from *D. licha* it usually occurs within the posterior half of the post-testicular region of the vitelline field (or even entirely posterior to the vitelline field). In the material from rays and both *Centro-scyllium fabricii* and *Centroscymnus coelolepis* it normally occurs in the anterior half of the post-testicular region of the vitelline field. This feature is not absolutely constant, however, as it depends to a great extent upon the distribution of the vitelline follicles, which is in itself a variable feature. As it was visible in only a small proportion of the material, its value as a specific criterion requires further study.
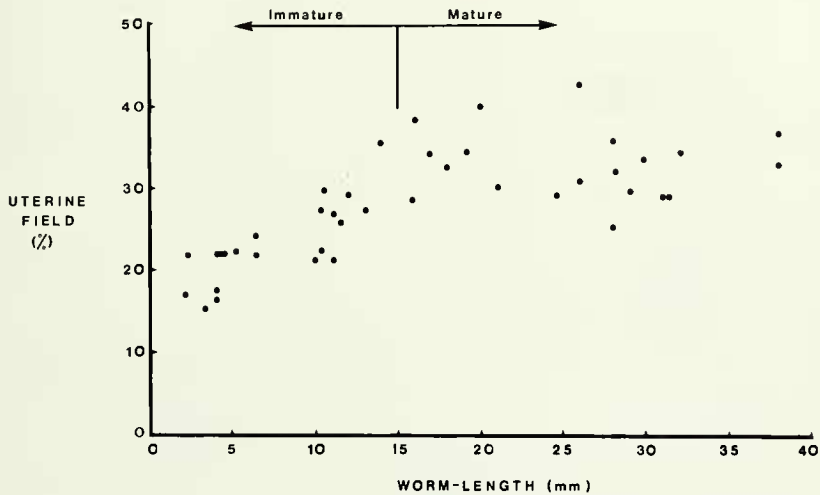

Fig. 2 Uterine field (measured from ventral sucker to posterior testis) as a percentage of body-length vs length of specimens from *Raja laevis*. These figures are calculated from measurements given by Manter (1926), and can be directly related to our measurements of the uterine field if reduced by 5 % to allow for the distance between the ovary and the posterior testis.

Table 5 A summary of the features which can be used to distinguish *Otodistomum veliporum* and *O. cestoides*.

Feature	*O. veliporum*	*O. cestoides*
Length (mm)	<135	<80
Sucker-ratio (breadth)	Normally 1 : 1·5–2·1	Normally 1 : 1·2–1·6
Anterior limit of vitellarium	1/3 to 2/3 of distance from ovary to ventral sucker	2/5 to 4/5 of distance from ovary to ventral sucker
Posterior limit of vitellarium	Does not normally extend into posterior third of body*	Normally extends into posterior third of body
Uterine field (in mature specimens)	Normally less than 1/6 of body-length	Normally more than 1/6 of body-length
Level of excretory bifurcation	Usually posterior to middle of post-testicular region of vitelline field	Usually anterior to middle of post-testicular region of vitelline field
Egg-length (μm)	80–130 (usually 90–115)	55–102 (usually 65–95)
Egg-shell thickness (μm)	4–10 (usually 6–8)	2·5–7 (usually 3–5)
Host	Hexanchiform, squaliform and squatiniform sharks and torpedoes	Rays and some small squaliform sharks

* The figure of a specimen from *Squatina californica* given by Caballero & Caballero (1969) shows the vitelline field just extending into the posterior third of the body and the uterine field reaches almost one-fifth of the body-length.

(3) Conclusion

The results presented above indicate quite clearly that there are two forms of *Otodistomum* present in the gut of the hosts examined, one from *Dalatias licha* and the other from the remainder. The form from *D. licha* is almost certainly *O. veliporum* (Creplin, 1837) as it appears to be morphologically identical with material described by other workers from *Hexanchus griseus*, the type-host of this species. The other form appears to be *O. cestoides* (van Beneden, 1871) which has been described by several authors, usually from rays. Another important point that this work has illustrated is that none of the features used for distinguishing these two species can be applied in isolation. At least three and preferably four or five of these criteria, which are summarized in Table 5, should be used.

We have not attempted to answer the question as to whether there are various subspecies present, as suggested by Dollfus (1937a), for, although there certainly are differences in size and morphology in specimens from different host-species, we do not know whether they are caused by environmental or genetic factors. Only with experimental work can one hope to solve this problem.

Key to the species of *Otodistomum* recorded from the northeast Atlantic

1 Parasitic in body-cavity of squaliform sharks and rays; breadth at least 1/3 of total length; uterine field normally at least 1/3 of body-length; eggs normally 100–120 μm with a shell-thickness of 6–9 μm .   .   *O. plunketi* Fyfe, 1953 (p. 192)

– Parasitic in gut, especially stomach of elasmobranchs; breadth normally much less than 1/3 total length in mature specimens   2

2 Parasitic in hexanchiform, squaliform and squatiniform sharks and torpedoes; sucker-breadth ratio normally 1 : 1·5–2·1; vitellarium does not usually extend into posterior third of body; uterine field rarely more than 1/6 of total length in mature specimens; eggs 80–130 (usually 90–115) μm with a shell-thickness of 4–10 (usually 6–7) μm .   .   .   *O. veliporum* (Creplin, 1837) (p. 176)

– Parasitic in rays and some small squaliform sharks; sucker-breadth ratio normally 1 : 1·2–1·6; vitellarium does not usually extend into posterior third of body; uterine field rarely less than 1/6 of total length in mature specimens; eggs 55–102 (usually 65–95) μm with a shell-thickness of 2·5–7 (usually 3–5) μm .   .   .   *O. cestoides* (van Beneden, 1871) (p. 181)

Otodistomum veliporum (Creplin, 1837) Stafford, 1904

(?) *Distoma scimna** Risso, 1826.
Distoma scymna or *scymni* Risso of various authors.
Otodistoma scymni (Risso) Guiart, 1938, in part.
Distoma veliporum Creplin, 1837.
Otodistomum veliporum leptotheca Dollfus, 1937.
Otodistomum veliporum pachytheca Dollfus, 1937.
Fasciola squali grisei Diesing, 1850 (attributed to, but not used by, Risso, 1810).
Distomum insigne Diesing, 1850.
Distoma microcephalum Baird, 1853.
Otodistomum plicatum Kay, 1947.

TYPE-HOST AND LOCALITY. *Hexanchus griseus*, Sicily.

RECORDS.

(i) Material studied
(a) From the NE Atlantic
Dalatias licha [stomach] SW of Barra Head, Scotland (March, 1954). Collected by E. W. White-head. BM(NH) Reg. No. 1954.9.13.59–79.
Dalatias licha [spiral intestine] Bay of Biscay (47°N, 06°W; depth 650 m; Jan., 1971). BM(NH) Reg. No. 1973.5.17.39–41 (see Bray, 1973 : 167).

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* It is possible that *Distoma scimna* of Risso (1826) is the senior synonym of *Otodistomum veliporum*; but, as Risso's description is very brief, we cannot be absolutely certain. In view of this, and after 130 years of common usage, it would seem inadvisable to replace the familiar appellation.

Dalatias licha [stomach] Off western Scotland (55°N, 10°W; depth 800–825 m; June, 1974). BM(NH) Reg. No. 1976.5.12.1–2.

Squalus acanthias [stomach] Falmouth Harbour, Cornwall, England. BM(NH) Reg. No. 49.12.29. 2–3. (Type specimens of *Distoma microcephalum* Baird, 1853.)

(b) From elsewhere

'Serrated Acanthias' [?] (?) Eastern coast of U.S.A. Collected by Dr Chapman. BM(NH) Reg. No. 1914.1.26.1–3.

(ii) NE Atlantic records from the literature

Dalatias licha [stomach] Biarritz, France (May, 1937). Dollfus (1937a : 450; 1937b : 72).

Dalatias licha [stomach] Oslo Fjord, Norway (Oct., 1962). Bråten (1964 : 73).

Dalatias licha [stomach] Shetland Is, Scotland (1953). Rae, in Bråten (1964 : 73).

Dalatias licha [spiral intestine] Northern Bay of Biscay (47°N, 06°W; depth 650 m; Jan., 1971). Bray (1973 : 167).

Echinorhinus brucus [stomach] Roscoff, Finistere, France. Villot (1875 : 477, as *Distoma scimna*; 1878 : 3, as *Distomum insigne*; redescribed by Dollfus, 1937a : 434).

Echinorhinus brucus [stomach] SW of Finistere (47°N, 05°W; depth 446 m; Sept., 1903). Guiart (1938 : 21, as *Otodistoma scymni*).

Hexanchus griseus [branchial region] Arcachon, France (March, 1902). Cuénot (1927 : 247; described by Dollfus, 1937a : 440).

Hexanchus griseus [stomach] French Atlantic Coast (47°N; April, 1934). Dollfus (1937a : 440).

Somniosus microcephalus [?] Origin unknown, but much of this shark's distribution is in NE Atlantic region. Mühlschlag (1914 ; 199).

Squalus acanthias [stomach] Falmouth Harbour, Cornwall, England. Baird (1853a : 58; as *Distoma microcephalum*).

Torpedo marmorata [stomach] St Jean-de-Luz, Bay of Biscay, France (July, 1914). Dollfus (1937a : 441; 1937c : 167).

Torpedo torpedo [stomach] Coast of Algarve, Portugal (July, 1954). Tendeiro & Valdez (1955 : 95). Host (?) [?] Vestmannaeyjar, Iceland (Aug., 1932). Brinkmann (1956 : 15).

Aspects of biology. Nothing appears to be known about the early stages in the life-history of this species, although much is known about some of the related azygiids in freshwater. In the latter cases prosobranch molluscs apparently become infested by eating embryonated eggs. The miracidia hatch within the molluscs and develop into sporocysts. These give rise to rediae, from which very large furcocystocerous cercariae are released. Upon release the body-wall of the cercaria absorbs water and expands greatly, leaving an immature adult within the anterior tail-region. The parasite enters its definitive host when the large, often colourful, cercaria is swallowed by a fish. Although it is possible that some of the fishes act as paratenic hosts, there appears to be no evidence that a crustacean host is involved. Detail of the life-histories of some these of freshwater azygiids are summarized by Yamaguti (1975).

As shown below (p. 196) metacercariae of *Otodistomum* have been found encysted, usually in the gut-wall, of teleosts, chimaeras, a ray and carcharhiniform sharks. As all the species of sharks and torpedoes infested with *O. veliporum* are piscivorous, it seems reasonable to suppose that they acquire this parasite by feeding on other fishes. These fishes, which in this instance may act as obligatory intermediate hosts, presumably acquire the parasite, if the freshwater azygiid life-history pattern can be used as a guide, by feeding directly on the cercariae, possibly by feeding on infected molluscs or by feeding on smaller infested teleosts. Most of the definitive hosts of *O. veliporum* are pelagic, but *Squatina* and *Torpedo* spp. are bottom-living, and although these fishes do feed upon small teleosts, they also feed upon molluscs; there is a possibility, therefore, that these fishes could acquire the parasites directly.

Previous descriptions. Villot (1878 : 3; as *D. insigne*); Poirier (1885 : 479; as *D. insigne*); Odhner (1911 : 516); Mühlschlag (1914 : 201); Dollfus (1937a : 433); Kay (1947 : 79; as *O. plicatum*); Tendeiro & Valdez (1955 : 95); Caballero y C. & Caballero R. (1969 : 958).

Description (Figs 3 & 4). This description is based on whole-mounts and sections of material mainly from the stomach of *Dalatias licha*. The size of these large worms is very variable, reaching
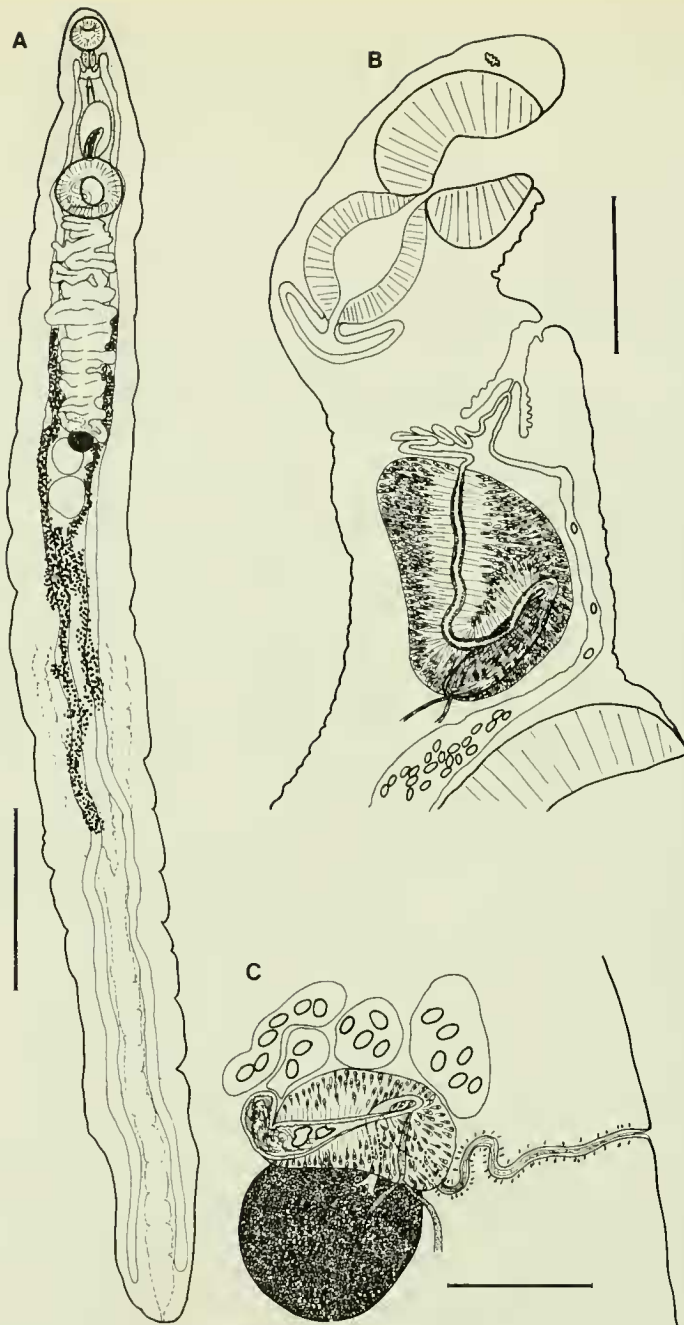
Fig. 3 *Otodistomum veliporum* ex *Dalatias licha*: (A) whole-mount; (B) sagittal section of forebody showing terminal genitalia; (C) lateral view of ovarian complex. Scale: (A) 5 mm; (B) 1 mm; (C) 500 μm.

up to 135 mm in length and 11 mm in breadth. The dimensions of the worms described are given in Table 6 and some measurements from the literature are given in Table 7. The worms are

Table 6 Measurements of *Otodistomum veliporum* from the material and hosts examined.

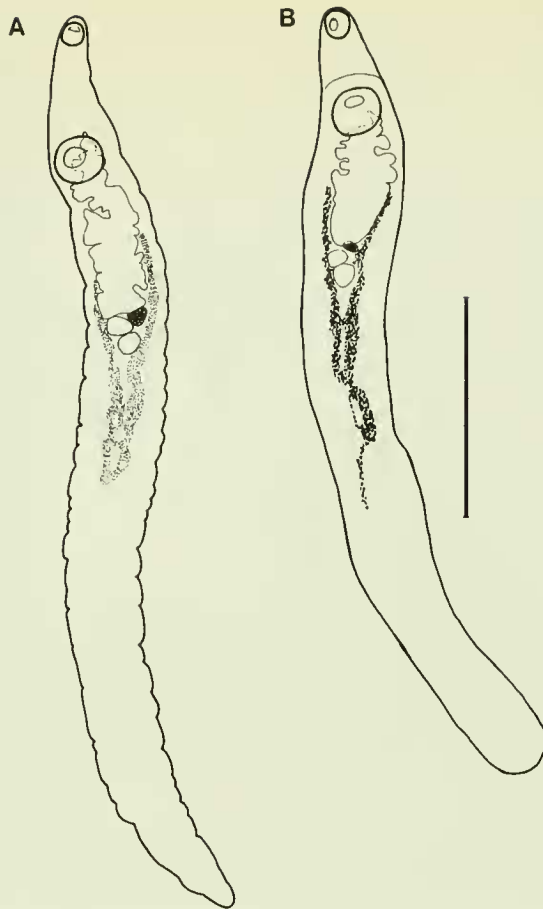|	Host		
	Dalatias licha	'Serrated Acanthias'	*Squalus acanthias*
Number of specimens	10	1	2
Length (mm)	13–92	40	10–14
Breadth (mm)	3–6	6	2·9–3·0
Forebody (mm)	1·7–7·5	7	–
Oral sucker (mm)	0·7–2·0 × 0·75–1·8	breadth 2·0	0·95 × 0·8–0·95
Ventral sucker (mm)	1·25–2·5 × 1·3–3·2	breadth 3·4	1·3 × 1·45
Sucker-ratio	1 : 1·5–2·1	1 : 1·7	1 : 1·5–1·8
Pharynx (mm)	0·5–1·0 × 0·4–0·7	–	–
Prostatic sac (mm)	1·1–2·0 × 0·75–1·3	–	–
Testes (mm)	0·5–1·8 × 0·5–1·5	diam. 1·25	–
Ovary (mm)	0·5–0·9 × 0·4–1·2	–	–
Uterine field/length × 100(%)	11–15	16	10–15
Egg-length (μm)	80–120 (usually 90–110)	110–115	c. 110
Egg-shell thickness (μm)	4–10 (usually 6–8)	7–8	c. 7–8

subcylindrical (Figs 3A & 4) and slightly dorso-ventrally flattened. There is evidence to indicate that the host may affect not only the size, but possibly also the appearance of the worm. The body-surface is smooth, although contraction may cause superficial transverse folding. The *oral sucker* is ventrally subterminal, as there is a relatively well-developed but not distinctly glandular pre-oral lobe, and significantly smaller than the *ventral sucker*, which usually protrudes. The forebody is relatively short, especially in the larger specimens, as the hindbody grows at a much faster rate than either the forebody or the suckers.

The structure of the body-wall is simple. There is a thick tegument beneath which is a region of relatively dense, but small, circular muscle-bundles, and beneath this lies a thick longitudinal muscle-layer. The structure of the body-wall is similar in both fore- and hindbodies, but with an additional layer of relatively large diagonal muscle-bundles lying within the longitudinal muscle-layer in the forebody.

There is no prepharynx. The well-developed *pharynx* gives rise to a very short, posteriorly or dorsally oriented oesophagus, which divides into two antero-laterally directed branches. These initial branches have a cuticular lining similar to that of the oesophagus. Laterally to the pharynx these two branches give rise to the gut-caeca which turn and run posteriorly in the dorso-lateral field, following a relatively straight to sinuous course, and end blindly near the posterior extremity. There are no 'Drüsenmagen' in the 'shoulder-region' of the gut. The gut-caeca, which are slightly diverticulate, are often fairly narrow and possess a thick, villous lining.

The *excretory vesicle* is Y-shaped. The terminal pore leads into a long stem which divides, giving rise to antero-laterally oriented arms, between half to two-thirds of the total body-length from the anterior end. This position normally corresponds to the posterior half of the post-testicular region of the vitelline field or just posterior to the vitellarium. The arms, which are slightly diverticulate, extend forward laterally into the forebody where, as can be seen in our sectioned material, they unite via a narrow commissure anterodorsally to the oral sucker (Fig. 3B).

Two oval, post-ovarian *testes* occur in tandem or slightly obliquely, usually well anterior to the middle of the body. The posterior testis is often slightly larger than the anterior. The vasa efferentia lead anteriorly from the testes, pass into the forebody and unite immediately anteriorly to the ventral sucker as they pass through the posterior wall of the prostatic sac. Within this large, ova

Fig. 4 *Otodistomum veliporum* ex *Dalatias licha*: (A) from SW of Barra Head, Scotland; (B) from Bay of Biscay. (These figures are directly comparable with the figures of *O. cestoides* in Fig. 6.) Scale: 10 mm.

sac (Fig. 3B) the male duct widens to become a seminal vesicle. This elongate, oval organ may be slightly arcuate and extends antero-ventrally to about the middle of the prostatic sac, where it narrows and joins the pars prostatica. The latter duct possesses a villous lining and a dense covering of gland-cells which fill all the available space within the prostatic sac. It initially turns and runs postero-dorsally, before passing towards the anterior region of the prostatic sac, where it passes through the thin, muscular wall of the prostatic sac and assumes the form of an ejaculatory duct. This duct is very long and usually convoluted, eventually leading into a well-developed and conical permanent *sinus-organ*. The sinus-organ is situated within a normally deep genital atrium, the pore of which opens mid-ventrally just posteriorly to the level of the pharynx. Near to the distal extremity of the sinus-organ, the ejaculatory duct unites with the metraterm to form a short hermaphroditic duct which opens terminally (Fig. 3B). The convoluted nature of the ejaculatory duct, the size of the sinus-organ and genital atrium and to some extent the position of the genital pore, are all variable.

The oval *ovary* is medially or sub-medially situated immediately anteriorly to the testes. Anteriorly from it leads a short oviduct, which enters a large Mehlis' gland, within which it receives firstly Laurer's canal and then, widely separated, the common vitelline duct (Fig. 3C). Laurer's canal is simple, tubular and opens to the exterior dorsally to the ovary. The eggs are formed within Mehlis' gland. The *uterus* is entirely pre-testicular and rarely reaches posteriorly to the ovary. Its main bulk, coiled between the ovary and the ventral sucker, occupies less than 20 % of the total body-length and normally only 10–15 % in mature specimens. The first coils of the uterus act as a uterine seminal receptacle, the only seminal store in the female system. Dorsal to the ventral sucker the uterus narrows, follows a sinuous or direct course anteriorly, passing ventrally or ventro-laterally to the prostatic sac, where it gradually narrows and becomes the metraterm, which unites with the ejaculatory duct within the sinus-organ. The eggs, which lack spines or filaments, and possess a relatively thick shell, occur in great numbers within the uterus. The *vitellarium* is in the form of numerous follicles in two lateral fields, which usually extend from about the middle of the uterine field, or just posterior to this, to a level just inside the posterior half of the body, very rarely extending into the posterior third of the body. The lateral fields of follicles tend to be more medially situated posteriorly to the gonads and are often confluent in this region. There is a good deal of variation with regard to both the anterior and posterior limits of the vitellarium and in regard to the degree of confluence of the vitelline fields in the post-testicular region.

DISCUSSION. One interesting feature of this species is that, not only is it absent from rays (Raji-formes), but, like the other species of *Otodistomum*, it does not occur in the adult form in galeo-morph sharks. Mühlschlag (1914) and Maclaren (1903b) have recorded specimens of *Otodistomum* from the carcharhiniform galeomorph sharks *Scyliorhinus caniculus* and *Mustelus laevis*, respec-tively; but on both occasions they occurred encysted in the stomach wall. This indicates that some kind of host-specificity is involved, for many of these sharks and rays occupy similar ecological niches and feed on similar foods. Admittedly, there is an apparent ecological difference in that most of the hexanchiform and squaliform sharks which harbour *O. veliporum* tend to be more pelagic and less benthic than the hosts of *O. cestoides*; but this does not apply to *Torpedo* spp. or *Squatina* spp. A further indication that host-specificity is involved is that there appears to be no record of adult *O. veliporum* from hosts which harbour *O. cestoides*, even though both parasites occur in squaliform sharks.

Another interesting feature of this species, and indeed of the other species of *Otodistomum*, is the different sizes attained in different hosts. *O. veliporum* is capable of reaching a massive size in *Dalatias licha* and *Hexanchus griseus*, and yet the largest recorded size for specimens from *Squalus acanthias* appears to be 30 mm, recorded by Layman (1930) off Vladivostok. This effect is probably exaggerated by the paucity of records from *S. acanthias*. The size at which maturity occurs also appears to be affected by the host, for while both of Baird's two specimens of *Distoma micro-cephalum* (= *O. veliporum*), which measure 10 and 14 mm in length, contain large numbers of eggs, a specimen from *D. licha* of 13 mm was immature.

Otodistomum cestoides (van Beneden, 1871) Odhner, 1911

Distoma cestoides van Beneden, 1871.
Otodistomum cestoides pacificum Dollfus, 1937.
Distoma(um) veliporum Creplin of Olsson (1868a, 1868b, 1876), Lönnberg (1889a, 1889b, 1890, 1898), Linton (1898, 1901), Jägerskiöld (1900) and Sleggs (1927).
Otodistomum veliporum (Creplin) of Stafford (1904), Lebour (1908), Manter (1926), Lloyd (1938), Dawes (1946, 1947, in part), Rees (1953), Myers (1959, in part), Templeman (1973) and Brinkmann (1975, in part).
Otodistoma scymni (Risso) Guiart, 1938, in part.
Aphanhystera monacensis Guiart, 1938.
Otodistomum sp. of Williams & Richards (1966), Williams *et al.* (1970) and Manger (1972).

TYPE-HOST AND LOCALITY. *Raja batis*, Belgian coast.

RECORDS.

Table 7 Measurements of specimens of *Otodistomum veliporum* from various hosts taken from the literature. Figures

Author	Villot (1878)	Odhner (1911)	Mühlschlag (1914)	Dollfus (1937a)	Dollfus (1937a
Name used	*Distomum insigne*	*Otodistomum veliporum*	*Otodistomum veliporum*	*Otodistomum veliporum veliporum*	*Otodistomum veliporum leptotheca*
Host	*Echinorhinus brucus*	Sharks	Sharks	*Hexanchus griseus*	*Torpedo marmorata*
Locality	Roscoff, France	Mediterranean and South European Atlantic	?	Atlantic coast of France	Moroccan coa
Number of specimens	?	?	?	5	2
Length (mm)	40–50 [35*]	up to 50	12–55	50–101	(25)–35
Breadth (mm)	6–10 [5·5*]	5–6	3·5–5·5	5·0–5·5	(3·5)–5·5
Forebody (mm)	–	–	–	–	(3·5)–?
Oral sucker (mm)	–	1·25–2 diam.	0·5–1·0 diam.	1·77–?	(1·2)–? × (1·5)–?
Ventral sucker (mm)	–	2–3·5 diam.	1–2 diam.	4·4–?	(2)–? × (2·5)–?
Sucker-ratio	–	(1 : 1·67)	(1 : 2)	(1 : 1·9)	(1 : 1·67)
Pharynx (mm)	–	–	–	–	(0·5)–? × (0·4)–?
Prostatic sac (mm)	–	–	–	–	(1·2)–? × (1·0)–?
Testes (mm)	–	–	–	–	(0·9)–? × (1·4)–?
Ovary (mm)	–	–	–	–	(0·7)–? × (0·8)–?
Uterine field/length × 100 (%)	–	–	(14)	–	(9·5)–?
Egg-length (μm)	90 × 70 [93–97 × 62–66*]	*c.* 86 × 60–63	90 × 53	110–130 × 69–92	82–88 × 62–70
Egg-shell thickness (μm)	4 [6–7*]	6	7	6–8	6–6·5

* Figures of Dollfus (1937).

Dollfus (1937a)	Guiart (1938)	Kay (1947)	Tendeiro & Valdez (1955)	Bråten (1964)	Caballero & Caballero (1969)
Otodistomum veliporum pachytheca	*Otodistoma scymni*	*Otodistomum plicatum*	*Otodistomum veliporum*	*Otodistomum veliporum*	*Otodistomum veliporum*
Torpedo marmorata & T. torpedo	*Echinorhinus brucus*	*Hexanchus griseus*	*Torpedo torpedo*	*Dalatias licha*	*Squatina californica*
Morocco, Mauritania & Bay of Biscay	Atlantic, SW of Finistere	Washington State, U.S.A.	Portuguese coast	Oslo Fjord, Norway	California, U.S.A
7	13	51	2	6	5
11–29 (9·5–16)	28–52	8–83	51·8	up to 135	40
2·1–6 (2·25–2·9)	4–5	3–7·5	4·3	up to 11	4·9
(2·0–2·5)	–	–	–	–	6·76
0·75 × 0·9–0)	–	0·9–1·5 diam.	2·2 diam.	–	1·41 × 1·46
1·5–1·7 × 6–1·75)	–	1·3–2·4 diam.	3·7 diam.	–	2·35 × 2·67
1 : 2)	–	(1 : 1·5)	(1 : 1·67)	–	1 : 1·8
0·35–0·4 × ·35)	–	–	–	–	0·65 × 0·58
0·9 × 0·6–·65)	–	average length 1·97	–	–	(1·8 × 0·85)
0·35 × 0·6–·75)	–	average ant. 1·17 × 1·05 post 1·08 × 0·99	–	–	1·26–1·44 × 1·15–1·2
0·39–0·4 × ·56–0·6)	–	average 0·61 × 0·3	–	–	0·91 × 0·84
11–12)	–	(15)	–	–	(19·5)
3–130 × 5–75	–	*c.* 110 × 70	97–103 × 66–75	–	107 × 73
–10	–	7·5–8	7·7–9·6	–	thick

(i) Material studied

(a) From the NE Atlantic

Raja batis [stomach] West of Orkney Is (60°N, 03°W; depth 273 m; Sept., 1959). Collected by H. H. Williams. BM(NH) Reg. No. 1959.10.14.24.

Raja batis [?] Faxa-Floi, Iceland (Oct., 1966). BM(NH) Reg. No. 1976.5.12.47–56 (see Manger, 1972 : 163; as *Otodistomum* sp.).

Raja batis [stomach] West of Scotland. Rees Collection. BM(NH) Reg. No. 1976.4.12.23.

Raja batis [stomach] Between Flannan Is and St Kilda off west coast of Scotland (58°N, 08°W; depth 130–134 m; July, 1976). BM(NH) Reg. No. 1976.9.8.1–2.

Raja batis [stomach] Oslo fjord, Norway. Collected by Esmark. Zoologisk Museum, Oslo Cat. Nos. C.53 (collected 1868), C.54, C.56 (collected 1863) and C.57 (collected 1863).

Raja nidarosiensis [stomach] Trondheim, Norway. Zoologisk Museum Oslo Cat. No. C.55 (collected March, 1889; probably material of Lönnberg, 1891 : 71) and C.72 (collected Dec., 1900).

Raja radiata [?] Vesterhorn, Iceland (Oct., 1966). BM(NH) Reg. No. 1976.5.12.57–66.

Raja radiata [?] Isafjordhur, Iceland (Oct., 1966). BM(NH) Reg. No. 1976.5.12.57–66.

Raja radiata [stomach and pyloric duct] (immature specimens in pyloric duct) Aberdeen, Scotland (Oct., 1973). BM(NH) Reg. No. 1976.5.12.67.

Raja radiata [stomach] Off eastern Iceland (63°N, 11°W; depth 410–420 m; June, 1974). BM(NH) Reg. No. 1976.5.12.37–40.

Raja radiata [stomach] Viking Bank, off coast of Norway (61°N, 03°E; depth 120–138 m; July, 1976). BM(NH) Reg. No. 1976.10.12.1.

Raja radiata [stomach] Kristineberg, Sweden (Jan., 1971). Material of J. Thulin.

Raja spinicauda [stomach] Off eastern Iceland (63°N, 11°W; depth 410–420 m; June, 1974). BM(NH) Reg. No. 1976.5.11.7–29.

Centroscymnus coelolepis [stomach] SW of St Kilda (58°N, 10°W; depth 1090–1120 m; April, 1973). BM(NH) Reg. No. 1976.5.11.30–34.

Chlamydoselachus anguineus [?] Varangerfjord, Norway (1896). Material referred to by Lönnberg (1898 : 4) and Odhner (1911 : 517). Zoologisk Museum, Oslo Cat. No. C.64.

(b) From elsewhere

Raja jenseni [stomach] Grand Bank, Newfoundland, Canada. Collected by W. Templeman. BM(NH) Reg. Nos 1963.9.6.1–2 and 1965.7.30.1–8.

Raja jenseni [stomach] Northern NW Atlantic (Sept., 1967 and May, 1968). Collected by W. Templeman. BM(NH) Reg. No. 1968.12.6.41–48.

Raja richardsoni [stomach] Northern NW Atlantic (Sept., 1967 and May, 1968). BM(NH) Reg. No. 1968.12.6.31–40 (see Templeman, 1973 : 1831; as *O. veliporum*).

Raja sp. (? *griseocaudata*) [stomach] North of Falkland Is (47°S, 61°W; depth 272–300 m; July, 1928). BM(NH) Reg. No. 1975.3.14.42–45 (see Gibson, 1976 : 200).

Centroscyllium fabricii [stomach] Grand Bank, Newfoundland, Canada. Collected by W. Templeman. BM(NH) Reg. No. 1965.7.30.9–12.

(ii) NE Atlantic records from the literature

Raja batis [stomach] Storeggen (Aug.) and Varberg (? date), Sweden. Olsson (1868a : 22; as *Distoma veliporum*).

Raja batis [stomach] Bohuslän, Sweden (Summer, 1868). Olsson (1868b : 478; as *Distoma veliporum*).

Raja batis [oesophagus] Belgium. van Beneden (1871 : 17; as *Distoma cestoides*).

Raja batis [stomach; occ. intestine] Skagerrak at Bohuslän, Sweden (July, Aug.). Olsson (1876 : 13; as *Distoma veliporum*).

Raja batis [?] Kristineberg, Sweden (Aug.). Lönnberg (1889a : 68; as *Distoma veliporum*).

Raja batis [?] Kärnigo, Sweden (Dec.). Lönnberg (1889b : 48; as *Distoma veliporum*).

Raja batis [?] Bergen, Norway (July, Aug.). Lönnberg (1890 : 46; as *Distoma veliporum*).

Raja batis [?] Aberdeen, Scotland. Scott, T. (1909 : 77; as *Distoma cestoides*).

Raja batis [?] Kristineberg, Sweden (1898). Odhner (1911 : 516).

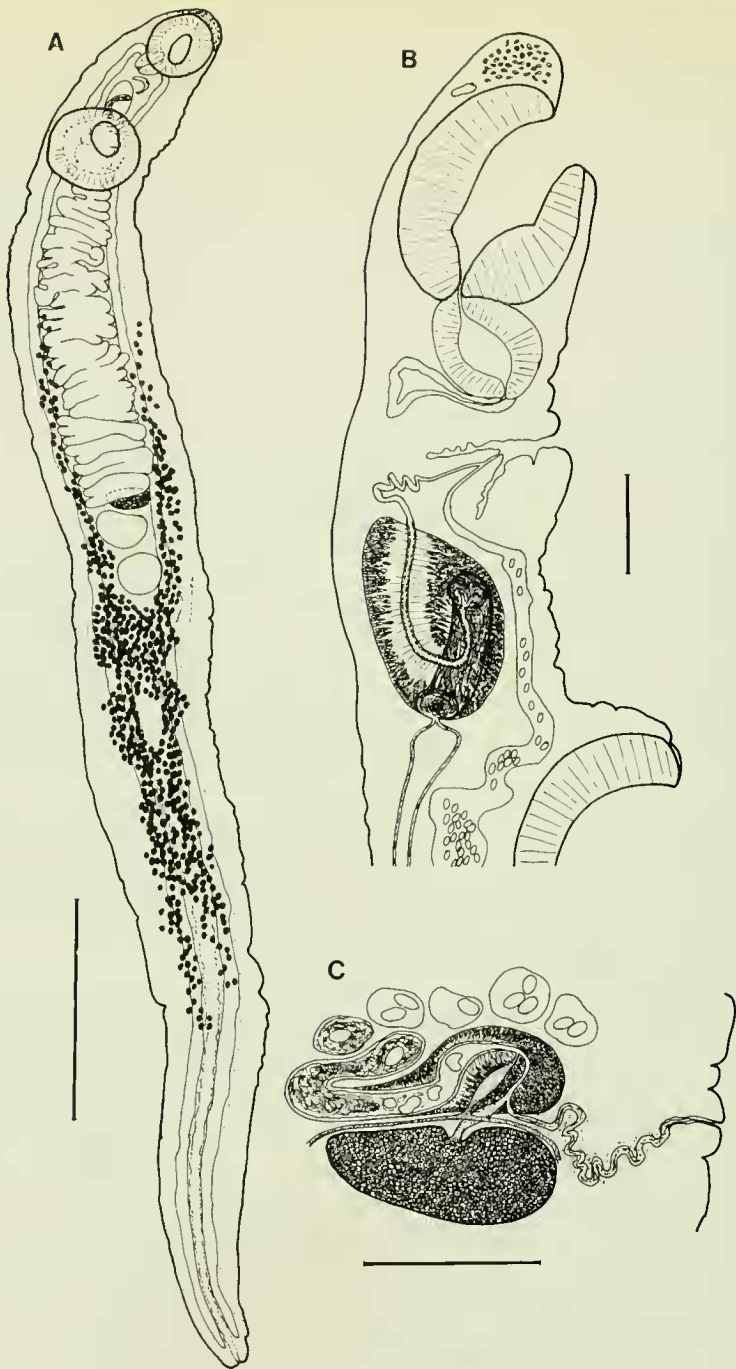*Raja batis* [stomach] Aberdeen, Scotland. Nicoll (1913 : 194).

Raja batis [stomach] Galway, Ireland. Little (1929 : 26).

Raja batis [stomach] Faxa-Floi, Iceland (64°N, 23°W; Oct., 1966). Manger (1972 : 163; as *Otodistomum* sp.).

Raja clavata [stomach] Varberg, Sweden (July). Olsson (1868a : 22; as *Distoma veliporum*).

Raja clavata [stomach] Bohuslän, Sweden (Summer, 1868). Olsson (1868b : 478; as *Distoma veliporum*).

Raja clavata [stomach] Skagerrak at Bohuslän, Sweden (July, Aug.). Olsson (1876 : 13; as *Distoma veliporum*).

Raja clavata [stomach] East coast of Iceland (66°N, 11°W; depth 142 m; Aug., 1948). Rees (1953 : 18; as *Otodistomum veliporum*).

Raja fullonica [stomach] Bohuslän, Sweden (Summer, 1868). Olsson (1868b : 478; as *Distoma veliporum*).

Raja fullonica [stomach, occ. intestine] Skagerrak at Bohuslän, Sweden (July, Aug.). Olsson (1876 : 13; as *Distoma veliporum*).

Raja fullonica [?] Bergen, Norway (July, Aug.). Lönnberg (1890 : 46; as *Distoma veliporum*).

Raja lintea [stomach] Bohuslän, Sweden (Summer, 1868). Olsson (1868b : 478; as *Distoma veliporum*).

Raja lintea [stomach] Skagerrak at Bohuslän, Sweden (July, Aug.). Olsson (1876 : 13; as *Distoma veliporum*).

Raja nidarosiensis [stomach] Trondheim, Norway (March, 1889). Lönnberg (1891 : 71; as *Distoma veliporum*).

Raja radiata [stomach] Bohuslän, Sweden (Summer, 1868). Olsson (1868b : 478; as *Distoma veliporum*).

Raja radiata [stomach] Skagerrak at Bohuslän, Sweden (July, Aug.). Olsson (1876 : 13; as *Distoma veliporum*).

Raja radiata [stomach] Northumberland, England. Lebour (1908 : 49; as *Otodistomum veliporum*).

Raja radiata [stomach] British waters. Williams & Richards (1966 : 556; as *Otodistomum* sp.).

Raja radiata [stomach] Scottish waters. Williams, McVicar & Ralph (1970, 46; as *Otodistomum* sp.).

Raja sp. [?] Swedish coast. Jägerskiöld (1900 : 72; as *Distomum veliporum*).

Centroscymnus coelolepis [stomach] Golfe de Gascogne, France (45°N, 03°W; depth 1431 m; July, 1903: 44°N, 02°W; depth 1483 m; August, 1903). Guiart (1938 : 23; as *Otodistoma scymni*).

Centroscymnus coelolepis [stomach] Off Portugal (39°N, 10°W; depth 1628 m; Aug., 1910). Guiart (1938 : 24; as *Otodistoma scymni*).

Chlamydoselachus anguineus [?] Varangerfjord, Norway. Lönnberg (1898 : 4; as *Distomum veliporum*).

ASPECTS OF BIOLOGY. As in the case of *O. veliporum* there appears to be little information available concerning the larval stages and early intermediate hosts of this species. It is confined to Manter's (1926) description of the non-ciliated miracidium. There is no evidence that a crustacean intermediate host is involved. Immature encysted specimens (metacercariae) of *Otodistomum* have been recorded from various marine fishes (see p. 196), but it is not known for certain to which species they belong.

If the life-history of the freshwater azygiids can be used as a guide, the rays and small sharks presumably acquire these parasites either by feeding directly upon the cercariae or by feeding on molluscs; but it would appear more likely that they become infested by feeding upon small fishes infested with metacercariae.

PREVIOUS DESCRIPTIONS. Lebour (1908 : 49; as *O. veliporum*); Odhner (1911 : 516); Layman & Borovkova (1926 : 11); Manter (1926 : 14); Linton (1940 : 107); Miller (1941 : 47); Gibson (1976 : 200).

DESCRIPTION (Figs 5 & 6). This description is based on specimens from several species of ray, but especially on material from *Raja spinicauda*, *R. batis*, *R. richardsoni* and *R.* sp. (? *griseocaudata*), and from the shark *Centroscymnus coelolepis*. Measurements taken from these worms are given in Table 8, and measurements from the literature in Table 9.

Fig. 5 *Otodistomum cestoides*: (A) whole-mount, ex *Raja spinicauda*; (B) sagittal section of forebody showing terminal genitalia, ex *R. spinicauda*; (C) lateral view of ovarian complex, ex *Raja* sp. (? *griseocaudata*). Scale: (A) 5 mm; (B, C) 500 μm.
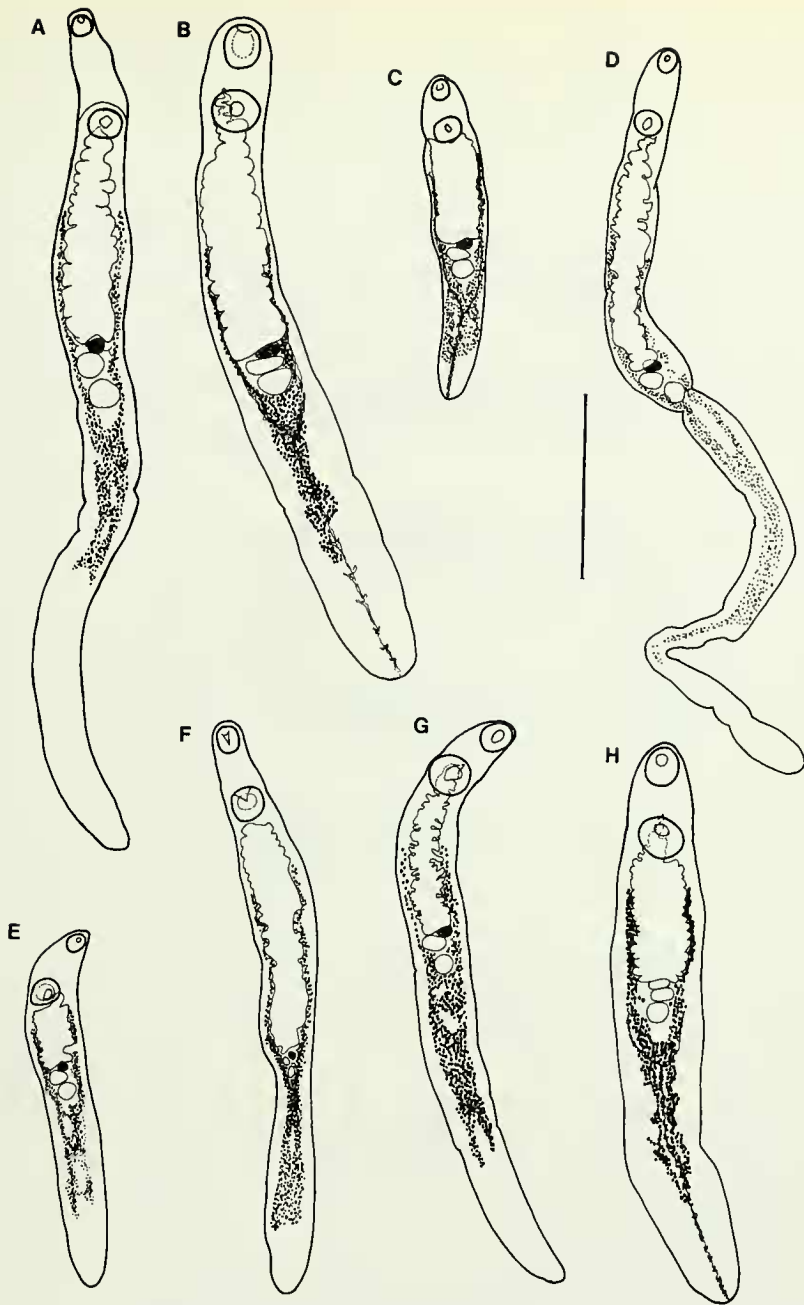
Fig. 6 *Otodistomum cestoides* from various hosts: (A) *Raja richardsoni*; (B) *R. batis*; (C) *R. radiata*; (D) *R. jenseni*; (E) *R.* sp. (? *griseocaudata*); (F) *Centroscyllium fabricii*; (G) *Raja spinicauda*; (H) *Centroscymnus coelolepis*. (All are drawn to the same scale and are directly comparable to the figures of *O. veliporum* in Fig. 4.) Scale: 10 mm.

Table 8 Measurements of specimens of *Otodistomum cestoides* examined from various hosts.

Host	Raja batis	Raja jenseni	Raja radiata	Raja richardsani	Raja spinicauda	Centroscymnus coelolepis	Centroscyllium fabricii	Chlamydoselachus anguineus
Number of specimens	12	8	12	9	12	7	7	1
Length (mm)	3–46	20–48	1·9–23	17–75	9–33	3·9–35	20–31	15
Breadth (mm)	1–5	1·5–3·3	0·4–3·4	1·7–5·5	1·25–4	1–5·5	3·2–3·7	2·2
Forebody (mm)	1–6	2·1–4·0	0·5–3·3	3·6–8·5	1·75–3	1–4·5	2·0–3·75	2·4
Oral sucker (mm)	0·45–2·0 × 0·35–2·0	0·75–1·2 × 0·82–1·25	0·22–1·25 × 0·23–1·3	0·95–1·8 × 1·0–1·95	0·85–1·6 × 0·92–1·55	0·53–1·8 × 0·53–1·6	1·1–1·25 × 1·1–1·5	1·1 × 1·2
Ventral sucker (mm)	0·55–2·8 × 0·45–2·8	1·0–1·6 × 1·1–1·6	0·3–1·8 × 0·34–1·8	1·5–2·6 × 1·5–2·6	1·4–2·25 × 1·35–2·25	0·68–2·5 × 0·7–2·4	1·55–1·9 × 1·5–2·4	1·9 × 1·7
Sucker ratio	1:2·15–1·6	1:1·3–1·4	1:1·2–1·6	1:1·25–1·6	1:1·3–1·5	1:1·25–1·5	1:1·3–1·6	1:1·4
Pharynx (mm)	0·23–0·9 × 0·15–0·8	0·38–0·6 × 0·35–0·5	0·12–0·68 × 0·07–0·6	0·4–0·7 × 0·44–0·7	0·4–0·7 × 0·35–0·6	0·12–1·1 × 0·15–1·2	—	0·6 × 0·5
Prostatic sac (mm)	up to 1·4 × 1·2	0·7–1·4 × 0·4–0·9	up to 1·2–1·1	0·6–2·0 × 0·45–1·0	up to 1·3 × 0·75	0·16–1·5 × 0·18–1·0	—	—
Testes (mm)	0·1–1·7 × 0·1–1·2	0·6–1·5 × 0·55–1·4	0·04–1·1 × 0·04–1·4	up to 2·0 × 1·75	0·6–1·25 × 0·6–1·2·5	0·12–1·1 × 0·15–1·25	0·5–1·75 × 0·9–1·1	c. 0·6 × 0·6
Ovary (mm)	up to 1·2 × 1·2	0·4–0·8 × 0·45–0·9	0·04–0·6 × 0·04–1·0	up to 1·0 × 1·2	0·4 × –0·8 0·4–1·0	0·1–0·7 × 0·1–1·0	—	—
Uterine field/length × 100 (%) (mature specimens only)	17–28	12·5–29	18–36	19–37	16–33	17–21	18–40	27
Egg-length (μm)	67–87	58–94	59–95	68–100	72–100	72–97	74–102	c. 75–90
Egg-shell thickness (μm)	3–7 (usually 3–4)	3–6	2·5–5	3·5–5	3–6	3–4	3–6·5	—

The body of this often large, elongate worm is subcylindrical, being slightly dorso-ventrally flattened and attenuated towards both extremities (Figs 5A & 6). The body-surface is smooth, although transverse folds do occur in contracted material. The subterminal *oral sucker* is about two-thirds to three-quarters the size of the slightly protruding *ventral sucker*. There is a very distinct pre-oral lobe which is unusual in that it contains a dense concentration of gland-cells, though this is much less apparent in the specimens from *C. coelolepis*. The forebody is short, especially in the larger specimens, as it apparently grows at a much slower rate than the hindbody. The structure of the body-wall is similar to that of *O. veliporum*.

There is no prepharynx, the oral aperture opening directly into a well-developed *pharynx*. The relatively short oesophagus passes dorsally and divides, giving rise to two very short lateral branches lined with a cuticle similar to that of the oesophagus itself. These in turn give rise antero-laterally to the gut-caeca which pass posteriorly in the dorso-lateral fields, following a straight or sinuous course, and end blindly near the posterior extremity. There are no 'Drüsenmagen'. The relatively narrow gut-caeca have a villous lining and tend to be slightly diverticulate.

The *excretory system* is Y-shaped, the terminal pore leading into a long, slightly diverticulate stem which bifurcates just posteriorly to the testes in the anterior half of the post-testicular region of the vitellarium. The two arms pass antero-laterally and into the forebody where they re-unite antero-dorsally to the oral sucker (Fig. 5B).

The two oval, post-ovarian *testes* lie in tandem or slightly obliquely in about the middle of the body. The posterior testis is often slightly larger than the anterior. The vasa efferentia unite just anteriorly to the ventral sucker as they pass through the posterior wall of the prostatic sac (Fig. 5B). This large, oval sac has a thin, muscular wall and contains the seminal vesicle which is tubular, broad and usually very arcuate, often being almost U-shaped. The length of the seminal vesicle is variable, and, although it is often the same length as the prostatic sac, it is sometimes considerably shorter. It leads into a tubular pars prostatica which passes posteriorly dorsal to the seminal vesicle, before reflexing and passing anteriorly. The pars prostatica has a villous lining and a dense covering of gland-cells which fill the prostatic sac. As the male duct passes through the anterior wall of the prostatic sac it assumes the form of an ejaculatory duct. This part of the duct is very long, has a thick, muscular wall and is usually coiled between the anterior extremity of the prostatic sac and the base of the *sinus-organ*. Towards the distal extremity of the conical sinus-organ the ejaculatory duct unites with the metraterm to form a short hermaphroditic duct which opens terminally. The genital atrium is usually relatively deep and possesses a thick, muscular wall. The genital pore is mid-ventral, usually a short distance posterior to the pharynx. The degree of coiling of the ejaculatory duct and the size and shape of the sinus-organ and the genital atrium are all extremely variable (see Gibson, 1976 : fig. 6).

The oval *ovary* lies medially or sub-medially immediately anterior to the testes. From it a short oviduct leads directly into a relatively large compact Mehlis' gland situated antero-dorsally to the ovary. Within Mehlis' gland the oviduct receives first Laurer's canal and then, some distance along, the common vitelline duct (Fig. 5C). Laurer's canal is a simple tube, passing dorsally and opening to the exterior at about the level of the ovary. The first coils of the *uterus* act as a uterine seminal receptacle, this being the only seminal store in the female system. The uterus is almost entirely pre-ovarian, rarely reaching posteriorly to the ovary. The bulk of the uterine field occurs between the ovary and the ventral sucker, and accounts for between 17 and 40% (usually 20–30%) of the total body-length. As it passes into the forebody the uterus narrows and is less convoluted. It usually passes ventrally or ventro-laterally to the prostatic sac, where it narrows further and gradually assumes the form of a metraterm. Anteriorly to the prostatic sac the metraterm passes antero-dorsally and enters the sinus-organ, where it unites with the ejaculatory duct. Eggs without spines or filaments are formed within Mehlis' gland: these possess a shell which is not as thick as that of some of the other species of *Otodistomum*. The follicular *vitellarium* occurs in two lateral fields between a level which is usually a short distance anterior to the middle of the uterine field and a level approximately halfway between the posterior testis and the posterior extremity. The anterior and posterior limits of the vitellarium are, however, extremely variable. The posterior limit can, for example, be almost anywhere within the posterior third of the body. Posteriorly to the gonads the lateral fields of follicles tend to be confluent, but the degree of confluence is also variable.

Table 9 Dimensions of *Otodistomum cestoides* from various hosts taken from the literature. Figures given in

Authority	Lebour (1908)	Odhner (1911)	Manter (1926)	Linton (1940)[1] van Cleave & Vaughn (1941)[2]
Name used	*Otodistomum veliporum*	*Otodistomum cestoides*	*Otodistomum cestoides*	*Otodistomum cestoides*
Host	*Raja radiata*	*Raja* spp.	*Raja laevis*	*Raja laevis*
Locality	Northumberland coast, England	North Atlantic	Maine, U.S.A.	Massachusetts[1] New Hampshire[2] U.S.A.
Number of specimens	1	?	Many	Many
Length (mm)	32	up to 65	1·9–65 (33)	10–54[1] 6·9–30·2[2]
Breadth (mm)	2·6	3–5	0·56–3·5* (3·8)	2–4·5[1]
Forebody (mm)	–	–	0·93–5* (4·2)	–
Oral sucker (mm)	1·2 diam.	1·5–2	0·28–1·56* diam. (1·6 × 1·6)	–
Ventral sucker (mm)	2·4 diam.	2–2·75	0·39–2·31* diam. (2·2 × 2·4)	–
Sucker-ratio	1 : 2	1 : 1·35	(1 : 1·25–1·67)*	–
Pharynx (mm)	0·4 × 0·35	–	(0·6 × 0·4)	–
Prostatic sac (mm)	–	–	(0·9 × 0·7)	–
Testes (mm)	1·3–1·5 diam.	–	(1·0 × 1·0)	–
Ovary (mm)	1·2 diam.	–	(0·5 × 0·8)	–
Uterine field/ length × 100 (%) (mature only)	(*c.* 18)	–	(*c.* 20–42)*	–
Eggs (μm)	60	65–72 × 43	average 69·4 × 46·2	*c.* 78 × 51[1] 55–90 × 36–58[2]
Egg-shell thickness (μm)	–	3	*c.* 4·5	3[1] 3–4[2]

* Figures from specimens of 1·9 to 39 mm in length.   † New measurements.

parentheses were calculated from the measurements or illustrations given in the literature.

Manter (1926)[1] Dollfus (1937a)[2] van Cleave & Vaughn (1941)[3]	Layman & Borovka (1926)	Miller (1941)	Guiart (1938)	Guiart (1938)	Gibson (1976)
Otodistomum veliporum[1] Otodistomum cestoides[2, 3]	Otodistomum cestoides	Otodistomum cestoides	Otodistoma scymni	Aphanhystera monacensis	Otadistomum cestoides
Raja ?inoculata	Raja radiata	Raja laevis	Centroscymnus coelolepis	Centroscymnus coelolepis	Raja sp. (? griseocaudata)
Pacific coast of U.S.A.	Barents Sea	Atlantic coast, Canada	Gulf of Gascogne	Off Monaco	Patagonian shelf
Many	14	3	16	3	10
3–50[1], up to 61·5[2] 3·9–69[3]	39–52	up to 12·5	17·5–38 (17·5–27)	16–20 (17)	7·5–20
average 3·81[1] up to 3·5[2] up to c. 9[2]	3·3–3·9 –	up to 1·6 1/5 body-length	3–5·5 (3–3·5) (3·2–4·8)	3·5–5 (3·5) (3·2)	0·9–2·0 –
·77[2]	0·9–1·4 × 1·18–1·59	up to 0·72 × 0·79	(1·2–1·4 × 0·95–1·6)	(c. 1·0 × 1·0)	0·65–1·1 × 0·65–1·1
·95[2]	2·13 × 2·05	up to 1·14 × 1·24	(1·7–2·25 × 1·7–2·4)	(2·25 × 2·25)	1·0–1·7 × 1·0–1·7
(1 : 1·67)[2]	(1 : 1·25–1·67)	(1 : 1·5)	(c. 1 : 1·67)	(c. 1 : 2)	1 : 1·25–1·67†
	0·52–0·56 × 0·59–0·66	0·31 length	–	–	0·35–0·4 × 0·25–0·35
	–	–	–	–	0·6–1·3 × 0·4–0·7
	1·38–1·89 × 1·23–1·64	–	–	–	0·6–1·2 × 0·3–1·2
	0·82–0·85 × 0·89–0·95	–	–	–	0·3–0·7 × 0·35–0·9
	(c. 30)	–	(c. 15–20)	–	18·5–30†
average 85·5 × 57·8[1] 7·5–73 × 41–49[2])–94 × 40–70[3]	82–98·5 × 49	(immature)	–	(immature)	74–89 × 50–59
4[1] 3–4[2] –5[3]	–	–	–	–	4–6

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DISCUSSION. One record, which apparently refers to *O. cestoides*, which should be commented upon is that of Lönnberg (1898) from the very rare hexanchiform shark *Chlamydoselachus anguineus* in a fjord in northern Norway, well outside the normal range of this fish. As *O. veliporum* is common in the related *Hexanchus griseus*, one might have assumed that Lönnberg's material, which he did not describe, also belonged to this species. However, Odhner (1911 : 517, footnote), presumably after examining the material, referred it to *O. cestoides*, and this was accepted by Dollfus (1937a). We had some doubts in accepting this record, for although it is possible that *O. cestoides* might occur in hexanchiform sharks, the life-style of *C. anguineus* is much more similar to the pelagic hosts of *O. veliporum* than to that of the squaliform hosts of *O. cestoides*. We have, however, examined the specimen referred to by Lönnberg and can confirm Odhner's determination (see Table 8). It is possible that this shark might have acquired this particular parasite accidentally by feeding upon an elasmobranch infested with *O. cestoides*.

Like *O. veliporum*, this species shows variation in development and size which seems to be affected by the host-species (see Fig. 6; Tables 8 & 9). Specimens from *Raja radiata* appear to mature at about 5–6 mm in length, whereas in specimens from *R. spinicauda* maturity apparently occurs at about 11 mm, which is similar to that found by Manter (1926), i.e. 11–15 mm, in material from *R. laevis*. Although our own specimens from *R. radiata* reached only 23 mm in maximum length, Layman & Borovkova (1926) recorded specimens of up to 52 mm. Specimens from *R. binoculata, R. laevis* and *R. richardsoni* often reach lengths of more than 50 mm, whilst Gibson (1976) recorded specimens from *Raja* sp. (? *griseocaudata*) of only up to 20 mm in length. Although the paucity of records, and the lack of knowledge of seasonal variation probably bias these results, it does appear that these worms reach a greater size in certain hosts, and they appear to mature at a smaller size in hosts which contain small worms. This suggests that some rays provide a more suitable habitat than others and, indeed, the total absence of this parasite from certain rays, such as *R. naevus* which has been examined in great numbers (500 +) by McVicar (1973), adds additional weight to this hypothesis.

Otodistomum plunketi Fyfe, 1953

TYPE-HOST AND LOCALITY. *Scymnodon plunketi*, Otago, New Zealand.

RECORDS.

(i) Material studied.
Etmopterus princeps [body-cavity] East Rockall (57°N, 13°W; depth 1000–1060 m; June, 1974). BM(NH) Reg. No. 1976.5.12.3–4.
(ii) NE Atlantic records from the literature.
None.

ASPECTS OF BIOLOGY. Nothing is known about the life-history of this species. It is probably similar to that of the gastric species of this genus, with the exceptions that the encysted metacercariae must penetrate the gut-wall in order to grow in the body-cavity, and the the eggs must, presumably, be lost through the abdominal pore.

PREVIOUS DESCRIPTIONS. Fyfe (1953 : 187); Skrjabin & Guschanskaja (1958 : figure only).

DESCRIPTION (Fig. 7). Due to the very large size of these worms and their bowed shape when fixed, the following description is based mainly on the smallest of the three specimens found, this being the only one which could be mounted on a slide. Even so, the thickness of this specimen prevented much of the internal structure being observed. Parts of one of the larger specimens, showing details of the terminal genitalia, and the proximal part of the female system, were sectioned. The dimensions of the worms and measurements from the literature are given in Table 10.

The worms are large, oval and very flattened dorso-ventrally (Fig. 7A), being similar in shape to the anaporrhutine gorgoderids, which also inhibit the body-cavity of elasmobranchs. Two of the present specimens, fixed without any pressure, have assumed a concave shape with the whole of the uterine field protruding ventrally. The body-surface is smooth. The *oral sucker* is sub-

terminal and about two-thirds as large as the *ventral sucker*. There is a pre-oral lobe, which, although containing numerous nuclei, does not contain the great number of gland-cells which usually occurs in *O. cestoides*. The forebody is short, conical and much narrower than the hindbody (Fig. 7A). The structure of the body-wall is basically similar to that of *O. veliporum* and *O. cestoides*, except that the tegument and the muscle-layers are much thinner, as is usual in coelomic parasites.

Details of the *pharynx* and oesophagus could not be made out in the whole-mount, but sections show that there is no prepharynx, a large, oval pharynx and a short oesophagus, which passes dorsally before joining the caecal bifurcation. There are no 'Drüsenmagen', and the relatively narrow gut-caeca pass back sinuously and end blindly close to the posterior extremity. The terminal region of the caeca is especially sinuous and slightly diverticulate.

Some of the details of the *excretory system* could not be determined in this material, but the pore is terminal and the vesicle Y-shaped, bifurcating at about the level of the posterior testis, according to Fyfe (1953). Our sectioned material indicates that, contrary to the usual condition in *Otodistomum* spp., the excretory arms, which are very diverticulate, end blindly on each side of the body dorso-laterally to the oral sucker. This latter feature is visible in the figure given by Skrjabin & Guschanskaja (1958).

Table 10 The dimensions of *Otodistomum plunketi*.

Authority	Fyfe (1935)	Skrjabin & Guschanskaja (1958)	Present material		
Host	*Scymnodon plunketi*	*Raja longirostris*	*Etmopterus princeps*		
Locality	Off New Zealand	Pacific coast of U.S.S.R.	East Rockall		
Number of specimens	30	? (1)	3		
Length (mm)	46–82	(*c.* 55)	27	*c.* 38	*c.* 42
Breadth (mm)	27–33	(*c.* 19)	14	20	21
Forebody (mm)	–	(*c.* 8)	3.1	–	–
Oral sucker (mm)	3·0–3·9 diam.	(*c.* 2·5) diam.	1·17 × 1·52	–	–
Ventral sucker (mm)	4·0–5·19 diam.	(*c.* 3·5) diam.	2·1 × 2·6	–	–
Sucker ratio	(1 : 1·5)	(*c.* 1 : 1·5)	1 : 1·7	–	–
Testes (mm)	2·5 × 3·0	(*c.* 1·5) diam.	0·8 × 1·5	–	–
Ovary (mm)	1·88 × 2·63	(*c.* 1·5 × 2·5)	*c.* 1·0 × 1·2	–	–
Uterine field/length × 100 (%)	(*c.* 40)	(*c.* 33)	40	–	–
Egg-length (μm)	111 × 75	–	102–118 × 70–80	–	–
Egg-shell thickness (μm)	9	–	6–8	–	–

The figures in parentheses were taken from an illustration in the literature.

The two *testes* are oval and situated obliquely about two-thirds of the body length from the anterior end. Details of the terminal genitalia are not clearly visible in the whole-mount, but are very distinct in the sections. The seminal vesicle, as in other azygiids, is broad, tubular, curved and, along with the tubular pars prostatica, contained in the oval prostatic sac (Fig. 7B). This latter organ, which measures about 2 × 1 mm in the sectioned specimen, is situated immediately anteriorly to the ventral sucker. The two vasa efferentia pass through the wall of the prostatic sac a short distance apart and not in union, as is the case in *O. veliporum* and *O. cestoides*. A long convoluted ejaculatory duct leads from the prostatic sac into a large, muscular conical *sinus-organ*. The fusion of the ejaculatory duct and metraterm occurs near the distal extremity of the
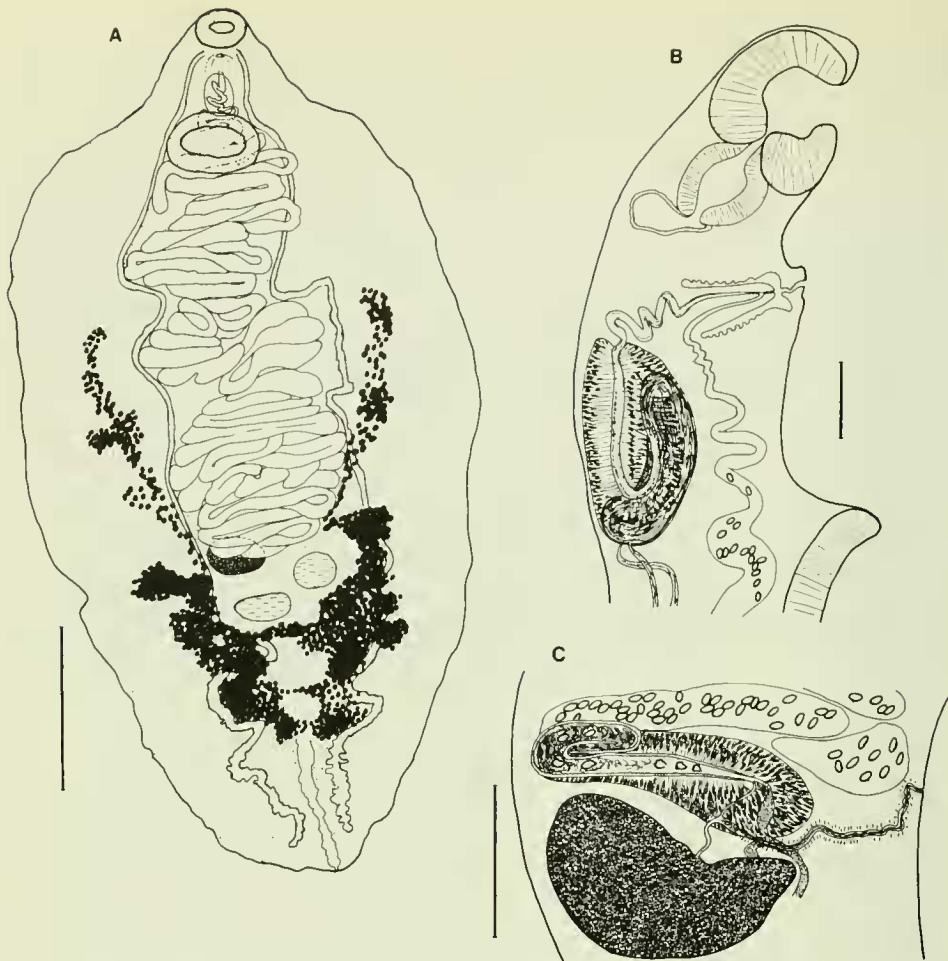
Fig. 7 *Otodistomum plunketi* ex *Etmopterus princeps*: (A) whole-mount; (B) sagittal section of fore-body; (C) lateral view of ovarian complex. Scale: (A) 5 mm; (B, C) 1 mm.

sinus-organ, and a very short hermaphroditic duct, opening terminally, is formed. There is no sinus-sac. The genital atrium is large, but almost completely filled by the sinus-organ, and the genital pore is situated mid-ventrally just posteriorly to the pharynx.

The *ovary*, which is apparently sometimes larger than the testes, is oval and almost immediately pre-testicular. A short oviduct leads anteriorly directly into a large, oval Mehlis' gland (Fig. 7C). Just within Mehlis' gland the oviduct unites with Laurer's canal. Towards the centre of Mehlis' gland, some distance from its union with Laurer's canal, the oviduct receives the common vitelline duct, and almost immediately dilates to form the oötype, which continues as the uterus. The first part of the *uterus* contains spermatozoa and thus acts as a uterine seminal receptacle. Laurer's canal is tubular and, although it may be slightly dilate proximally and contain sperma-tozoa and vitelline material, it does not appear to form a distinct rudimentary seminal receptacle as figured by Fyfe (1953). This canal, which has a thick wall and is surrounded by gland-cells, opens dorsally at the level of Mehlis' gland. The uterus does not reach posteriorly to the ovary,

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but coils inter-caecally between the ovary and the ventral sucker, occupying about 40 % of the total body-length. Anteriorly to the ventral sucker the uterus narrows to form a metraterm, which unites with the ejaculatory duct within the sinus-organ. The numerous eggs, which are without spines or filaments, are large and possess thick shells. At the proximal extremity of the uterus the eggs are light brown in colour, as in other species of *Otodistomum*, presumably being untanned; but as they pass down the uterus they become darker. The follicular *vitellarium* occurs in two sublateral fields between a level just anteriorly to the middle of the uterine field and a level half-way between the testes and the posterior extremity. These fields are confluent in parts of the post-testicular region. This species differs markedly from *O. veliporum* and *O. cestoides* in that the extra-caecal region of the body is very wide, which means that the anterior half of the vitelline field is isolated and not compressed between the body-wall and the uterine field.

DISCUSSION. This species has been recorded previously from *Scymnodon plunketi* off New Zealand by Fyfe (1953) and *Raja longirostris* off the Pacific coast of the U.S.S.R. by Skrjabin, in Skrjabin & Guschanskaja (1958). Despite the opinions of Dawes (1946, 1947) and Brinkmann (1975), who apparently consider all of the species of *Otodistomum* of which they were aware to belong to a single variable species, *O. veliporum*, we believe that this species can be distinguished from the other species of the genus, except for *O. pristiophori* (Johnston, 1902) and *O. hydrolagi* Schell, 1972, by its location, the body-cavity, and by the broad shape of the body. *O. pristiophori* has been recorded from *Pristiophorus cirratus* in Australian waters by Johnston (1902) and Woolcock (1935) and from *Psammobatis microps* and *Squatina argentina* in the Atlantic ocean off northern Argentina by Ostrowski de Nunez (1971). *O. hydrolagi* was recorded from the chimaera *Hydrolagus colliei* off the Pacific coast of the U.S.A. by Schell (1972). *O. plunketi* differs from the other two remarkably similar species in its larger size, wider extra-caecal region of the body, longer uterine field, more posterior position of the gonads, and in the absence of a union of the excretory arms in the forebody. As few specimens of these coelomic forms of *Otodistomum* have been found, little is known of the morphological variability of these species. Further workers may in fact find that some or all of these forms tend to grade into one another, thus presenting similar problems to those of their gastric relatives.

Gibson & Bray (in preparation) suggest that the reason why adult helminths are fairly common in the coelom of elasmobranchs may have something to do with the fact that these fish possess an abdominal pore which permits the escape of eggs. Forms associated with this habitat tend to have a broad or spatulate body, sometimes in contrast to their near relatives from the gut. This may be an adaptation which has developed to prevent individual specimens being lost through the abdominal pore. Helminths from similar habitats, such as the urinary and swim bladders, where the relatively static conditions permit a reduction in sucker-size and where there is an outlet through which the parasite might be lost, tend to have similar adaptations.

Otodistomum sp. metacercaria

Distoma veliporum Creplin of Wagener (1852).
Otodistomum veliporum (Creplin) of Mühlschlag (1914, in part), Dollfus (1937a, in part), Ronald (1959, 1960), Olson & Pratt (1973), Scott, J. S. (1975).
Distoma (similar to *D. veliporum*) of Olsson (1868b).
Distoma nigrescens Olsson, 1876.
Agamodistomum chimaerae Ariola, 1899.
Xenodistomum melanocystis Stafford, 1904.
Distomum cestoides van Beneden of Scott, T. (1909).
Cercaria cestoides van Beneden of Nicoll (1913).
Otodistomum cestoides (van Beneden) of Nicoll (1913), Linton (1940, in part), Miller (1941, in part).
'Metacercaria' of Ruszkowski (1934).
Otodistomum (?) sp. of Manter (1934).

RECORDS.

(i) Material studied

Coelorinchus caelorhinchus [encysted on liver] Off St Kilda (57°N, 10°W; depth 650–660 m; June 1974). BM(NH) Reg. No. 1976.5.11.54.

Conger conger [stomach] Skagerrak, 35–40″ NW of Hirtshals (depth *c*. 250 m; Sept., 1973). Material of J. Thulin.

Hippoglossoides platessoides [encysted in stomach wall] SW of Iceland (64°N, 24°W; depth 152–164 m; May, 1974). BM(NH) Reg. No. 1976.5.11.55.

Hippoglossoides platessoides [encysted in stomach wall] Off eastern Iceland (63°N, 11°W; depth 410–420 m; June, 1974). BM(NH) Reg. No. 1976.5.11.35–43.

Raja fyllae [encysted in stomach wall] East Rockall (57°N, 13°W; depth 800–820 m; June, 1974). BM(NH) Reg. No. 1976.5.11.44–53.

Rhinonemus cimbrius [liver] Gothenburg fish market (March, 1973); Skagerrak (Dec., 1970; Feb., 1971); Tjänö Marine Zoological Station, Bohuslän, Sweden (June, 1971). Material of J. Thulin.

(ii) From the literature

Chimaera monstrosa [encysted in wall of stomach and spiral intestine] Herdla, Norway. Ruszkowski (1934 : 487; as 'metacercaria'; see Dollfus, 1937a : 449 footnote).

Chimaera monstrosa [encysted in stomach wall] Bay of Setubal, Portugal (38°N, 09°W, depth 350 m; Nov., 1933). Dollfus (1937a : 447).

Chimaera monstrosa [encysted in wall of spiral intestine] Berlin Museum material, locality unknown. Mühlschlag (1914 : 200).

Glyptocephalus cynoglossus [encysted in stomach wall] Moray Firth, Scotland, Scott, T. (1909 : 77; as *Distomum cestoides* in *Pleuronectes microcephalus* – host corrected by Nicoll, 1915 : 360).

Glyptocephalus cynoglossus [stomach wall] Aberdeen, Scotland (Sept., 1908). Nicoll (1913 : 194; as *Cercaria cestoides* and *Otodistomum cestoides*).

Lophius piscatorius [stomach] Skagerrak, Sweden. Olsson (1868b : 477; as *Distoma* similar to *D. veliporum*: 1876 : 19; as *Distoma nigrescens*: see Dollfus, 1937a : 446).

Molva molva [branchial arch] Skaggerrak, Sweden. Olsson (1876 : 19; as *Distoma nigrescens*).

PREVIOUS DESCRIPTIONS. Ariola (1899 : 8; as *Agamodistomum chimaerae*); Nicoll (1913 : 194; as *Cercaria cestoides* and cercaria of *Otodistomum cestoides*); Manter (1934 : 324; as *Otodistomum* (?) sp.); Ruszkowski (1934 : 487; as 'metacercaria'); Dollfus (1937a : 447; as *Otodistomum veliporum* metacercaria); Linton (1940 : 108; as *Otodistomum cestoides*).
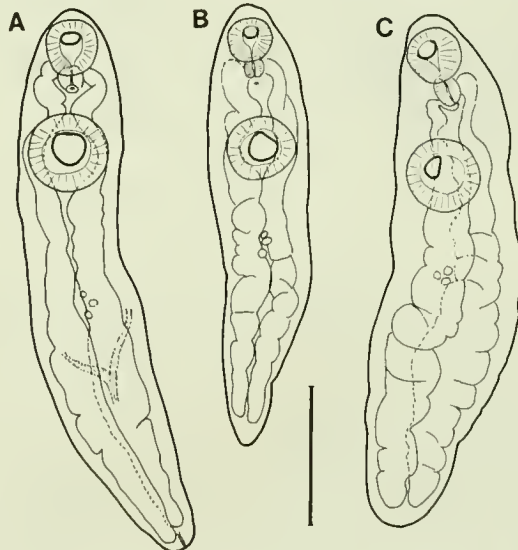

Fig. 8   *Otodistomum* sp. metacercariae: (A) ex *Coelorinchus caelorhinchus*; (B) ex *Hippoglossoides platessoides*; (C) ex *Raja fyllae*. Scale: 1 mm.

DESCRIPTION (Fig. 8). Morphologically these metacercariae are very similar to immature specimens of *O. cestoides* and differ from mature specimens in that the hindbody is much shorter in relation to the size of the forebody and the suckers (Fig. 8). The dimensions of the metacercariae are given in Tables 11 and 12.

Table 11 Dimensions of *Otodistomum* sp. metacercariae from various hosts.

Host	*Hippoglossoides platessoides*	*Coelorinchus caelorhinchus*	*Raja fyllae*	*Conger conger*	*Rhinonemus cimbrius*
Number of specimens	5	2	6	1	5
Length (mm)	1·9–4·1	4·5–5·6	2·35–3·8	7·6	1·76–6·5
Breadth (mm)	0·6–0·9	0·9–1·6	0·65–1·25	1·5	0·49–1·4
Forebody (mm)	0·6–1·0	0·8–1·1	0·52–0·95	2·1	0·59–1·5
Oral sucker (mm)	0·25–0·41 × 0·27–0·42	0·42–0·58 × 0·42–0·55	0·25–0·4 × 0·26–0·41	0·47–0·63	0·18–0·49 × 0·22–0·59
Ventral sucker (mm)	0·35–0·56 × 0·37–0·54	0·6–0·8 × 0·63–0·81	0·35–0·57 × 0·36–0·56	0·82–0·87	0·27–0·89 × 0·28–0·84
Sucker ratio	1 : 1·3–1·5	1 : 1·5	1 : 1·3–1·5	1·4	1·3–1·4
Testes (mm)	0·025–0·07 diam.	0·07–? diam.	0·035–0·07 diam.	0·13 diam.	0·03–0·11 diam.
Ovary (mm)	0·02–0·05 diam.	0·04–? diam.	0·025–0·05 diam.	–	up to 0·08 diam.
Uterine field/ length × 100 (%)	11–15	18–?	10–14	15	10–15

The metacercariae, which are surrounded by a host-tissue reaction in addition to their own cyst-wall, are usually elongate oval. One of the most noticeable features is the great breadth of the gut-caeca which may be more than half of the total body-width and thus overlap. The gonads are not always visible, but normally are very small. The distance between the ovary and the ventral sucker, the equivalent of the uterine field, is normally shorter than that of the adult specimens (cf. Fig. 2). No sign of any development of the vitellarium or the uterus is visible in whole-mounts, though the primordium of Mehlis' gland is often visible.

DISCUSSION. *Otodistomum* metacercariae have been attributed by various authors to both *O. veliporum* and *O. cestoides*. The only features of the key which can be applied to the metacercariae are the sucker-ratio and, to a limited extent, the presumptive uterine field (the distance between the ovary and the ventral sucker). The value of the latter feature is severely restricted for, as shown in Fig. 2, allometric growth is involved in its early development. The sucker-ratio of all the specimens we have measured and the majority of those in the literature (see Tables 11 & 12) strongly suggest that they belong to *O. cestoides*. In addition, the large size of the presumptive uterine field in some specimens tends to preclude the presence of *O. veliporum*, especially as further growth in this region would be expected as the worms mature. As shown in Figs 8 and 9 and Tables 11, 12 and 13, these metacercariae do tend to resemble immature specimens of *O. cestoides* from the definitive hosts.

The results of Linton (1940) are worth noting. He recorded *Otodistomum* metacercariae from *Alutera schoepfi*, *Lophius piscatorius* and *Palinurichthys perciformis*. The specimens from *A. schoepfi* were up to 13 mm long and possessed sucker-ratios, especially in the largest specimens, within the *O. veliporum*-range. *A. schoepfi* differs from the majority of hosts from which *Otodistomum* metacercariae have been recorded in that it is pelagic rather than benthic, and this corresponds to the preferred habitat of the majority of the definitive hosts of *O. veliporum* and contrasts with the benthic habit of the majority of the definitive hosts of *O. cestoides*. This ecological distinction is not clear-cut, however, as Linton also found large specimens from the benthic fish *Lophius piscatorius* which have a sucker-ratio on the border-line between the *O. veliporum* and

Table 12 Dimensions of *Otodistomum* sp. metacercariae recorded in the literature.

Authority	Ariola (1899)	Ruszkowski (1932)	Dollfus (1937a)	Nicoll (1913)	Manter (1934)
Name used	*Agomodistomum chimaeroe*	'Metacercaria'	*Otodistomum veliporum* metacercaria	*Cercaria cestoides*	*Otodistomum* (?) sp.
Host	*Chimaera monstrosa*	*Chimaera monstrosa*	*Chimaera monstrosa*	*Glyptocephalus cynoglossus*	*Coelorinchus carminatus*
Locality	Genoa	Norway	Portugal	Aberdeen	Florida
Length (mm)	3·5–7	1·7–5·8	7–8·0	2·4	(3·55)
Breadth (mm)	–	0·5–1·0	1·6–1·8	0·66	(0·75)
Forebody (mm)	–	(1·2–1·5)	–	0·96	(0·9)
Oral sucker (mm)	c. 0·5 diam.	0·24–0·41 × 0·3–0·45	0·47×0·53	0·29×0·35	(0·28×0·3)
Ventral sucker (mm)	less than 1·0 diam.	0·36–0·68 × 0·37–0·67	0·85×0·79	0·43×0·59	(0·38×0·42)
Sucker-ratio	–	(1:1·3–1·5)	(1:1·5)	(1:1·7)	(1:1·4)
Uterine field/length × 100 (%)	–	(11)	(31)	–	(11)

Authority	Linton (1940)	Linton (1940)	Linton (1940)	Linton (1940)
Name used	*Otodistomum cestoides*	*Otodistomum cestoides*	*Otodistomum cestoides*	*Otodistomum cestoides*
Host	*Palimurichthys perciformis*	*Lophius piscatorius*	*Lophius piscatorius*	*Alutera schoepfi*
Locality	New England	New England	New England	New England
Length (mm)	4·34	3–4	8–10·5	2·24–13
Breadth (mm)	0·70	0·87–1·5	1·4–1·65	0·73–3·5
Forebody (mm)	–	–	–	–
Oral sucker (mm)	0·30×0·38	0·35×0·46–0·49	0·66–0·67×0·53–0·74	0·17–0·6×0·22–0·6
Ventral sucker (mm)	0·46×0·53	0·5×0·6–0·64	0·95–1·09×0·92–1·09	0·31–1·18×0·35–1·18
Sucker-ratio	(1:1·4)	(1:1·3–1·5)	(1:1·5–1·75)	(1:1·6–2·0)
Uterine field/length × 100 (%)	–	–	–	–

The figures in parentheses have been calculated from measurements or illustrations given by these authors.

Table 13 Dimensions of immature specimens of *Otodistomum veliporum* and *O. cestoides* from various hosts.

Species	O. veliporum	O. cestoides		
Host	Dalatias licha	Raja batis	Raja radiata	Centroscymnus coelolepis
Number of specimens	1	4	4	2
Length (mm)	13	3·0–5·1	1·9–5·5	3·9–5·0
Breadth (mm)	3	1·0–1·8	0·4–0·9	1·05–1·1
Forebody (mm)	1·7	1·0–1·2	0·53–1·07	1·05–1·1
Oral sucker (mm)	0·9 × 0·75	0·45–0·75 × 0·35–0·6	0·22–0·57 × 0·23–0·58	0·53 × 0·52–0·53
Ventral sucker	1·25 × 1·3	0·55–1·0 × 0·45–0·93	0·3–0·75 × 0·34–0·75	0·68–0·75 × 0·7
Sucker ratio	1 : 1·7	1 : 1·3 × 1·5	1 : 1·2 × 1·5	1 : 1·3
Testes (mm)	0·5 diam.	?–0·1 diam.	0·04–0·3 diam.	0·12–0·24 diam.
Ovary (mm)	–	–	0·04–0·2 diam.	0·1–0·13 diam.
Uterine field/length × 100 (%)	12	c. 10–11	15–20	6–9

Fig. 9 Immature specimens of *Otodistomum cestoides*: (A) ex *Centroscymnus coelolepis*; (B) ex *Raja batis*; (C) two specimens ex *Raja radiata*. (These illustrations are directly comparable with those in Fig. 8.) Scale: 1 mm.

O. cestoides and a small specimen from the pelagic species *Palinurichthys perciformis* whose sucker-ratio fits well within the *O. cestoides*-range (Table 12). The large metacercariae, which may be *O. veliporum*, correspond with the large immature specimens of *O. veliporum* which we record from *Dalatias licha* (Table 13).

A further interesting result is recorded by Dollfus (1937a), who found specimens from *Chimaera monstrosa* off Portugal with a very large presumptive uterine field. Although they come within the range of *O. cestoides*, there is a possibility that they may be metacercariae of *O. plunketi*. The identity of this metacercaria is, however, further complicated by the existence of an adult coelomic form, *O. hydrolagi* Schell, in chimaeras.

We have referred to these metacercariae as *Otodistomum* sp., as we cannot with any confidence attribute them to any species of *Otodistomum*. We consider, however, that the vast majority of the forms recorded in the northeast Atlantic probably belong to *O. cestoides*.

Family HIRUDINELLIDAE Dollfus, 1932

Botulidae Guiart, 1938.
Lampritrematidae Yamaguti, 1940.
Mediolecithidae Oshmarin, 1968.

DIAGNOSTIC FEATURES. Body large; stout or elongate; very contractile. Body-surface smooth, may be papillate in forebody or around suckers and usually wrinkled transversely. Oral and ventral suckers well developed; latter well inside anterior half of body. Prepharynx absent. Pharynx well developed. Oesophagus usually short. Gut-caeca terminate blindly or form uroproct; may fuse subterminally forming a cyclocoel; usually diverticulate. Testes two; in tandem, oblique or symmetrical; pre-ovarian; in hindbody. Seminal vesicle tubular; normally thin-walled, occasionally anterior region may be thick-walled; convoluted in forebody. Pars prostatica well developed; tubular, usually long. Ejaculatory duct long; muscular; surrounded by muscular 'cirrus-sac'; opens into genital atrium through well-developed, conical or cylindrical 'cirrus'. Hermaphroditic duct, sinus-sac and sinus-organ absent. Genital atrium large, usually capable of being everted through genital pore. Genital pore mid-ventral in forebody. Ovary oval; post-testicular; in middle or anterior half of body. Laurer's canal and uterine seminal receptacle normally present (not reported in *Lampritrema*). Mehlis' gland post-ovarian. Juel's organ and canalicular or blind seminal receptacle absent. Uterus descends ventrally and ascends more dorsally; coiled mainly at level of vitellarium; but often extending more anteriorly into pre-ovarian region; mainly inter-caecal, occasionally reaching extra-caecally. Metraterm opens into genital atrium either directly or through a papillate organ immediately posterior to 'cirrus'. Eggs numerous; small; without filaments. Vitellarium composed of two to numerous long, straight or convoluted, branched tubules; mainly post-ovarian; inter- or extra-caecal. Excretory vesicle Y-shaped; stem short; arms initially in dorsal and ventral fields, very convoluted; unite in forebody. Parasitic in stomach (occasionally gills) of large, piscivorous teleosts.

COMMENT. Other workers, such as Yamaguti (1971), have considered that *Hirudinella* de Blainville, 1828, *Botulus* Guiart, 1938, and *Lampritrema* Yamaguti, 1940, form three distinct families. Our observations indicate that these three genera are morphologically very similar and, although we initially intended to distinguish *Lampritrema* at the subfamily level, we believe that the distinguishing features are not significant enough to be used at this level. We consider it likely, therefore, that the family Hirudinellidae consists, at present, of three monotypic genera.

Key to the genera of the Hirudinellidae

1 Body stout, elongate or 'key-hole' shaped; uroproct present; 'cirrus-sac' small, globular;
    seminal vesicle entirely thin-walled 2

– Body slender, very elongate; uroproct absent; 'cirrus-sac' large, elongate; distal part of seminal
    vesicle with muscular wall . . . . . *Lampritrema* Yamaguti, 1940 (p. 213)

2 Vitellarium in two lateral fields between level of testes and mid-hindbody; uterus mainly inter-
    caecal, post-ovarian, at level of vitellarium . . *Hirudinella* de Blainville, 1828 (p. 201)

–   Vitellarium massed close to ventral surface, in single field, inter-caecally between ovary and
    posterior extremity; uterus reaching extra-caecally, mainly in anterior hindbody .   .
    .   .   .   .   *Botulus* Guiart, 1938 (p. 208)

HIRUDINELLA de Blainville, 1828

Hirudinella Garcin, 1730 [Pre-Linnaean; see Gibson, 1976]
Uroproctinella Skrjabin & Guschanskaja, 1957.

DIAGNOSTIC FEATURES. Body stout, elongate or 'key-hole' shaped. Body-surface often transversely
wrinkled. Uproct present; gut-caeca may fuse subterminally in old specimens forming cyclocoel.
Testes symmetrical to oblique; in anterior hindbody. Seminal vesicle thin-walled throughout its
length. 'Cirrus-sac' relatively small; globular. 'Cirrus' conical to digitiform. Genital atrium
capable of being everted through genital pore. Ovary in anterior hindbody. Uterus mainly inter-
caecal; coils extending posteriorly from ovary to near posterior limit of vitellarium. Vitellarium
in two lateral fields between testes and middle of hindbody. Parasitic in stomach of large, pisci-
vorous marine teleosts (usually scombroids).

TYPE-SPECIES. *Hirudinella ventricosa* (Pallas, 1774) (by monotypy).

Hirudinella ventricosa (Pallas, 1774) Baird, 1853

Hirudinella marina Garcin, 1730.
Fasciola ventricosa Pallas, 1774.
Distomum ventricosum (Pallas) Monticelli, 1893.
Distomum ventricosum minor Shipley, 1900.
Fasciola clavata Menzies, 1791.
Distoma clavatum (Menzies) Rudolphi, 1808.
Hirudinella clavata (Menzies) de Blainville, 1828.
Fasciola fusca Bosc, 1802.
Distoma fuscum (Bosc) Poirier, 1885.
Hirudinella fusca (Bosc) Manter, 1926.
Fasciola coryphaenae Bosc, 1802.
Distoma coryphaenae (Bosc) Rudolphi, 1809.
Fasciola coryphaenae hippuridis Tilesius, in Rudolphi, 1809.
Fasciola scombri pelamidis Tilesius, in Rudolphi, 1809.
Distoma heurteli Poirier, 1885.
Distoma dactylipherum Poirier, 1885.
Distoma verrucosum Poirier, 1885.
Distoma personatum Poirier, 1885.
Distoma pallasii Poirier, 1885.
Hirudinella pallasii (Poirier) Guiart, 1938.
Distoma ingens Moniez, 1886.
Hirudinella ingens (Moniez) Darr, 1902.
Distomum validum von Linstow, 1886.
Brachylaemus validum (von Linstow) Stossich, 1892.
Distoma poirieri Moniez, 1891.
Hirudinella poirieri (Moniez) Dollfus, 1935.
Distoma siemersi Buttel-Reepen, 1900.
Hirudinella siemersi (Buttel-Reepen) Skrjabin & Guschanskaja, 1959.
Distoma ampullaceum Buttel-Reepen, 1900.
Hirudinella ampullacea (Buttel-Reepen) Skrjabin & Guschanskaja, 1957.
Hirudinella beebei Chandler, 1937.
Hirudinella spinulosa Yamaguti, 1938.
Uroproctinella spinulosa (Yamaguti) Skrjabin & Guschanskaja, 1957.
Hirudinella oxysoma Guiart, 1938.
Hirudinella phalloidea Guiart, 1938.
Hirudinella bonnacouri Guiart, 1938.
Hirudinella ahi Yamaguti, 1970.
Uroproctinella attenuata Hafeezullah, 1971.

Type-host. Unknown.

Type-locality. Amboyna, South China Sea.

Records.

(i) Material studied

(a) From the NE Atlantic

None.

(b) From elsewhere

Acanthocybium solandri [stomach] Powell Islet, New Guinea (July, 1972). Collected by B. R. Smith. BM(NH) Reg. No. 1973.4.6.13–14.

Acanthocybium solandri [stomach] Zanzibar. Collected by J. F. C. Morgans. BM(NH) Reg. No. 1961.6.26.113–116.

Acanthocybium solandri [intestine] West Coast of Aldabra Atoll, Indian Ocean (Nov., 1974). Collected by C. R. Huxley. BM(NH) Reg. No. 1976.5.17.36–37.

Coryphaena hippurus [stomach] Between New Britain and New Ireland (Aug., 1972). Collected by B. R. Smith. BM(NH) Reg. No. 1973.4.6.12.

Euthynnus affinis [stomach] Cape Liguan, New Britain (May, 1972). Collected by B. R. Smith. BM(NH) Reg. No. 1973.4.6.5.

Euthynnus affinis [gut] Pondo harbour, New Britain (May, 1972). Collected by B. R. Smith. BM(NH) Reg. Nos 1973.4.6.4. and 1973.4.6.9–10.

Euthynnus affinis [stomach] East coast of South Africa (Dec., 1975). Collected by R. van der Elst. BM(NH) Reg. No. 1976.9.21.1.

Euthynnus alletteratus [gut] Port Moresby, New Guinea (Oct., 1971). Collected by B. R. Smith. BM(NH) Reg. No. 1973.4.6.8.

Katsuwonus pelamys [stomach] Locality (?). Unregistered.

Katsuwonus pelamys [gut] Gasmata, New Britain (Dec., 1971). Collected by B. R. Smith. BM(NH) Reg. No. 1973.4.6.1–3.

Katsuwonus pelamys [body-cavity] West Coast of Africa just north of Dakar, Senegal (19°N, 18°W; Oct., 1925). BM(NH) Reg. No. 1975.3.13.123 (see Gibson, 1976 : 232).

Naucrates ductor [?] North of Canary Isles (29°N, 15°W; depth 0–900 m; Oct., 1925). BM(NH) Reg. No. 1975.3.13.124 (see Gibson, 1976 : 232).

Neothynnus macropterus [stomach] Zanzibar (Aug., 1958). Collected by F. Williams. BM(NH) Reg. No. 1960.1.12.63–66.

Scomberomorus commerson [gut] New Guinea (June, 1972). Collected by B. R. Smith. BM(NH) Reg. No. 1973.4.6.11.

Scomberomorus commerson [stomach] NNW of Cape Liguan, New Britain (May, 1972). Collected by B. R. Smith. BM(NH) Reg. No. 1973.4.6.5.

Thunnus albacares [?] Mapelana, Natal, South Africa (May, 1975). Collected by R. van der Elst. BM(NH) Reg. No. 1975.9.17.20.

Thunnus albacares [stomach] Formosa Bay, North of Malindi, Kenya. BM(NH) Reg. No. 1969.11.11.3–4.

'Bonito' [?] Locality (?). BM(NH) Reg. No. 52.10.7.3.

'Bonito' [intestine] St Helena, SE Atlantic. Collected by A. E. Craven. BM(NH) Reg. No. 81.10.8.6–7.

'Dolphin' [liver] Atlantic Ocean. Collected by Capn Fraser. BM(NH) Reg. No. 95.11.15.1 (as *Distomum validum*).

'Kingfish' [stomach] Cosmoledo Is, Indian Ocean (Nov., 1952). BM(NH) Reg No. 1969.11.11.1–2.

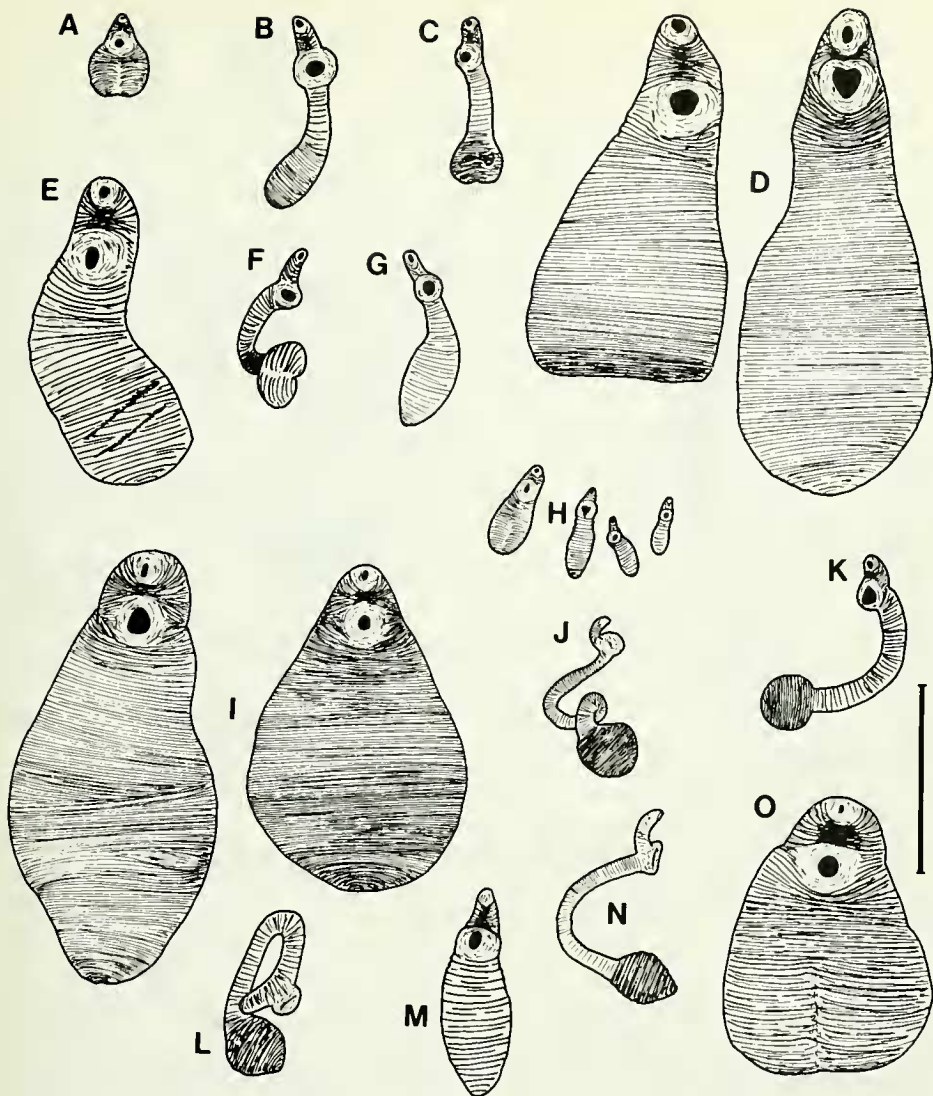Host (?) [?] Atlantic Ocean. BM(NH) Reg. No. 1914.1.22.2–4.

Host (?) [?] 'South of Europe'. BM(NH) Reg. No. 45.9.26.–.

Host (?) [?] Locality (?). BM(NH) Reg. No. 1914.1.22.1.

(ii) NE Atlantic records from the literature

Thunnus alalunga [stomach] Northern Bay of Biscay (47°N, 10°W; Sept., 1888). Guiart (1938 : 30; as *Hirudinella fusca*).

Thunnus alalunga [stomach] West of Cape Finistere, Spain (44°N, 13°W; July, 1888). Guiart (1938 : 31; as *Hirudinella poirieri*).

Fig. 10 Representatives of *Hirudinella ventricosa* from the collection of the British Museum (Natural History) to illustrate some of the variations in size and shape which occur in fixed specimens: (A) ex stomach of *Coryphaena hippurus* off New Guinea; (B) ex *Thunnus albacares* off Natal, South Africa; (C) ex intestine of *Katsuwonus pelamys* off St Helena; (D) two specimens ex stomach of 'Kingfish' off Cosmoledo Is, Indian Ocean; (E) ex unknown host from '? South of Europe'; (F) ex 'Bonito'; (G) ex unknown host from Atlantic Ocean; (H) four specimens ex stomach of *Thunnus albacares* off Zanzibar; (I) two specimens ex stomach of *Acanthocybium solandri* off Zanzibar; (J) ex gut of *Euthynnus affinis* off New Guinea; (K) ex stomach of *Scomberomorus commerson* off New Guinea; (L) ex gut of *Katsuwonus pelamys* off New Guinea; (M) ex 'Liver of Dolphin' from Atlantic Ocean (specimen labelled '*Distomum validum*'); (N) ex gut of *Euthynnus alletteratus* off New Guinea; (O) ex stomach of *Thunnus albacares* off Kenya. Scale: 20 mm.
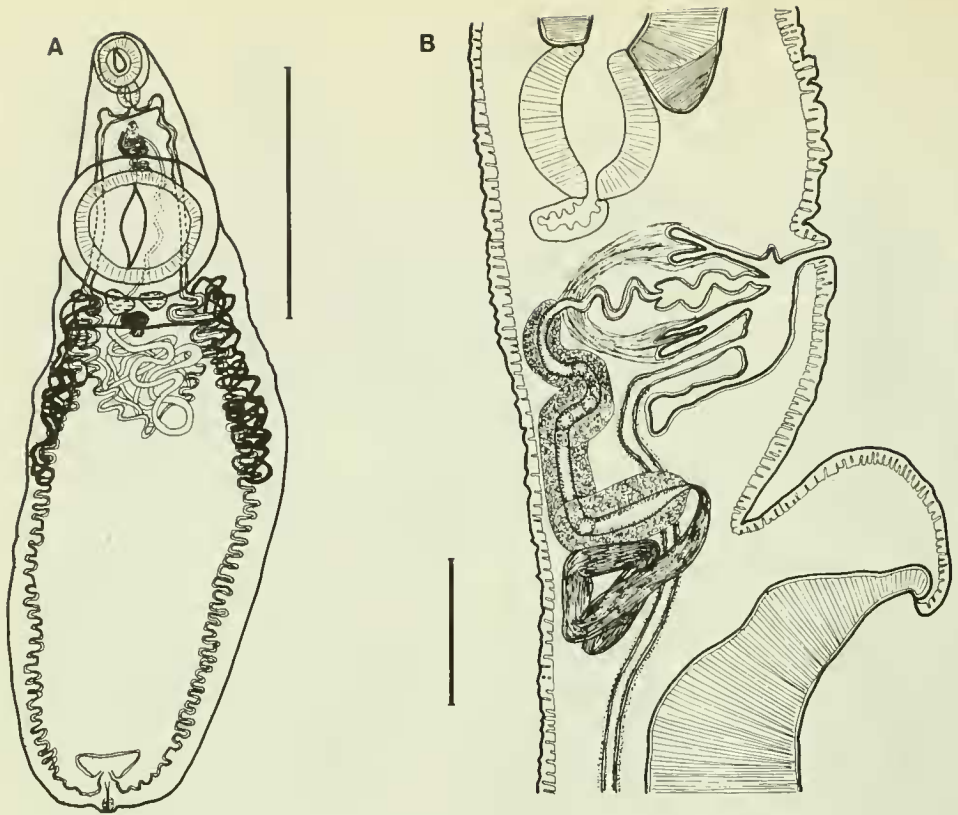
Fig. 11 *Hirudinella ventricosa* ex *Naucrates ductor* off Canary Isles: (A) internal details of worm reconstructed from sections; (B) sagittal section of terminal genitalia. Scale: (A) 10 mm; (B) 1 mm.

Thunnus alalunga [?] Concarneau, southern Brittany, France. Dollfus (1940 : 278; as *Hirudinella fusca*).

Thunnus alalunga [?] Golfe de Gascogne, Bay of Biscay. Aloncle & Delaporte (1970 : 297; 1973 : 568; 1974 : 10; as *Hirudinella fusca*).

Thunnus alalunga [?] Cote Cantabrique, Bay of Biscay, northern Spain. Aloncle & Delaporte (1970 : 297; as *Hirudinella fusca*).

Xiphias gladius [?] Norfolk, England (Aug., 1863). Cobbold (1867 : 200; 1883 : 404; as *Distoma clavatum*).

Although recorded from only two fishes in the northeast Atlantic region, it is likely that this parasite also occurs in *Katsuwonus pelamys*, *Euthynnus alletteratus*, *Coryphaena hippurus*, *Sarda sarda* and *Thunnus thynnus*, especially in the southern latitudes of this region. There are several 19th-century records of this parasite (see Nigrelli & Stunkard, 1947) from these hosts in the Atlantic Ocean, but the precise region is not listed.

ASPECTS OF BIOLOGY. The life-history of this species is not known. Aloncle & Delaporte (1970, 1973, 1974) have used this parasite as a 'biological tag'.

PREVIOUS DESCRIPTIONS. Poirier (1885 : 471; as *Distoma clavatum, D. verrucosum, D. pallasii*, etc.); Moniez (1886 : 531; as *D. ingens*); Buttel-Reepen (1900 : 586; 1902 : 175; as *D. ampullaceum* and *D. siemersi*); Darr (1902 : 670; as *D. clavata*); Mühlschlag (1914 : 232; as *D. ingens*); Chandler (1937 : 348; as *Hirudinella beebei*); Yamaguti (1938b : 40; as *H. spinulosa*: 1970 : 150; as *H. ahi* and *H. beebei*); Guiart (1938 : 28; as *H. phalloidea, H. fusca, H. poirieri* and *H.* sp.); Nigrelli & Stunkard (1947 : 189; as *H. marina* and *H. ventricosa*); Manter (1947 : 365); Hafeezullah (1971 : 76; as *Uroproctinella attenuata*); Gibson (1976 : 232).

DESCRIPTION (Figs 10 & 11). This giant species of digenean is very variable in both size and shape. Small fixed specimens, which are still large when compared to most other digeneans, tend to be elongate and usually possess a bulbous terminal portion (Fig. 10). The larger fixed specimens tend to be more robust and oval, but with the hindbody much broader than the forebody. Due to the great size of these worms, and the relatively weakly-muscled nature of the hindbody, larger specimens often become distorted during fixation, sometimes being flattened posteriorly or laterally where the specimens have rested on the base of the receptacle (Fig. 10D). Live specimens are reported to be extremely variable in shape. Nigrelli & Stunkard (1947), for example, note the following: 'Extended, it measures 170 mm long by 30 mm wide and it contracted to a length of only 40 mm . . . . When the worm was held up by the anterior end, the cecal contents passed to the posterior end which swelled in a balloon-like fashion. When placed in 10 % formalin it contracted vigorously and when fixed it measured 98 by 40 mm. . . .'

The body-surface is smooth, although contracted live and fixed specimens are usually encircled by dermal folds (rugae). In addition, small papillae may be apparent, especially around the suckers. Beneath the thick tegument there is a thick interstitial matrix and several muscle-layers. A difference between the musculature of the body-wall in the fore- and hindbodies is apparent (see Gibson, 1976). In the forebody there are four layers of muscles: (1) circular; (2) outer longitudinal; (3) diagonal; and (4) inner longitudinal. In the hindbody, the outer layer of longitudinal muscles is very weakly developed and the diagonal muscles are very reduced and indistinguishable from the circular muscles which are reduced and sparse. The fibres appear to be hollow. The measurements of this species are given in Table 14.

The *oral* and *ventral suckers* are well developed, both being overlain by folds of the body wall. The oral sucker, which opens subterminally, is much smaller than the ventral sucker and the forebody is relatively short. There is no prepharynx, the well-developed *pharynx* is oval and the oesophagus short and narrow. The two gut-caeca each form a glandular sac (Drüsenmagen) in the 'shoulder'-regions, before running posteriorly. In the forebody, the caeca are usually relatively narrow and sinuous, but in the hindbody they dilate forming very large sac-like structures with small external diverticula (Fig. 11A). Close to the posterior extremity the caeca unite with the excretory vesicle through narrow ducts to form a uroproct. In mature specimens the caeca appear to be fused medially throughout much of the hindbody. In the majority of specimens the caeca contain the black residues of digesting blood.

The *excretory system* is very complex and difficult to follow, especially as the vesicle is almost obliterated by the giant sac-like gut. The terminal excretory pore leads into a (?) Y-shaped vesicle, the stem of which is probably short. The (?) two arms, which initially appear to be in dorsal and ventral fields, follow a very convoluted course extra-caecally throughout the hindbody. They pass into the forebody where they are sinuous, slightly wider and appear to unite dorsally to the oral sucker. This system is further complicated by the presence of two other much narrower systems of branching tubules (see Gibson, 1976): these may be branches of the excretory system or possibly a lymphatic system, a feature common in very large digeneans.

The two relatively small, oval *testes* are situated symmetrically just posteriorly to the ventral sucker (Fig. 11A). The small, tubular and convoluted seminal vesicle lies antero-dorsally to the anterior margin of the ventral sucker. This may be situated a little further forward, especially in immature forms, but its actual position depends somewhat upon the degree of contraction of the body. There is a long, tubular and convoluted or sinuous pars prostatica, which may be slightly wider in its mid-region. It is surrounded by a broad layer of gland-cells, which are strictly delimited by the surrounding tissue. There is a large, diffusely-muscled 'cirrus-sac', which surrounds the male terminal genitalia; this appears to be absent or very poorly developed in immature forms.

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Table 14 Dimensions of *Hirudinella ventricosa* given in the literature.

Authority	Buttel-Reepen (1902)	Chandler (1937)	Yamaguti (1938b)	Manter (1947)	Nigrelli & Stunkard (1947)
Name used	*Distomum ampullaceum*; *D. siemersi*; *D. ingens*	*Hirudinella beebei*	*Hirudinella spinulosa*	*Hirudinella ventricosa*	*Hirudinella marina*; *H. ventricosa*
Host	(?) *Coryphaena* sp.; (?) *Sphyraena barracuda*	*Acanthocybium petus*	*Thunnus alalunga*	*Coryphaena hipparus*	Various scombriform fishes
Locality	(?) Indian and Atlantic Oceans	Bermuda	Pacific Ocean	Tortugas, Florida	Various
Number of specimens	?	1	20	1	56
Length (mm)	33–60	32	up to 37	22·5	8·5–98
Breadth (mm)	16–22	19–20	up to 5·5	8·5	2–40
Forebody (mm)	–	–	–	–	–
Oral sucker (mm)	0·8–1·5 diam.	2·35 depth	1·12–1·7 diam.	1·74 diam.	2–4 diam. (not full range)
Ventral sucker (mm)	3–4 × 3	4 depth	2·5–3·6 diam.	3·88 diam.	3–7·5 diam. (not full range)
Pharynx (mm)	–	1·35 diam.	0·6–0·87 × 0·58–0·75	–	–
Testes (mm)	–	1·7 × 3–3·5	0·8–1·1 × 1·1–1·7	–	–
Ovary (mm)	–	1·5 × 2·5–3	0·8 × 1·0–1·7	–	–
Eggs (μm)	38–39·5 × 23	35–37 × 24–26	39–47 × 21–24	33 × 19	31–44 × 19·5–24

Authority	Yamaguti (1970)	Yamaguti (1970)	Yamaguti (1970)	Yamaguti (1970)	Gibson (1976)
Name used	*Hirudinella ahi*	*Hirudinella beebei*	*Hirudinella marina*	*Hirudinella ventricosa*	*Hirudinella ventricosa*
Host	*Neothunnus macropterus*	*Acanthocybium solandri*	*Katsuwonus pelamys*		*Naucrates ductor*
Locality	Hawaii	Hawaii	Hawaii		Canary Isles
Number of specimens	1	2	5		1
Length (mm)	28	16–22	45–55		31
Breadth (mm)	4	5–6	5–7		10
Forebody (mm)	–	–	–		4·4
Oral sucker (mm)	1·15 × 1·7	1·0–1·2 × 1·3–1·6	1·3–1·7 × 1·4–2·0		1·45 × 1·3 (depth)
Ventral sucker (mm)	3·7 diam.	2·3–2·5 × 2·4–2·8	2·5–3·0 × 2·8–3·0		3·4 × 2·0 (depth)
Pharynx (mm)	0·6 diam.	0·6 diam.	0·7–0·85 × 0·55–0·75		0·8 diam.
Testes (mm)	0·56–0·8 × 0·8–1·1	0·33–0·41 × 0·3–0·54	0·5–1·0 × 0·4–0·85		1·1 × 0·8 (depth)
Ovary (mm)	0·75 × 0·95	0·13 × 0·25	0·5–0·9 × 0·5–0·75		0·5 × 0·3 (depth)
Eggs (μm)	35–42 × 18–24	39–42 × 23–26	23–33 × 18–23*		30–36 × 20–22

Due to the extreme morphological variability of this species, the value of this table is severely limited.
* 28–35 × 20–24 in live material.

As the male duct passes through the wall of the 'cirrus-sac', it assumes the form of an ejaculatory duct. This duct passes forward sinuously within the 'cirrus-sac' and into a well-developed conical 'cirrus', which projects into a large, wide genital atrium and may be surrounded by a small collar (Fig. 11B). The small genital aperture is situated mid-ventrally, close to the middle of the forebody.

The small, oval *ovary* is situated immediately posteriorly to the testes. Posteriorly to the ovary, Laurer's canal and the common vitelline duct unite with the oviduct prior to its entry into the small, oval Mehlis' gland. Laurer's canal opens dorsally, having followed a long, convoluted course. There is no blind or canalicular seminal receptacle. No spermatozoa were seen in the uterus of our sectional material, but as a uterine seminal receptacle was reported by Yamaguti (1938b) in his description of *H. spinulosa* and is present in the closely related genus *Botulus* (see below), we can be confident that it usually occurs. The *uterus* is coiled intercaecally in a space between the gonads and the anterior margin of the union of the gut-caeca in the hindbody. Dorsally to the posterior half of the ventral sucker the diameter of the uterus is reduced and it forms a metraterm which passes forward. Short villous projections line the metraterm, which is surrounded by small gland-cells. Just dorsally to the genital atrium, but posteriorly to the 'cirrus-sac', the metraterm loses its villous lining and outer gland-cells, acquires a cuticular wall and leads into the genital atrium through a finger-like process, which is often flattened distally (Fig. 11B). Whereas in mature specimens this female process is not closely associated with the 'cirrus', in immature forms, before the development of the 'cirrus-sac', these two organs may be fused over much of their length. Both male and female organs may be everted together through the genital pore (see Nigrelli & Stunkard, 1947 : Fig. 2); but they are usually withdrawn. The eggs, considering the size of the worm, are very small. According to Moniez (1891) and Nigrelli & Stunkard (1947), egg-size is correlated with the size of the worm, although Nigrelli & Stunkard present a table which does not show this correlation. Egg-size is, therefore, probably too variable to serve as a reliable specific character. The tubular vitellarium forms two regions lying extra-caecally and symmetrically, between the posterior margin of the ventral sucker and the middle of the body.

DISCUSSION. The name *Hirudinella ventricosa* (Pallas, 1774) has been accepted by Gibson (1976) as the oldest available name for this species, as *H. marina* Garcin, 1730, is pre-Linnaean. Over the course of the past century there has been a certain amount of controversy over the number of species in this genus. Following the work of Moniez (1891) and Buttel-Reepen (1900, 1902), Nigrelli & Stunkard (1947), in their revision of the genus, considered that there were only two valid species, despite the large number of species attributed to the genus in the past. Recently, however, in line with the thoughts of some early workers, such as Cobbold (1879) and Blanchard (1891a, 1891b), Gibson (1976) has suggested that there is no substantial reason for accepting the presence of more than one species in the genus *Hirudinella*. We accept the latter opinion until there is substantial proof to indicate the presence of a second species. The great variability in shape and size appears to have led to the confused situation with regard to the taxonomy of the worm. The weak circular muscle in the hindbody and the fusion of the gut-caeca in the hindbody of larger individuals may account for the tendency they show to differ in shape from the smaller ones (Fig. 10). In addition, significant changes in the shape of the hindbody can be caused by differences in the orientation of the specimens or small changes in the contraction of the longitudinal musculature, when the voluminous gut-caeca are distended with the very fluid residues of digesting blood.

It is noticeable that there is a certain morphological similarity between *H. spinolusa* of Yamaguti (1938b) from *Thunnus alalunga*, *Uroproctinella attenuata* of Hafeezullah (1971) from *Neothunnus macropterus* and *H. marina* of Caballero y C. & Caballero R. (1971) from *Euthynnus lineatus*. Yamaguti claimed that his material possessed body-spines, Hafeezullah noted that spines were 'very sparse' and Caballero y C. & Caballero R.'s material was covered with digitiform papillae. We have examined material from *Euthynnus affinis* (Fig. 10J), *E. alletteratus* (Fig. 10N), *Neothunnus macropterus*, *Thunnus albacores* (Fig. 10H & O) and several other scombrids. Although some are morphologically similar to the specimens described by these authors, there is a variety of shapes present. Certainly papillae are apparent in certain specimens, especially around the oral and ventral suckers; but some of these papillae and the rugate nature of contracted material can present a spinulate appearance when viewed from certain angles, and it is possible that these papillae may be extensible under certain conditions. In addition, as pointed out by Gibson

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(1976 : 234 footnote), the apparent spines in Yamaguti's material may have been caused by subtegumentary projections exposed after the loss of the tegument.

We have listed *Distomum validum* von Linstow, 1886, as a synonym of *H. ventricosa* despite the fact that it has been placed in *Brachylaemus* Dujardin, 1843, by workers such as Stossich (1892) and ('*sub judice*') by Yamaguti (1971), because the original description, although very incomplete, resembles the latter species very strongly. *D. validum* was described by von Linstow (1886) from a species of *Delphinus*. At first sight this appears to be a peculiar host for *Hirudinella*; but a search of the literature revealed that the original description of *D. pallasii* by Poirier (1885), a readily recognizable synonym of *H. ventricosa*, was based on material from *Delphinus phocaena* (= *Phocaena phocaena*). Similarly, *D. ampullaceum* Buttel-Reepen, 1900, was originally recorded from a cetacean. As it seems unlikely that a digenean parasite of teleosts could survive for long in a mammalian host, it must be assumed that these were accidental infestations acquired from the teleost-prey. There is, however, another possibility, as we consider that there may been have some confusion with regard to the common name of the host. The appellation 'dolphin', in addition to being the vernacular name for certain species of cetaceans, is also a vernacular name of the teleost *Coryphaena hippurus*, which is one of the normal hosts of *H. ventricosa*, and may have been applied by 19th-century fishermen to various scombroids. If the collector had recorded 'dolphin', then this would have been ambiguous for later workers. As an example, we have in the collection of the British Museum (Natural History) one specimen of *D. validum*, collected in the 19th century, the host of which is listed as 'dolphin'. The confusion between the vernacular names of *Coryphaena* and *Delphinus* has been appreciated for many years and was pointed out by Forster, in Osbeck (1771 : 117); but, although some authors now refer to *Coryphaena* as the 'dolphin-fish', this confusion still exists. For the above reason, Price (1932) did not include *Distoma validum*, *D. pallasii* or *D. ampullaceum* in his monograph on the trematode parasites of marine mammals.

BOTULUS Guiart, 1938

Profundiella A. S. Skrjabin, 1958.
Mediolecithus Oshmarin, 1968.

DIAGNOSTIC FEATURES. Body normally stout. Uroproct present. Testes symmetrical to oblique; in anterior hindbody; relatively large. Seminal vesicle thin-walled throughout its length. 'Cirrussac' relatively small; globular. 'Cirrus' conical to digitiform. Genital atrium often everted through genital pore. Ovary in anterior hindbody. Uterus reaching extra-caecally in anterior hindbody. Vitellarium a densely tangled mass of tubules in one ventral, inter-caecal field between ovary and posterior extremity. Parasitic in stomach of large piscivorous marine teleosts (*Alepisaurus*) and (?) accidentally in piscivorous sharks.

TYPE-SPECIES. *Botulus microporus* (Monticelli, 1889) n. comb. (by monotypy).

COMMENT. A certain amount of discussion has centred around the systematic position of *Botulus* and its synonyms. Giuart (1938) erected a new family, related to the Azygiidae and Hirudinellidae, for this genus. Stunkard (1965) considered the Botulinae to be a subfamily within the Hirudinellidae and synonymous with the Profundiellinae, which has been erected, within the Dinuridae, by A. S. Skrjabin (1958) for *Profundiella*. Yamaguti (1971) maintained the Botulidae as a distinct family, and recently Parukhin & Nikolaeva (1974) considered the Botulinae a subfamily within the Dinuridae and accepted the appelations Profundiellinae and Mediolecithidae, erected by Oshmarin (1968) for *Mediolecithus*, as synonyms. In our opinion (Gibson, 1976; Gibson & Bray, in preparation), *Botulus* is a monotypic genus within the Hirudinellidae which cannot be distinguished from *Hirudinella* and *Lampritrema* at the subfamily level. A main reason for recent major disagreements in the systematic position of *Botulus* is the erroneous descriptions of the terminal genitalia. Contrary to all the previous detailed descriptions of the genus, there is no sinus-sac or hermaphroditic duct present.

Botulus microporus (Monticelli, 1889) n. comb.

Distoma microporum Monticelli, 1889.

Apoblema microporum (Monticelli) Monticelli, 1891.
Hemiurus microporum (Monticelli) Looss, 1899.
Botulus alepidosauri Guiart, 1938.
Profundiella skrjabini A. S. Skrjabin, 1958.
Botulus skrjabini (A. S. Skrjabin) Parukhin & Nikolaeva, 1974.
Botulus cablei Stunkard, 1965.
Profundiella alepisauri Parukhin & Nikolaeva, 1967.
Botulus skrjabini alepisauri (Parukhin & Nikolaeva) Parukhin & Nikolaeva, 1974.
Mediolecithus pacificus Oshmarin, 1968.

Type-host and locality. *Alepisaurus ferox.* Madeira,

Records.

(i) Material studied
(a) From the NE Atlantic
Alepisaurus ferox [stomach] SE coast of Iceland. (depth 46 m). BM(NH) Reg. No. 1976.5.12.35–36.
(b) From elsewhere
Alepisaurus ferox [?] Madeira. Type-specimens of *Distoma microporum* Monticelli, 1889. BM(NH) Reg. No. 1914.4.22.1–6.
Alepisaurus ferox [stomach] Off Miami Beach, Florida. (Nov., 1964). Specimens donated by Dr R. M. Overstreet. BM(NH) Reg. No. 1976.5.11.3–6.
(ii) NE Atlantic records from the literature
None.

Aspects of biology. The life-history of *B. microporus* is not known. This species appears to be restricted to *Alepisaurus* spp., where they normally occur in the stomach. Oshmarin (1968), however, recorded a single specimen, which he named *Mediolecithus pacificus*, in the shark *Lamna cornubica*; but this, as Parukhin & Nikolaeva (1974) suggest, was probably an accidental infestation. Recently, Aleshkina (1976) claimed to have found *Botulus* sp. in *Thunnus obesus* from the 'equatorial and tropical' region of the Atlantic Ocean, and Parukhin (1976) records a specimen under the name *Botulus skrjabini* from the ovary of *Coryphaenoides striatura* off the east coast of Africa. As these worms were not described we do not know, assuming that they were correctly determined, whether they were adults or larvae, or whether these hosts were accidentally infested or form part of the life-history of this parasite. Aleshkina (1976) also records *Botulus* sp. from *Alepisaurus ferox* and *A. brevirostris* (as *A. breviductus*).

Previous descriptions. Monticelli (1889 : 322); Guiart (1938 : 26; as *Botulus alepidosauri*); A. S. Skrjabin (1958 : 340; as *Profundiella skrjabini*; English translation in K. I. Skrjabin & Guschanskaja, 1960 [1965] : 295); Stunkard (1965 : 488; as *Botulus cablei*); Parukhin & Nikolaeva (1967 : 757; as *Profundiella alepisauri*; 1974 : 117, as *Botulus skrjabini alepisauri*); Oshmarin (1968 : 272; as *Mediolecithus pacificus*).

Description (Fig. 12). These are very large, usually spindle-shaped worms; but they may vary between oval and almost cylindrical (Fig. 12), depending on the degree of contraction during fixation. They are circular or oval in cross-section. The relatively short forebody is much narrower than the hindbody: in some of the type-specimens the forebody is extended, thus giving the specimens an ampullaceous outline. In many specimens the oral sucker and pre-oral lobe form a short, subterminal, ventrally directed proboscis-like protrusion. The unarmed body-surface may be transversely wrinkled. The measurements of this species are given in Table 15.

As in *Hirudinella* the musculature of the body-wall differs in the fore- and hindbodies. In the forebody the muscle-layers occur as follows: (1) outer circular; (2) longitudinal; and (3) inner circular and/or diagonal. The inner layer of longitudinal muscles, present in *Hirudinella*, appears to be absent in *Botulus*. The musculature of the hindbody is similar to that in *Hirudinella*: there is a very poorly-developed layer of circular muscle, external to a narrow, but relatively well-developed, layer of longitudinal muscle.

A pre-oral lobe is present. The musculature of the well-developed oral and ventral suckers is overlain by the body-wall. The *oral sucker* is significantly smaller than the *ventral sucker*. The
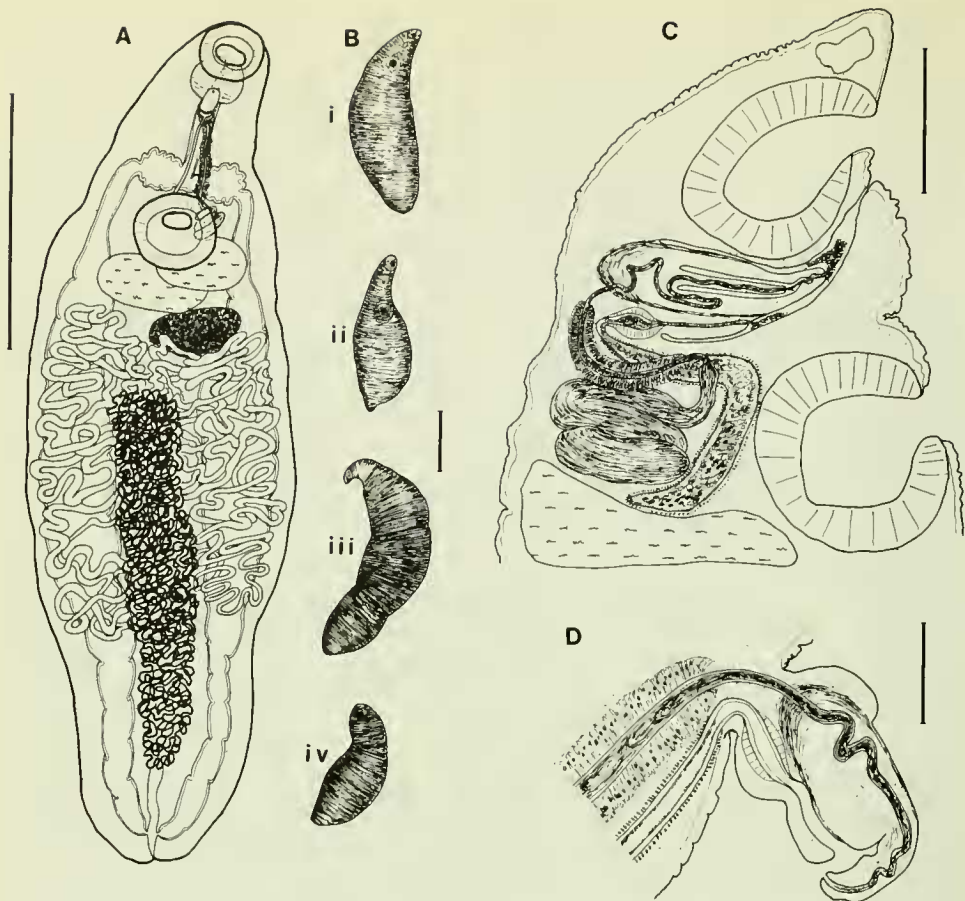
Fig. 12 *Botulus microporus* ex *Alepisaurus ferox*: (A) internal details of worm reconstructed from sections (Iceland); (B) specimens from various localities; (i) off Iceland; (ii) off Madeira (type-specimen); (iii) and (iv) off Miami Beach, Florida; (C) sagittal section of forebody showing terminal genitalia (Miami Beach); (D) sagittal section showing extruded genital atrium (Iceland). Scale: (A, B) 10 mm; (C) 1 mm; (D) 300 μm.

former, which is usually protruded ventrally, leads dorsally or postero-dorsally directly into a large muscular *pharynx*. An oesophagus of variable length, lined with thick, irregular cuticle, leads in an antero-dorsal to posterior direction, depending on contraction, to join the bifurcation of the gut-caeca. The caeca form 'Drüsenmagen' in the 'shoulder'-region, before running into the hindbody, where they dilate considerably and possess greatly folded walls. They are lined with a layer of very long, darkly staining, glandular, villous epithelium. Close to the posterior extremity the caeca are connected to the stem of the excretory vesicle by narrow ducts to form a uroproct (Fig. 12A). The caeca do not appear to fuse medially, as occurs in the larger specimens of *Hirudinella*, for they are separated over much of their length by the vitellarium.

The terminal excretory pore leads into a short, sinuous or sigmoid stem of the *excretory vesicle*. It reaches forward to about the level of the posterior extremity of the vitellarium, where it divides giving off dorsal and ventral arms. These arms are extremely convoluted and very difficult to follow; but they appear to pass dorsally and ventrally within the hindbody. In the forebody,

Table 15 Dimensions of *Botulus microporus* from the present material and from the literature.

Authority	Type-specimens	Guiart (1938)	A. S. Skrjabin (1958)	Stunkard (1965)	Parukhin & Nikolaeva (1967)	Oshmarin (1968)	Present material	
Name used	*Distomum microporum*	*Botulus alepidosauri*	*Profundiella skrjabini*	*Botulus cablei*	*Profundiella alepisauri*	*Mediolecithus pacificus*	*Botulus microporus*	
Host	*Alepisaurus ferox*	*Alepisaurus ferox*	*Alepisaurus aesculapius*	*Alepisaurus borealis*	*Alepisaurus* sp.	*Lamna cornubica*	*Alepisaurus ferox*	
Locality	Madeira	Madeira	Pacific Ocean	Easter Island, South Pacific	Gulf of Mexico	NW Pacific	Miami, Florida	Iceland
Number of specimens	2 of 6 (remainder twisted)	1 of 2	1 of (?)	13	4	1	4 (contracted)	2 (contracted)
Length (mm)	19–25 (20–32)*	27	18·4	11–33·5	23–40	27	11–35	19–31·5
Breadth (mm)	7–9	7	4·0	6·5–12·0	13–15	10	5–11	6–10·5
Forebody (mm)	5–7	—	—	—	—	—	2·3–5	4·2–7
Oral sucker (mm)	extended 1·9–2·3 × 1·7–2·2	—	1·6 diam.	0·9–1·5 diam.	1·35–1·77 × 1·12–2·00	2·22 × 2·34	1·5–2·6 × 1·2–1·7	2·3 × 1·8–2·8
Ventral sucker (mm)	2·3–2·7 × 2·0–2·8	—	1·7 diam.	1·44–2·25 diam.	1·72–2·56 × 1·96–2·66	2·31 × 2·61	1·3–2·5 × 1·3–2·8	2·8–3·1 × 2·5–2·8
Pharynx (mm)	—	—	1·15 × 1·3	—	1·5–1·26 × 1·68	1·62 × 1·98	—	1·5–1·9 × 1·7
Testes (mm)	—	—	2·4 × 1·6	—	2·1–3·08 × 0·84–4·06	1·2 × 3·4 and 1·76 × 2·2	—	—
Ovary (mm)	—	—	1·6 × 1·1	1·0–1·6 × 1·5–1·75	3·3–6·4 × 1·5–2·0	1·6 × 2·2	—	—
Eggs (µm)	35–37 × 26–27	—	36–38 × 23–28	30–34 × 23–25	35–38 × 22–26	30–38 × 19–28	33–36 × 24–28	33–38 × 22–27

* Figures in parentheses from Monticelli (1889).

where they are still extremely convoluted, they appear to pass laterally and unite dorsally or antero-dorsally to the oral sucker. A small number of muscular ducts are also present within the hindbody; but it is not known whether they are branches of the excretory system or some form of lymphatic system.

The two *testes* are usually situated symmetrically to obliquely, with the left usually being slightly antero-dorsally to the right, immediately posterior or postero-dorsal to the ventral sucker. A relatively large, convoluted, tubular seminal vesicle lies dorsally to the ventral sucker. It leads into a tubular pars prostatica, which is surrounded by a delimited layer of gland-cells and lined with anuclear cells. The pars prostatica leads directly or sinuously anteriorly towards the wall of a diffusely muscled 'cirrus-sac' which surrounds the base of a large, muscular 'cirrus' (Fig. 12C). Just prior to reaching the wall of the 'cirrus-sac', the male duct assumes the form of an ejaculatory duct which passes into the 'cirrus-sac' and opens terminally on the 'cirrus'. The 'cirrus' is peculiar in that it can be invaginated within itself, thus forming a 'cirrus' within a 'cirrus' (Fig. 12C); this is presumably a mechanism associated with the protrusion and storage of a copulatory organ capable of great extension, while requiring only a relatively small 'cirrus-sac' (cf. *Lampritrema*). There is a well-developed genital atrium (Fig. 12C), which is often completely everted (Fig. 12D), and is thus capable of adding length to the 'cirrus'. The genital pore lies mid-ventrally just posterior to the oral sucker.

The *ovary* is transversely oval and lies immediately postero-ventral to the testes, medially or submedially towards the left side of the body. From the postero-dextral margin of the ovary a short oviduct passes, entering a large Mehlis' gland almost immediately. Just within Mehlis' gland it receives the common vitelline duct and Laurer's canal. The muscular Laurer's canal, which may be dilate proximally, winds dorsally to the ovary and opens on the dorsal surface just posteriorly to the testes. The common vitelline duct is fed by a large reservoir lying dorsally to the anterior extremity of the vitellarium. Mehlis' gland extends a short distance along the first part of the uterus, which may be convoluted. Egg and egg-shell formation occur in the next part of the uterus, which we refer to as the uterine ootype*. This region also contains spermatozoa and leads into a broader region of the uterus, the uterine seminal receptacle, which is packed with spermatozoa. The *uterus* then widens further and leaves the region of the ovary, passing posteriorly to a level about two-thirds of the distance from the ventral sucker to the posterior extremity. This region of the uterus is greatly convoluted, lying mainly in the ventral plane, and reaches towards the lateral margins of the body, overlying the caeca. It then passes anteriorly and, as it approaches the level of the ovary, it passes dorsally and begins to develop a thick, muscular wall, forming a metraterm. The metraterm, which is surrounded by gland-cells and lined with a villous epithelium, runs forward either sinuously or directly towards the base of the 'cirrus-sac'. Here it loses its sheath of gland-cells and turns to run, parallel with, but posterior to, the 'cirrus-sac' through a duct, the proximal region of which has a thick, muscular wall (Figs 12C & D). This duct opens into the genital atrium about halfway along the main body of the male organ, but external to the 'cirrus-sac'. When the genital atrium is everted the female pore is protruded through the genital pore with the 'cirrus'. In one of the sectioned specimens spermatozoa could be seen in the genital atrium and inside the metraterm (Fig. 12C). The uterus contains numerous, relatively small, non-filamented eggs. The *vitellarium* consists of many tightly coiled tubules, which fill the ventro-median region of the worm between a level just posteriorly to the ovary and a short distance from the posterior extremity.

DISCUSSION. The two specimens of *Botulus alepidosauri* originally described by Guiart (1938) were in poor condition (they were dried out) and this prohibited a sound description. We have, however, been able to examine specimens of *Botulus* from the type-host, *Alepisaurus ferox*, and this has allowed us to refine the concept of the genus (see Gibson & Bray, in preparation). We have also examined the type-specimens of *Distoma microporum* Monticelli, 1889, which were collected from the type-host (*A.* [=*Plagyodus*] *ferox*) and type-locality (off Madeira) of *B. alepidosauri*.

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* In a small sectioned specimen from *A. ferox* off Florida, the proximal region of the uterus contains a tubular, convoluted structure which extends into the uterine seminal receptacle. This may be the detached lining of the female duct from within Mehlis' gland. Distally it can be seen to contain very small eggs which apparently swell to normal size on release. No sign of this structure was found in a larger sectioned specimen.

Although *D. microporum* has been listed as a species of *Hemiurus* by authors such as Looss (1899) and Yamaguti (1971), our examination has convinced us that it is a senior synonym of *B. alepidosauri*.

The genus *Profundiella* was erected for a new species, *P. skrjabini*, from *Alepisaurus aesculapius* (possibly a synonym of *A. ferox*) in the Pacific Ocean by A. S. Skrjabin (1958). There appears to be no significant difference between this genus and *Botulus*, except for the reported presence of a globular seminal vesicle in the former; if true this would be an unusual feature in a 'primitive' hemiuroid (see Gibson & Bray, in preparation). A second species, *P. alepisauri*, was described by Parukhin & Nikolaeva (1967) from *Alepisaurus* sp. in the Gulf of Mexico (*A. ferox* appears be to the only species of the genus recorded in this region); but this species possesses a seminal vesicle which is tubular and coiled. Through the generosity of Dr R. M. Overstreet we have been able to examine specimens of *Botulus* from off Miami Beach, Florida, and these appear to be indistinguishable from *B. microporus*. We agree, therefore, with Stunkard (1965) and Parukhin & Nikolaeva (1974), who consider *Profundiella* a synonym of *Botulus*, and in addition we consider *P. skrjabini* and *P. alepisauri* to be synonyms of *B. microporus*.

In 1965 Stunkard described *B. cablei* from *Alepisaurus borealis* (possibly a synonym of *A. ferox*) near Easter Island in the south-eastern Pacific Ocean. This species appears to be indistinguishable morphologically from *B. microporus*.

In agreement with Parukhin & Nikolaeva (1974), we are of the opinion that *Mediolecithus pacificus* Oshmarin, 1968, known from a single specimen from *Lamna cornubica* in the northwest Pacific Ocean, is also *Botulus* and we consider further that it is probably a specimen of *B. microporus* accidentally swallowed by this piscivorous host.

LAMPRITREMA Yamaguti, 1940

DIAGNOSTIC FEATURES. Body very elongate, slender. Papillae present on surface of forebody. Uroproct absent. Testes in tandem; near middle of hind body. Most of seminal vesicle thin-walled, but distal portion forms thick-walled, muscular 'pars musculosa'. Thick-walled pars prostatica lies ventrally to posterior part of 'cirrus-sac'. Male duct leads into 'cirrus-sac' some distance from its posterior extremity. 'Cirrus-sac' very large, elongate; club-shaped. 'Cirrus' long or short; capable of being extended through genital pore. Genital atrium deep. Ovary near middle of hindbody. Laurer's canal (?) absent. Uterine seminal receptacle (?). Uterus extends back to near posterior limit of vitellarium; mainly coiled intercaecally in post- and pre-ovarian regions of hindbody. Vitellarium a pair of lateral tubules with short, dorsal branches; mainly extra-caecal; passing posteriorly to ovary about halfway to posterior extremity. Parasitic in stomach (occasionally on gills) of marine teleosts (*Lampris* and *Brama*). Immature forms recorded from salmonoids.

TYPE-SPECIES. *Lampritrema miescheri* (Zschokke, 1890) (by monotypy).

Lampritrema miescheri (Zschokke, 1890) Margolis, 1962

Distomum miescheri Zschokke, 1890.*
Lampritrema nipponicum Yamaguti, 1940.
Lampritrema atlanticum Delyamure & Serdyukov, 1970.
Lampritrema hawaiiense Yamaguti, 1970.

TYPE-HOST AND LOCALITY. *Salmo salar*, River Rhine.

RECORDS.

(i) Material studied
(a) From the NE Atlantic
None.

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* The appellation *Distomum miescheri*, as pointed out by Margolis (1962), was first used by Zschokke in 1889; but without a description.

(b) From elsewhere

Lampris guttatus [=*regius*] [stomach] Hamazima, Japan (April, 1939), type-material of *L. nipponicum* Yamaguti, 1940. Fragments in transverse serial section. Meguro Parasitological Museum, Tokyo.

(ii) NE Atlantic records from the literature

(a) Mature

None. It is likely that it does occur in this region in *Lampris guttatus* and possibly *Brama rayi* [stomach, oesophagus and (?) possibly gills].

(b) Immature

Salmo salar [oesophagus] River Rhine. Zschokke (1889 : 88; 1890 : 764; 1892 : 831); [stomach] Heitz (1918 : 339; 1919 : 510).

Salmo salar [?] River Elbe. Fritsch (1894 : 110).

Salmo salar [oesophagus] River Tweed, Great Britain. Tosh (1905 : 115).

ASPECTS OF BIOLOGY. The life-history of this species is not known. Its normal definitive host appears to be the opah *Lampris guttatus* [=*L. regius*, =*L. luna*]; but it also reaches maturity in *Brama rayi* (see Margolis, 1962), although these specimens are smaller. Immature forms are found in salmonoids which, although several of the records are from freshwater, presumably acquire the parasite at sea. It does not appear to be capable of maturing in salmonoids. Records from salmonoids, in addition to those given above, are those from *Oncorhynchus nerka* and *O. gorbuscha* [stomach and gills] in the Sea of Okhotsk and northern Pacific Ocean (Margolis, 1962) and from *Argentina silus* off the eastern coast of Canada (Scott, 1969). The occurrence of the immature form only in salmonoids is surprising unless these records are not entirely accidental as at first suspected. *Lampris guttatus* is essentially piscivorous, and it may be that these teleosts, apparently acting as paratenic hosts, will, in fact, prove to be obligatory.

PREVIOUS DESCRIPTIONS. Zschokke (1890 : 781; immature form only); Heitz (1918 : 339; 1919 : pl. 5, fig. 1; immature form only); Yamaguti (1940 : 100; as *L. nipponicum*: 1970 : 119; as *L. hawaiiense*); Margolis (1962 : 942; adult and immature forms as *L. nipponicum*); Scott (1969 : 139; immature form, measurements, only; as *L. nipponicum*); Delyamure & Serdyukov (1970 : 213; as *L. atlanticum*).

DESCRIPTION (Fig. 13). [Taken from Yamaguti, 1940, 1970; Margolis, 1962; Delyamure & Serdyukov, 1970.] Mature specimens of this species have a very long, slender and cylindrical body (Fig. 13A). Measurements for this species are given in Table 16. The short forebody may be arched ventrally and covered by numerous small papillae. The body-surface is otherwise smooth, except for transverse wrinkles possibly caused by contraction during fixation. Yamaguti (1940) notes that the body-wall contains a well-developed layer of longitudinal muscle both in the fore- and hindbodies; but in the hindbody a thick layer of diagonal muscles, which lies within the longitudinal muscle in the forebody, is absent.

The *oral sucker* is ventrally subterminal and surmounted by a pre-oral lobe. The *ventral sucker* is very prominent and significantly larger than the oral sucker (Table 16). The latter leads directly into a large muscular *pharynx*, which in turn leads into a vesicular oesophagus. The gut-caeca possess 'Drüsenmagen' in the 'shoulder'-region and pass back sinuously into the hindbody apparently ending blindly close to the posterior extremity. In the posterior half of the body they develop dorsally-oriented diverticula (Fig. 13E).

The *excretory system* has not been elucidated in detail, as it is very difficult to follow. Judging from the figures of Zschokke (1890), Hertz (1919) and Yamaguti (1970), however, the terminal pore leads into an excretory vesicle with a short stem which divides into dorsal and ventral arms. The arms appear to be very convoluted in both the fore- and hindbodies; but, according to Yamaguti (1940), they do not unite in the forebody. Our examination of his sections, however, suggests otherwise.

The oval *testes* are situated in tandem close to the middle of the hindbody. A tubular, convoluted seminal vesicle lies immediately anteriorly to the ventral sucker, the distal region of which has a muscular wall. It leads into a sinuous or sigmoid, tubular pars prostatica that is surrounded by a dense covering of gland-cells. The elongate, club-shaped '*cirrus-sac*' extends posteriorly
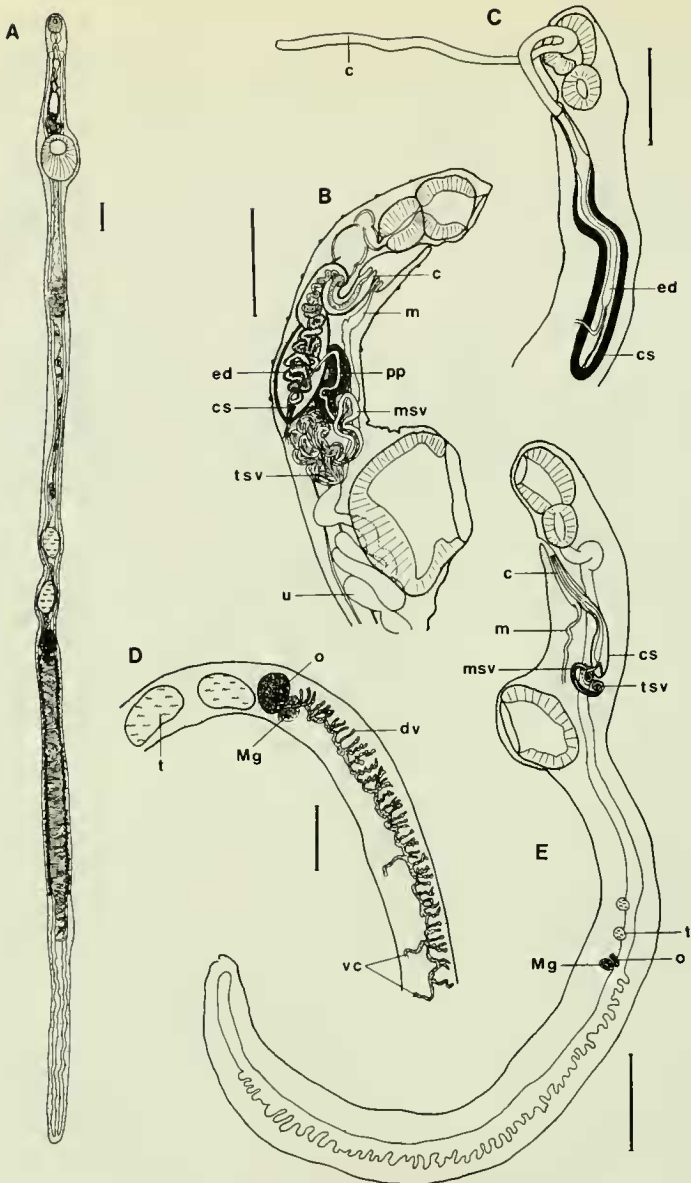
Table 16 Dimensions of *Lampritrema miescheri* from the literature

Authority	Zschokke (1890, 1892)	Tosh (1905)	Heitz (1918)	Margolis (1962)	Scott (1969)
Name used	*Distomum miescheri*	*Distomum miescheri*	*Distomum miescheri*	*Lampritrema nipponicum*	*Lampritrema nipponicum*
Host	*Salmo salar*	*Salmo salar*	*Salmo salar*	*Oncorhynchus* spp.	*Argentina silus*
Locality	River Rhine	River Tweed	River Rhine	Northern Pacific	East coast of Canada
Maturity	Immature	Immature	Immature	Immature	Immature
Length (mm)	10–15	9–17	up to 12	2·7–6·1	6·2–12·9
Breadth (mm)	0·7–0·8	—	—	0·23–0·39	0·46–0·8
Forebody (mm)	2·0–2·5	—	—	—	—
Oral sucker (mm)	—	—	—	0·23–0·32 × 0·22–0·29	0·25–0·36 × 0·30–0·34
Ventral sucker (mm)	—	—	—	0·34–0·46 × 0·25–0·39	0·49–0·63 × 0·34–0·53
Pharynx (mm)	—	—	—	0·13–0·21 × 0·12–0·18	0·18–0·26 × 0·18–0·24
Testes (mm)	—	—	—	up to 0·062 × 0·07	0·02–0·11 × 0·02–0·09
Ovary (mm)	—	—	(?) 1·705*	up to 0·028 × 0·057	up to 0·06 × 0·11
Eggs (μm)	—	—	—	—	—

Authority	Margolis (1962)	Yamaguti (1940)	Yamaguti (1970)	Delyamure & Serdyukov (1970)
Name used	*Lampritrema nipponicum*	*Lampritrema nipponicum*	*Lampritrema hawaiiense*	*Lampritrema atlanticum*
Host	*Brama rayi*	*Lampris regius* (=*L. guttatus*)	*Lampris regius* (=*L. guttatus*)	*Lampris luna* (=*L. guttatus*)
Locality	Gulf of Alaska	Off Japan	Off Hawaii	South Atlantic
Maturity	Mature	Mature	Mature	Mature
Length (mm)	12·3–28·2	30–53	17–70	55·9
Breadth (mm)	0·48–1·4	0·9–1·8	0·8–1·6	1·9
Forebody (mm)	—	—	c. 1/7 length	7·3
Oral sucker (mm)	0·34–0·66 × 0·33–0·54	0·6–0·92 × 0·62–0·9	0·3–0·75 × 0·34–0·76	0·72 × 0·85
Ventral sucker (mm)	0·53–1·06 × 0·53–0·88	1·5–2·25 × 1·1–1·88	0·75–2·0 × 0·7–1·75	1·47 × 1·35
Pharynx (mm)	0·25–0·41 × 0·24–0·36	0·5–0·6 × 0·47–0·72	0·25–0·45 × 0·2–0·5	0·56 × 0·56
Testes (mm)	0·5–0·73 × 0·31–0·73	0·92–2·0 × 0·65–0·1	0·55–2·2 × 0·25–1·0	1·62–1·35 and 1·72 × 1·16
Ovary (mm)	0·25–0·4 × 0·32–0·62	0·6–1·1 × 0·53–0·83	0·33–1·15 × 0·25–0·8	0·93 × 0·97
Eggs (μm)	47–57 × 18–24	45–51 × 18–20	52–58 × 21–28	54 × 21

* According to Margolis (1962) this should be 0·1705 and is probably a measurement of Mehlis' gland.

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Fig. 13 *Lampritrema meischeri*: (A) mature specimen ex *Lampris guttatus* (modified after Yamaguti, (1940); (B) lateral view of anterior extremity of mature specimen from *L. guttatus* (modified after Yamaguti, 1940); (C) lateral view of anterior extremity of mature specimen ex *L. guttatus* (modified after Margolis, 1962); (D) ventro-lateral view of gonads and one side of vitellarium of mature specimen from *Brama rayi* (modified after Margolis, 1962); (E) lateral view of immature specimen from *Oncorhynchus nerka* [rudimentary vitellarium may be visible in larger specimens] (modified after Margolis, 1962). Scale: (A, B, C) 1 mm; (D, E) 500 μm. [c, 'cirrus'; cs, 'cirrus-sac'; dv, dorsal branches of vitellarium; ed, ejaculatory duct; m, metraterm; Mg, Mehlis' gland; msv, muscular region of seminal vesicle; o, ovary; pp, pars prostatica; t, testis; tsv, thin-walled region of seminal vesicle; u, uterus; vc, vitelline commissures.]

from the base of the genital atrium to the level of the seminal vesicle (Fig. 13B). The pars prostatica passes through the wall of the 'cirrus-sac' subterminally and immediately assumes the form of an ejaculatory duct. This duct is initially narrow, but then becomes broader and more muscular as it passes distally within the 'cirrus-sac', being either straight or convoluted, depending on the extension of the 'cirrus'. The 'cirrus' is a very contractile structure, which may be very short or protruded through the genital pore for a distance of up to 4 mm (Margolis, 1962) (Fig. 13C). The small genital pore lies mid-ventrally to the pharynx.

The globular *ovary* lies just posteriorly to the hinder testis. Mehlis' gland is immediately post-ovarian (Fig. 13D). Although found in other hirudinellids, no Laurer's canal or uterine seminal receptacle have yet been reported. Yamaguti (1940) reports the presence of a minute seminal receptacle within Mehlis' gland; but it is very unlikely that this is a canalicular seminal receptacle and its presence requires confirmation. The *uterus* winds posteriorly from the ovarian complex in the ventral plane, passing the posterior extremity of the vitellarium and overlapping the gut-caeca laterally. It then winds forward between the caeca and dorsally to the descending limb, passing the gonads laterally and becoming the metraterm as it passes into the forebody. The metraterm leads directly or sinuously towards the female pore, which is situated in the genital atrium immediately posterior to the 'cirrus' (Fig. 13B). The oval eggs lack spines or filaments. The vitellarium is tubular and extends laterally between the ovary and the posterior extremity. It appears, essentially, to consist of two main lateral tubules which run posteriorly and give rise to numerous small, dorsally-directed branches (Fig. 13D). According to the literature these small branches are mainly extra-caecal but occasionally unite medially forming commissures. The two main tubules unite in the region of Mehlis' gland, forming a vitelline reservoir.

Immature specimens, from both the final hosts and salmonoids, appear to have a much smaller length to breadth ratio (see Table 18). The gonads and vitellarium may be very reduced or apparently absent in the youngest specimens, but the terminal genitalia and Mehlis' gland are usually quite well developed even at this stage (Fig. 13E).

DISCUSSION. *Distoma miescheri* was described by Zschokke (1890, 1892) and Heitz (1918, 1919) as an immature form from the oesophagus and stomach of *Salmo salar* in fresh water. Further specimens were recorded from this host by Fritsch (1894) and Tosh (1905). The systematic position of this species remained undetermined until the valuable work of Margolis (1962), who recognized it as an immature form of the genus *Lampritrema* Yamaguti, 1940. Margolis found that the description of *D. miescheri* are remarkably similar to immature specimens of *Lampritrema nipponicum* which he had collected from *Oncorhynchus* spp., along with mature and immature specimens from *Lampris guttatus* [=*L. regius*] and *Brama rayi* from the Pacific Ocean. He concluded his study of this problem as follows: 'From the foregoing comparison of the morphology of *D. miescheri* and *L. nipponicum*, and taking into consideration the probable errors in the description of *D. miescheri*, it seems reasonable to conclude that the former species belongs to *Lampritrema*, becoming *L. miescheri* (Zschokke, 1890) nov. comb. Furthermore, it is not unlikely that *L. miescheri* and *L. nipponicum* are identical, but synonymizing these two species must await the discovery and description of adult *L. miescheri* from the Atlantic. If they prove to be synonymous, *L. nipponicum* will have to fall in favor of *L. miescheri*. The occurrence of the same species of *Lampritrema* in the Atlantic and the Pacific Oceans is quite tenable since the two known normal hosts (*Lampris regius* and *Brama rayi*) of *L. nipponicum* in the Pacific have a similarly wide distribution in both oceans.' Since Margolis' work immature specimens of *L. nipponicum* have been recorded from the salmonoid *Argentina silus* in the NW Atlantic by Scott (1969), a new species, *L. atlanticus*, has been described from *Lampris guttatus* [=*L. luna*] in the South Atlantic by Delyamure & Serdyukov (1970), and Yamaguti (1970) has described a new species, *L. hawaiiense*, from *Lampris guttatus* [=*L. regius*] from off Hawaii. Surprisingly, Yamaguti (1971) still maintains that *Distomum miescheri* is unrecognizable, despite the fact that several errors in Zschokke's (1890) description have been explained by Heitz (1918) and Margolis (1962).

L. nipponicum was originally described by Yamaguti (1940) from *L. guttatus* [=*L. regius*] from off Japan and, prior to Margolis' records, had been recorded from the same host off the Californian coast by Arai (1963). The differences between this species and *L. atlanticum* listed by Delyamure & Serdyukov (1970) can all be explained by differences in size and contraction.

Yamaguti (1970) claims that *L. hawaiiense* is a distinct species because of differences in egg-size and the smaller size of the oral sucker and pharynx, when compared with the type-specimens of *L. nipponicum*. These measurements, however, especially that of egg-size, tend to overlap when those of Margolis (1962) and Delyamure & Serdyukov (1970) are included. We are of the opinion, therefore, that, like the related genera *Hirudinella* and *Botulus*, *Lampritrema* is monotypic, and that, as suggested by Margolis (1962), *L. miescheri* is the oldest available name for the type-species.

Family **PTYCHOGONIMIDAE** Dollfus, 1937

DIAGNOSTIC FEATURES. Body medium sized; oval. Body-surface smooth, without spines or plications. Oral and ventral suckers well developed; oral sucker larger than ventral sucker; latter situated in anterior half of body. Prepharynx absent. Pharynx well developed. Oesophagus short. Gut-caeca form uroproct. Testes two; post-ovarian; tandem in middle of hindbody. Seminal vesicle dilate, tubular; thin-walled; extending posteriorly into anterior hindbody. Pars prostatica tubular. Ejaculatory duct and hermaphroditic duct short. Permanent sinus-organ a small cone. Sinus-sac absent. Genital atrium contains three distinct concentric folds in its wall which surround sinus-organ. Genital pore mid-ventral in forebody. Ovary oval; pre-testicular in hindbody. Mehlis' gland pre-ovarian. Laurer's canal and uterine seminal receptacle present. Juel's organ and canalicular or blind seminal receptacle absent. Uterine field extends between ventral sucker and a level posterior to testes. Eggs numerous; without filaments. Vitellarium follicular; in lateral fields extending throughout most of hindbody. Excretory vesicle Y-shaped; arms unite twice in forebody. Parasitic in stomach of elasmobranchs (normally carchariniform sharks).

PTYCHOGONIMUS Lühe, 1900

DIAGNOSTIC FEATURES. As family.

TYPE-SPECIES. *Ptychogonimus megastoma* (Rudolphi, 1819) (by monotypy).

Ptychogonimus megastoma (Rudolphi, 1819) Lühe, 1900

Distoma megastomum Rudolphi, 1819.
Distomum soccus Molin, 1858.
Distoma lymphaticum von Linstow, 1903.
Cercaria dentalii Pelseneer, 1906.

TYPE-HOST AND LOCALITY. *Galeorhinus galeus*, Rimini, Adriatic Sea.

RECORDS.

(i) Material studied
(a) From the NE Atlantic
Mustelus mustelus [stomach] Plymouth, Devon, England. BM(NH) Reg. No. 1932.12.6.9. (material of Baylis & Jones, 1933).
(b) From elsewhere
Mustelus mustelus [stomach] Split, Yugoslavia (Sept., 1975). BM(NH) Reg. No. 1976.5.12.5–34.
(ii) NE Atlantic records from the literature
Mustelus mustelus [oesophagus and stomach] Belgium. van Beneden (1871 : 6).
Mustelus mustelus [stomach] Arcachon, Gironde, France. Monticelli (1890 : 426).
Mustelus mustelus [stomach] Plymouth, Devon, England. Nicoll (1914 : 481); Baylis & Jones (1933 : 631); Baylis (1939 : 481).

ASPECTS OF BIOLOGY. Records of intermediate hosts in the NE Atlantic region:
(a) Molluscan host
Antalis vulgaris [= *Dentalium tarentinum*] Wimereux, France. Pelseneer (1906 : 170; as *Cercaria dentalii*).

(b) Crustacean hosts

Atelecyclus sp. [?] Arcachon, Gironde, France. Bouvier, in Dollfus (1937a : 468).

Carcinus maenas [body-cavity] Arcachon, Gironde, France (Nov., 1922). Dollfus (1937a : 461, 468).

Hyas araneus [body-cavity] Luc, Calvados, France. Vaullegeard (1896 : 665).

Maia sp. [body-cavity] Arcachon, Gironde, France. Viallanes, in Monticelli (1890 : 426).

Portunus depurator [body-cavity] Luc, Calvados, France. Vaullegeard (1896 : 665).

Adult specimens of *P. megastoma* occur in the stomach of carchariniform sharks, especially in *Mustelus mustelus* and especially in the Mediterranean region. Outside the northeast Atlantic region this parasite has been recorded from a variety of these sharks. The miracidium enters scaphopod molluscs of the genus *Antalis* [*A. vulgaris* (= *Dentalium tarentinum*) and *A. inaequicostatum* (= *D. alternans*)] and develops, presumably into a mother-sporocyst. Within the daughter-sporocysts almost tailless cercariae develop, but are not released. The daughter-sporocysts, containing the cercariae, leave the scaphopod and fall prey to a wide variety of crabs. Once within the crab, the cercariae penetrate the gut-wall and pass into the body-cavity, where they become unencysted metacercariae. These metacercariae, which may develop progenetically, usually mature when the crab is eaten by a shark (Palombi, 1942b : 117; also information in Palombi, 1941 : 127; 1942a : 1; 1966 : 10). Occasionally immature specimens of *P. megastoma* have been recorded in teleosts (Maclaren, 1903a : 261; Chandra Sekhar & Threlfall, 1970 : 175); but these are presumably accidental infestations, although it is possible that teleosts may serve as transport hosts.

There appears to be no record of this species north of the Belgian coast. This may be connected with the distribution of the first intermediate host in this region, *Antalis vulgaris*, which is not found north of Britain. Other species of *Antalis* occur in more northerly waters, but as yet have not been incriminated.

PREVIOUS DESCRIPTIONS. Willemoes-Suhm (1871 : 179); Jacoby (1899 : 16); Jägerskiöld (1900 : 68); von Linstow (1903 : 354); Dollfus (1937a : 459); Yamaguti (1938a : 65; eggs only); Nikolaeva (1966 : 63); de Oliveira Rodrigues *et al.* (1972 : 89).

DESCRIPTION (Figs 14 & 15). This description is based mainly on specimens collected from the stomach of *Mustelus mustelus* from the Adriatic Sea off Split, Yugoslavia. The measurements are given in Table 17. The specimens are relatively large, oval and dorso-ventrally flattened (Fig. 14). The hindbody is slightly broader than the forebody. They have a very prominent, large *oral sucker* and a smaller *ventral sucker* which is situated well inside the anterior half of the body. The body-surface appears smooth, although in fixed specimens it is rugate. Under high magnification, however, it can be seen that the tegument has a villous nature. Acetic acid-fixed specimens are curved dorsally. Specimens fixed under pressure differ considerably from those not flattened: they appear much larger, the ventral sucker tends to be of a slightly different shape, the course of the uterus is much more easily seen and the body-surface is less rugate (Figs 14A & B). For this reason measurements of flattened and unflattened specimens from the present material are given separately in Table 17. It should be noted that prior to fixation all of these specimens were of a similar size.

There is no prepharynx, the oral aperture leading directly into a well-developed *pharynx*. A very short oesophagus passes antero-dorsally from the base of the pharynx. It bifurcates giving rise to two caeca which pass laterally and slightly anteriorly before curving back and leading posteriorly. These broad caeca reach back almost to the posterior extremity of the body, where they narrow considerably and connect directly to the base of the excretory vesicle, very close to the excretory pore, through a very small aperture to form a uroproct.

The *excretory system* is peculiar. The vesicle is Y-shaped, but the stem is very short and narrow, receiving narrow connections from the gut-caeca laterally. The vesicle bifurcates well posteriorly to the posterior limit of the uterus, to form two broad, moniliform arms, which pass laterally dorsal to the caeca and then continue anteriorly dorso-lateral to the caeca. Close to the level of the posterior margin of the oral sucker, the arms bifurcate and re-unite dorsally anterior and posterior to the oral sucker (Fig. 14). Thus the excretory system forms a complete ring around the oral sucker.
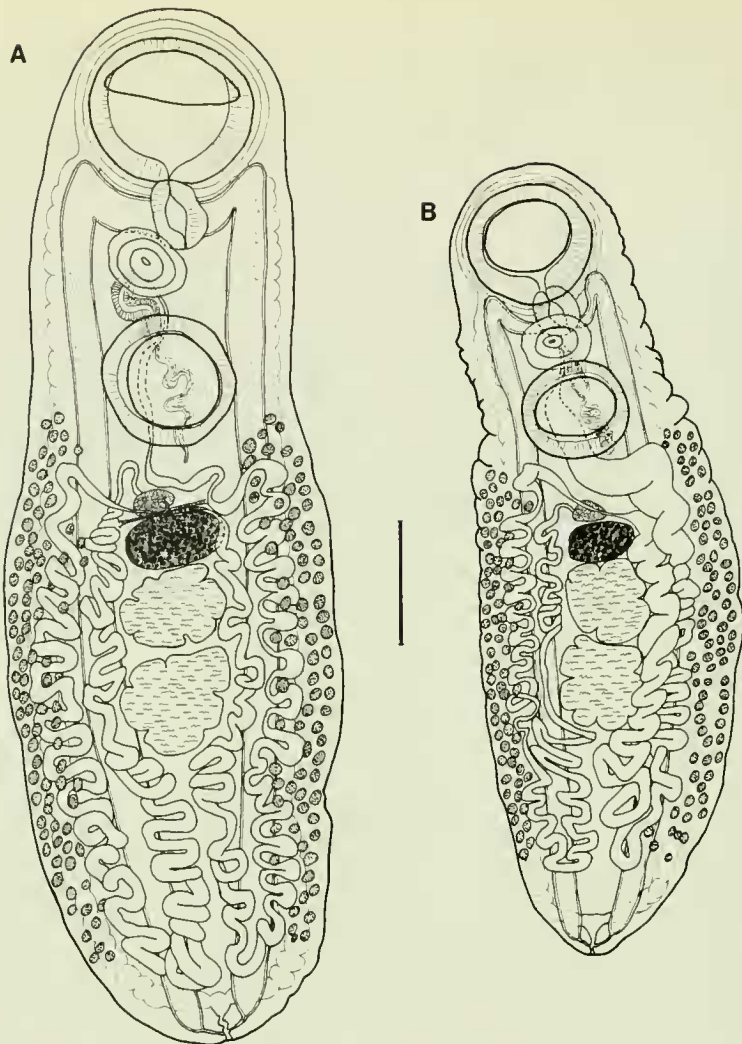
Fig. 14   *Ptychogonimus megastoma* ex *Mustelus mustelus* in Adriatic Sea: (A) specimen fixed under pressure; (B) specimen fixed without pressure. Scale: 1 mm.

The two irregularly-indented, subglobular *testes* occur in tandem close to the middle of the hindbody. A convoluted, tubular seminal vesicle lies dorsally to the ventral sucker; it usually extends from just posterior to just anterior to this sucker. Anteriorly it joins a relatively sinuous or sigmoid pars prostatica. This latter region of the male duct is tubular, although slightly wider in its middle region, surrounded by a dense layer of prostatic cells which are delimited by the surrounding parenchyma, and lined with a layer of cells which project into the lumen (Fig. 15A). There is no prostatic sac. The pars prostatica leads into a very short, oval ejaculatory duct, and this in turn leads into a very short hermaphroditic duct, which occurs within a very small papillate *sinus-organ* (Fig. 15B). The genital atrium is large and its thick wall is convoluted, forming three distinct concentric muscular collars which surround the sinus-organ. The inner collar is the smallest, and the outer collar which is the largest, fills much of the atrium and possesses a terminal glandular

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lip which tends to curve over and overlap the inner collars. There is no sinus-sac; but the diffuse musculature of the collars forms a distinct region which extends across the base of the genital atrium. The small genital pore is situated in the middle of the forebody postero-ventrally to the pharynx.

The transversely oval *ovary* is immediately pre-testicular in the anterior region of the hindbody. Closely anterior and slightly dextral to the ovary lies a well-developed Mehlis' gland. Dorsally to Mehlis' gland a relatively short, glandular Laurer's canal opens to the exterior. No canalicular or blind seminal receptacle is present (see Gibson & Bray, in preparation), but a uterine seminal receptacle does occur. The proximal part of the uterus prior to the uterine seminal receptacle apparently acts as an oötype, as the eggs do not appear to form within the region of the ovo-vitelline canal surrounded by Mehlis' gland. The *uterus* winds back to the right of the gonads to within a short distance from the posterior extremity of the body. It then winds anteriorly lateral to the descending region, reaching to the level of Mehlis' gland, where it crosses the body ventrally

Fig. 15 Terminal genitalia of *Ptychogonimus megastoma*: (A) sagittal section of forebody; (B) enlarged view of region of sinus-organ. [ed, ejaculatory duct; f, first (inner) fold of wall of genital atrium; ga, genital atrium; hd, hermaphroditic duct; m, metraterm; so, sinus-organ.] Scale: (A) 500 µm.

Table 17 Dimensions of *Ptychogonimus megastoma* from the present material and from the literature.

	Jacoby (1899)	von Linstow (1903)	Dollfus (1937)	Nikolaeva (1966)	de Oliveira Rodrigues et al. (1972)	Present material	
Authority						*Mustelus mustelus*	
Host	*Mustelus mustelus Galeorhinus galeus*	*Mustelus mustelus*	*Mustelus mustelus*	*Squalus acanthias*	*Mustelus mustelus*		
Locality	Mediterranean and Adriatic Seas	?	Coast of Mauritania	Adriatic Sea	Atlantic coast of North Africa	Adriatic Sea	
Number of specimens	?	?	?	?	?	Flattened 5	Unflattened 3
Length (mm)	10–12 (immat. 4–5)	2·1–2·7	6–8·5	1·5–4·62	3·04–6·34	7·5–8·3	6·0–6·3
Breadth (mm)	3–4 (immat. 1–1·5)	1·1–1·2	2·5–3·5	0·58–1·63	0·66–1·98	2·4–2·7	1·96–2·06
Forebody (mm)	—	—	—		—	2·2–2·5	1·62–1·64
Oral sucker (mm)	1·5 diam.	0·63	—	0·41–1·05 × 0·42–0·94	0·77–1·2 diam.	1·0–1·2 × 1·22–1·4	0·98–1·08 × 1·00–1·2
Ventral sucker (mm)	1·2 × 1·37	0·55	—	0·33–0·84 × 0·33–0·75	0·48–0·94 diam.	1·0–1·12 × 0·98–1·12	0·76–0·8 × 0·84–0·92
Pharynx (mm)	—	—	—	0·23–0·46 × 0·19–0·48	0·27–0·58 × 0·33–0·58	0·5–0·55 × 0·45–0·5	0·4–0·47 × 0·38–0·45
Genital atrium (mm)	—	—	—	—	+ 0·3–0·78 diam.	0·5–0·58 × 0·63–0·7	0·3–0·45 × 0·5–0·56
Testes (mm)	0·63–0·93 × 0·7–0·73	—	—	0·16–0·52 × 0·10–0·34	0·52–0·72 × 0·48–0·72	0·5–0·82 × 0·75–0·95	0·45–0·7 × 0·56–0·75
Ovary (mm)	0·41 × 0·77	—	—	0·14–0·43 × 0·08–0·28	0·36–0·56 × 0·24–0·52	0·4–0·48 × 0·75–0·8	0·26–0·35 × 0·53 × 0·56
Eggs (μm)	57 × 34	73 × 44	62–67 × 36–38	47–71 × 25–34	52–72 × 32–40	52–62 × c. 28–32 (collapsed)	56–62 × c. 30

and winds posteriorly again to the left of the gonads (Fig. 14). Just short of the posterior extremity it again loops forward laterally, forming an ascending limb on the left side, and then passes medially just posteriorly to the ventral sucker. Dorsally to the ventral sucker, where it is often very dilate, the uterus usually narrows suddenly, forming a metraterm which is surrounded by small gland-cells. This relatively long metraterm leads directly towards the terminal genitalia, where it unites with the ejaculatory duct to form a very short hermaphroditic duct (Fig. 15A & B). The numerous eggs lack filaments or spines. Their shells appear to be soft and untanned in the first descending limb of the uterus. The *vitellarium* is follicular and lies in lateral fields which extend from the posterior margin of the ventral sucker to a region approximately level with the posterior limit of the uterus, i.e. just short of the posterior extremity. The two fields are not confluent. The main collecting ducts unite ventrally to Mehlis' gland, and the common duct joins the oviduct within Mehlis' gland.

DISCUSSION. *Ptychogonimus* resembles the azygiid *Otodistomum* in having a wide range of egg-size, although our Adriatic Sea material has a relatively constant egg-size. Yamaguti (1938a) noted that young and fully-developed eggs showed variation of $42–96 \times 27–63$ μm, and Willemoes-Suhm (1871) recorded even larger differences, 28×21 to 86×57.* This emphasizes the need for measuring eggs only from the distal region of the uterus. It seems likely that, as in *Otodistomum*' some variation in the egg-size of *Ptychogonimus* is due to growth of the oötype.

Distomum megacotyle Monticelli, 1893, was briefly described from *Mustelus mustelus* at Wimereux, Artois, France, by Monticelli (1893b : 52). This species is based on a single immature specimen which had previously been figured by Monticelli (1890 : 426, fig. 17) as '*Distoma* (forma giovane)'. It was considered by Palombi (1942b : 149) to be a synonym of *P. megastoma*; but the position of the ventral sucker and the apparent structure of the excretory system suggest that this is somewhat unlikely. Monticelli's figure indicates that *D. megacotyle* might be an immature specimen of *Derogenes* accidentally ingested by the shark.

We have not included the description by Vigueras (1956) amongst our 'previous descriptions', as it differs from other descriptions of *P. megastoma*. Vigueras' specimens, from *Cynias canis* off Cuba, appear to possess an oral sucker smaller than the ventral sucker, a vitellarium which is confluent in the post-testicular region and an almost pre-testicular uterus.

Family **SCLERODISTOMIDAE** Odhner, 1927

Prosogonotrematidae Vigueras, 1940.
Mabiaramidae Teixeira de Freitas & Kohn, 1967.

DIAGNOSTIC FEATURES. Body usually large; stout or elongate. Body-surface smooth, but may be rugate. Oral and ventral suckers well developed; ventral sucker just posterior to middle of body, in middle of body or well inside anterior half of body. Prepharynx absent. Pharynx well developed. Oesophagus short. Gut-caeca terminate blindly close to posterior extremity. Testes two, symmetrical, in tandem or oblique; pre-ovarian; in forebody, dorsal to ventral sucker or in anterior hindbody. Seminal vesicle tubular; convoluted or winding in forebody. Pars prostatica tubular, occasionally with wide lumen; relatively long; convoluted or not; external gland cells may be delimited. Ejaculatory duct present, uniting with metraterm within sinus-organ forming short hermaphroditic duct. Sinus-sac well developed, weakly developed or absent. Permanent sinus-organ present; usually well developed; conical to cylindrical. Genital atrium well developed; often almost entirely filled by sinus-organ. Genital pore mid-ventral in forebody. Ovary globular to oval; post-testicular; in posterior forebody, dorsal to ventral sucker or in anterior to mid-hindbody. Mehlis' gland usually posterior or postero-lateral, occasionally antero-lateral, to ovary. Laurer's canal present; opens dorsally or into rudimentary Juel's organ (see 'Terminology'). Rudimentary seminal receptacle present or absent. Uterine seminal receptacle present. Uterus mainly in either fore- or hindbody; mainly pre- or post-ovarian. Eggs small, very numerous; non-filamented. Vitellarium four to seven convoluted, tubular branches, which may subdivide; either mainly pre-

* There may be some doubt as to the identity of some of Willemoes-Suhm's specimens, as he recorded them up to 20 mm in length. This is much larger than has been recorded by any other author.

or mainly post-ovarian; either mainly in fore- or hindbody. Excretory vesicle Y-shaped; arms united in forebody. Manter's organ (accessory excretory vesicle) present; single or double; dorsal to stem of excretory vesicle. Parasitic in gut (mainly stomach), occasionally body-cavity, of marine teleosts.

Subfamily **PROSORCHIINAE** Yamaguti, 1934

DIAGNOSTIC FEATURES. Body elongate-oval to very elongate. Ventral sucker normally within anterior half of body, but occasionally in middle. Testes tandem to almost symmetrical; in fore-body or dorsal to ventral sucker. Pars prostatica broad; external gland-cells delimited. Sinus-sac absent or very weakly developed. Ovary in hindbody. Laurer's canal long and opening into rudi-mentary Juel's organ or short and opening to exterior on dorsal surface; may or may not be dilated proximally forming rudimentary seminal receptacle. Uterus mainly post-ovarian in hind-body. Vitellarium two or four branching, or seven, convoluted and filamentous tubules; mainly post-ovarian, in hindbody; reaching near to posterior extremity. Manter's organ single.

Prosorchiopsis Dollfus, 1947

DIAGNOSTIC FEATURES. Laurer's canal short; opening dorsally to exterior; distal region may be slightly dilate and possess glandular wall; no rudimentary seminal receptacle present.

TYPE-SPECIES. *Prosorchiopsis legendrei* Dollfus, 1947 (by original designation and monotypy).

Prosorchiopsis legendrei Dollfus, 1947

Prosorchis (Prosorchiopsis) legendrei Dollfus, 1947.
(?) *Prosorchiopsis aluterae* Yamaguti, 1970.
(?) *Prosorchiopsis nasonis* Yamaguti, 1970.

TYPE-HOST AND LOCALITY. *Centrolophus niger*, Concarneau, Bay of Biscay.

RECORDS.

(i) Material studied
(a) From the NE Atlantic
None.
(b) From elsewhere
Pachymetopon grande [stomach] Ramsgate, nr Durban, South Africa. Collected by R. van der Elst. BM(NH) Reg. No. 1975.9.16.118.
(ii) NE Atlantic records from the literature
Centrolophus niger [body-cavity] Concarneau, Brittany, France (April, 1946). Dollfus (1947 : 314).

ASPECTS OF BIOLOGY. There appears to be no information available with regard to the life-history of the sclerodistomids; but it is interesting to note that, to date, the prosorchiine species appear to be restricted to stromateoid, acanthuroid and percoid members of the order Perciformes.

PREVIOUS DESCRIPTION. Dollfus (1947 : 314).

DESCRIPTION (Fig. 16). This description is based on four specimens of which three are whole-mounts and one has been serially sectioned. Measurements are given in Table 18. This relatively large worm is elongate and subcylindrical, the forebody being broader than the hindbody (Fig. 16A). The *oral* and *ventral suckers* are large and well developed, the latter being slightly larger than the former and situated well inside the anterior half of the body. The hindbody of these specimens is contracted, being in several places invaginated within itself for a short distance, and thus presenting a 'segmented' appearance. These invaginations (Fig. 16A) resemble the invagina-tion of the ecsoma of hemiurids, but do not appear to have been present in Dollfus' (1947) more extended specimens. In the sectioned specimen the oral sucker is withdrawn deeply into the fore-body (Fig. 16B). Surprisingly, the body-surface is not entirely smooth, as much of the surface is covered with minute, pointed projections which tend to occur in rows. Closer study of this surface

Table 18 Dimensions of *Prosorchiopsis legendrei* from the present material and from the literature.

Authority	Dollfus (1947)		Yamaguti (1970)		Present material
Name used	*Prosorchis (Prosorchiopsis) legendrei*		*Prosorchiopsis aluteroe*	*Prosorchiopsis nosonis*	*Prosorchiopsis legendrei*
Host	*Centrolophus niger*		*Alutera scripto*	*Naso hexacanthus*	*Pachymetopon grande*
Locality	Off Brittany		Hawaii	Hawaii	South Africa
Number of specimens	12	1 immature	2	9	4
Length (mm)	2·5–9·5	5	5·5–8·5	17–31	11–17·5
Breadth (mm)	1/7–1/10 length	0·27	1·0–1·1	up to 2·5	2·4–3·0
Forebody (mm)	–	1·45	–	1/4 length	3·3–5·6
Oral sucker (mm)	–	0·41 × 0·33 depth	0·32–0·5 × 0·43–0·6	1·0–1·8 diam.	1·4–2·05 × 1·0–2·05
Ventral sucker (mm)	–	0·75 × 0·45 depth	0·6–0·95 × 0·65–0·97	1·8–2·5 diam.	1·9–2·6 × 1·8–2·6
Pharynx (mm)	–	–	0·12–0·18 × 0·13–0·21	0·25–0·4 × 0·34–0·5	0·5–1·1 × 0·3–0·7
Testes (mm)	–	–	0·25–0·38 × 0·18–0·43	0·3–0·7 × 0·18–0·33	0·5–0·9 × 0·4–0·7
Ovary (mm)	–	–	0·2–0·32 × 0·18–0·33	0·27–0·6 × 0·13–0·35	0·7–1·0 × 0·5–0·6
Eggs (μm)	28·5–31 × 17–20	–	25–28 × 16–21	23–28 × 14–19	26–31 × 17–21 (usually 28–30 × 18–20)

in sections and comparison with the related *Prosogonotrema*, indicates that the tegument is missing in the region where these projections occur*.

No prepharynx occurs between the oral sucker and the well-developed, oval *pharynx*. It feeds a short dorsally to postero-dorsally directed oesophagus which joins a short, dilate transverse piece which may be the so-called 'diverticulum' observed by Yamaguti (1934) and Srivastava (1936) in whole-mounts of *Prosorchis* spp. The transverse piece is united on each side with the caeca via stout muscular sphincters (Fig. 16E). There are no 'Drüsenmägen'. The caeca, which are narrow and very diverticulate, pass antero-laterally before reflexing laterally to the oral sucker and passing posteriorly in the dorso-lateral field. They follow a direct or sinuous course, depending on contraction, into the hindbody where they terminate blindly near to the posterior extremity.

The *excretory vesicle* is Y-shaped. The arms divide immediately posteriorly to the ventral sucker and re-unite antero-dorsally to the pharynx. The sectioned specimen has a wide, very diverticulate vesicle, filled with granular material. Also present, lying dorsally to the stem of the excretory vesicle, is a single Manter's organ ('accessory excretory vesicle'). This elongate sac has an irregular wall and extends anteriorly almost to the level of the ovary. It is surrounded by a thin muscle-layer which is particularly evident anteriorly and which suggests that it can be evacuated. Manter's organ opens ventrally into the excretory vesicle very close to the terminal pore through a stout sphincter (Fig. 16D). The terminal pore may be slightly withdrawn within the animal.

Two relatively small, oval to rectangular *testes* lie obliquely to tandem in the posterior half of the forebody (Dollfus', 1947, description indicates that they may extend back to a level dorsally to the ventral sucker). Immediately anteriorly to the testes is a long, tubular seminal vesicle which possesses a thin, muscular wall and winds from side to side. It may occasionally extend between the testes. It leads to a tubular, but very broad, pars prostatica with a thick external layer of delimited gland-cells and a thick villous lining (Fig. 16C). It may be relatively straight or arcuate and gives rise to a narrow ejaculatory duct which passes directly into an elongate conical sinus-organ. Towards the tip of the sinus-organ the ejaculatory duct and the metraterm amalgamate to

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* It is likely that this is an artifact caused by fixation, and it probably does not occur in nature, although such a shedding of the tegument has been observed in senile sporocysts (Gibson, 1974). As pointed out by Gibson (1976 : 234, footnote), this phenomenon may explain the apparent presence of spines on the surface of *Hirudinella spinulosa* as described by Yamaguti (1938b).
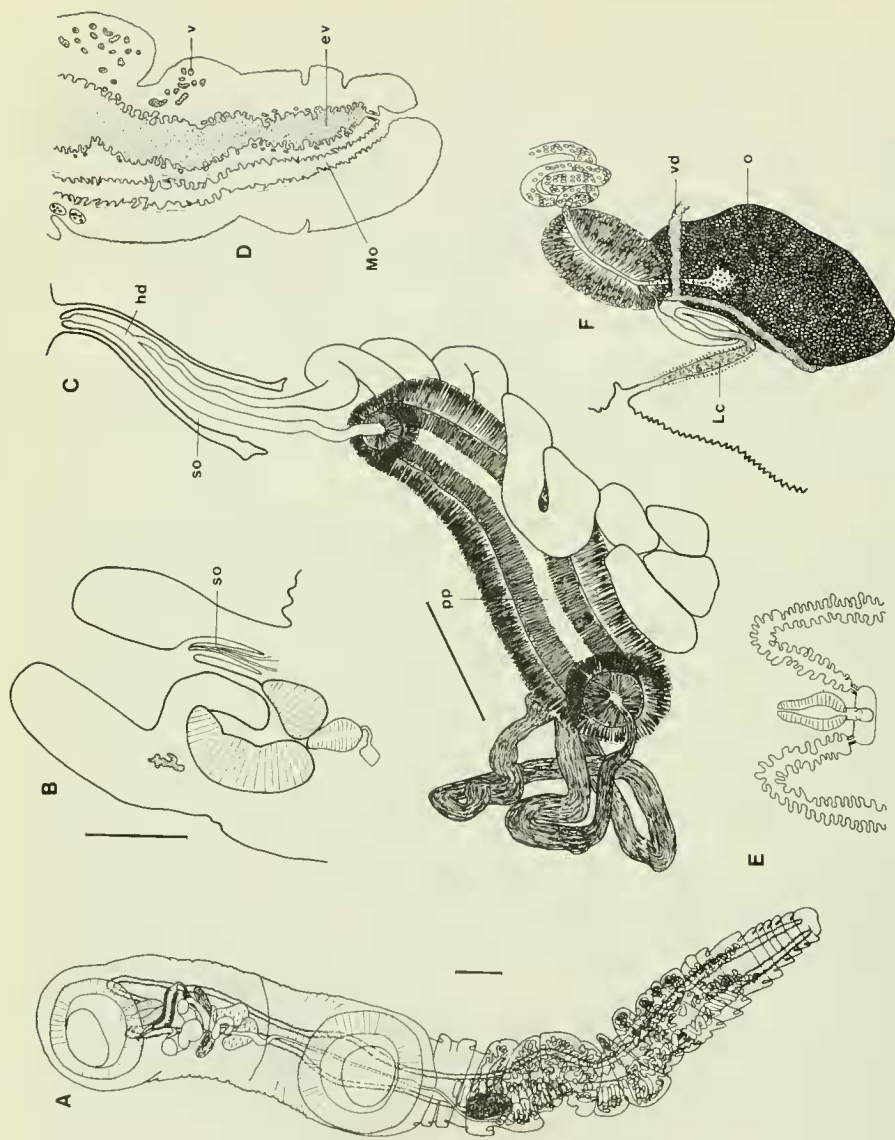
Fig. 16 *Prosorchiopsis legendrei* from *Pachymetopon grande*: (A) whole-mount; (B) anterior extremity of sectioned specimen to show invaginated oral sucker; (C) terminal genitalia; (D) posterior extremity to show stem of excretory vesicle and Manter's organ; (E) anterior region of gut; (F) ovarian complex. Scale: (A, B) 1 mm; (C) 500 μm. [ev, excretory vesicle; hd, hermaphroditic duct; lc, Laurer's canal; mo, Manter's organ; o, ovary; so, sinus-organ; v, vitellarium; vd, vitelline duct.]

form the short hermaphroditic duct. The sinus-organ is probably variable, but in the sectioned specimen it measured 800 μm long and 200 μm at its base. There is no distinct *sinus-sac*. The sinus-organ fills much of the genital atrium, and the genital pore lies mid-ventrally at the level of the pharynx. The arrangement and position of the reproductive organs in the forebody are probably quite variable.

The irregularly oval *ovary* lies submedially a short distance posteriorly to the ventral sucker. It is just dextral and lies in a dorsal plane. Antero-medially it gives rise to an oviduct which passes a short distance into the well-developed Mehlis' gland. Within this gland the oviduct receives Laurer's canal and the common vitelline duct (Fig. 16F). Egg-shell formation occurs within Mehlis' gland. Laurer's canal is short, leads postero-dorsally from Mehlis' gland and opens dorsally at the level of the ovary. It is quite dilate and the distal region contains diffuse material. In the sectioned specimen there is no sign of any type of seminal receptacle, although a uterine seminal receptacle would be expected. The *uterus* loops backwards from the region of Mehlis' gland, gradually widens and continues posteriorly, following a convoluted course, until it reaches a level about a fifth of the length of the hindbody from the posterior extremity. Here it reflexes and retraces its course anteriorly, ventrally to the descending portion, but dorsal or dorso-lateral to Manter's organ. At about the level of the ovary it narrows considerably and continues anteriorly past the ventral sucker either directly or sinuously, depending on the contraction of this region of the body. In the forebody it again expands and follows a winding path before becoming narrower and assuming the form of a short, simple metraterm, which unites with the ejaculatory duct within the sinus-organ (Fig. 16C). The small eggs lack spines or filaments. The *vitellarium* consists of a small number of very long, convoluted tubules which lie ventrally and laterally in the hindbody between the level of the ovary and a level which varies between just anteriorly to the posterior limit of the uterus and the posterior extremity. Whether or not these tubules are branched could not be determined; but they do unite ventro-laterally on either side of the ovary and form single, short, lateral ducts which combine just posteriorly to Mehlis' gland to form a short common duct.

DISCUSSION. There is some disagreement with regard to the validity of the genus *Prosorchiopsis*. It was originally erected as a subgenus of *Prosorchis* by Dollfus (1947) and raised to generic level by Skrjabin & Guschanskaja (1954) because of: (1) the absence of a diverticulum at the junction of the oesophagus and the transverse connection of the gut-caeca; (2) the testes being present dorsal to the ventral sucker instead of entirely within the forebody; and (3) the presence of a short Laurer's canal without a 'distal bulb' and a small proximal 'seminal receptacle'. In our opinion the only valid criterion is the nature of Laurer's canal, as small variations in the position of the testes within the species of this subfamily occur with age and contraction (see Lebedev, 1970 : fig. 7 of *Prosorchis chainanensis*), and because the presence of the oesophageal diverticulum has not been investigated in sectioned material (see above). On this basis we (Gibson & Bray, in preparation) have retained *Prosorchiopsis*. Specimens with a short, tubular Laurer's canal which opens dorsally, we consider to belong to *Prosorchiopsis*, and specimens which have been described as possessing a long Laurer's canal with a proximal swelling (a rudimentary seminal receptacle) and open distally into a terminal 'bulb' (rudimentary Juel's organ*), we consider to be *Prosorchis*. Kurochkin *et al.* (1971) reject *Prosorchiopsis* because '. . . the structure of Laurer's canal at present may be considered for only 3 species (*P. psenopsis*, *P. breviformis* and *P. australis* sp. n.) and such a feature can hardly have taxonomic importance'. This remarkable statement is even more startling when one considers that, of the nine species they accept in *Prosorchis*, six are described in the very same paper. It seems unadvisable to neglect a possibly phylogenetically important taxonomic character because it has not been mentioned in all of the descriptions, some of which are very perfunctory.

The only species of the subfamily Prosorchiinae which can definitely be included in *Prosorchiopsis* are the type-species *P. legendrei* Dollfus, 1947, and *P. aluterae* Yamaguti, 1970. Some of the remaining 13 species which have been described by Yamaguti (1934, 1970), Srivastava (1936), Lebedev

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* The nature of Juel's organ, discussed briefly by Gibson & Bray (1975), will be described elsewhere (Gibson & Bray, in preparation) in more detail.

(1970), Bilqees (1971), Kurochkin *et al.* (1971) and Fischthal & Thomas (1972) can definitely be allocated to *Prosorchis*; but in several cases, and especially those described by Kurochkin *et al.* (1971), Laurer's canal has not been mentioned. We suggest that in many of these descriptions the uterine seminal receptacle may have been mistaken for a seminal receptacle. Considering the fact that several workers have described relatively young specimens, that contraction has a considerable influence on body-length and that the eggs of all of these species are of a very similar size, it is likely that future work will show that most of these species of *Prosorchis* are synonymous.

To return to *Prosorchiopsis*, the present material appears to be morphologically very similar to, but larger than, *P. legendrei*. It must be remembered, however, that the latter species is known only from the 12 specimens, several of which were immature, described by Dollfus (1947). It is clear from the specimens of *Prosorchis* and *Prosorchiopsis* so far described that the hindbody of the larger specimens tends to be relatively longer and the gonads relatively smaller than in younger specimens. We have little hesitation, therefore, in considering the present material to be *P. legendrei*, and it is very possible that *P. aluterae* is a synonym. Yamaguti (1970) distinguishes the two species on the grounds that: (1) the testes of *P. aluterae* are within the forebody rather than dorsal to the ventral sucker; (2) Dollfus' figure of the pars prostatica indicates that it is enclosed in a sac (but Dollfus' description makes no mention of this, nor is a sac present in our material; the delimited nature of the external gland-cells of the pars prostatica tend to give this impression in whole-mounts, and this may account for the slightly misleading nature of Dollfus' figure); and (3) Manter's organ is present in *P. aluterae*, but is not mentioned in *P. legendrei*. These characters being rather unconvincing, we have tentatively included *P. aluterae* in the list of synonyms of *P. legendrei*. As it appears to differ from *P. aluterae* only in size (Laurer's canal is not described), we have also tentatively considered *P. nasonis* Yamaguti, 1970, a synonym of *P. legendrei*.

Manter's organ is not normally visible in whole-mounts and, we believe, is probably common to all or most genera within the family Sclerodistomidae. We have seen it as a single structure in *Prosorchiopsis* and *Prosogonotrema* and paired in *Sclerodistomum*, where it is present dorsally or dorso-laterally to the excretory vesicle with which it communicates ventrally and subterminally. Yamaguti (1970) is apparently in error when he states that in *P. aluterae* Manter's organ is 'ventral to the excretory vesicle' and 'communicates with the excretory vesicle dorsally'. It is clear from the distribution of the vitelline tubules (mainly ventral in our specimens) and the uterus (mainly dorsal in our specimens) that some of Yamaguti's transverse sections (see his fig. 217 E) are inverted in relation to the others, and this probably accounts for his remarks.

Family SYNCOELIIDAE Looss, 1899

DIAGNOSTIC FEATURES. Body elongate, cylindrical or dorso-ventrally flattened; usually with pedunculate ventral sucker. Body-surface smooth, but commonly papillate on forebody and peduncle. Oral and ventral suckers well developed; may possess accessory suckers around rim. Glandular cells common in subtegumentary parenchyma and within musculature of suckers. Prepharynx absent. Pharynx well developed. Oesophagus short. Cyclocoel usually present, but caeca may end blindly (?) or form uroproct. Testes 11–18 distinct, oval follicles (usually arranged in pairs), 7–8 transverse rows of follicles, or a large number of irregular follicles; pre-ovarian, in hindbody. Seminal vesicle thin-walled, tubular, winding or sinuous; in forebody. Pars prostatica tubular. Ejaculatory duct short. Hermaphroditic duct and genital atrium present, but indistinguishable when sinus-organ is absent. Permanent sinus-organ and sinus-sac present or absent. Genital pore mid-ventral in anterior forebody. Ovary post-testicular; composed of five large, oval and isolated lobes, numerous regular follicles, or (?) a single oval structure. Mehlis' gland post-ovarian. Laurer's canal and uterine seminal receptacle present. Juel's organ and both canalicular and blind seminal receptacles absent, but rudimentary seminal receptacle may be present. Uterus passes posteriorly, but coils mainly in pre-ovarian hindbody. Eggs numerous, small, not filamented. Vitellarium seven (occasionally five or six) isolated, oval lobes, or irregular acinous bunches or rows of follicles; post-ovarian. Excretory vesicle Y-shaped; arms unite in forebody, may initially run in dorsal and ventral fields. Free-floating metacercarial

stage present. Parasitic in branchial and buccal cavities, on skin, in (?) oviduct and in (?) gut of elasmobranchs and marine teleosts.

Subfamily SYNCOELIINAE Looss, 1899

DIAGNOSTIC FEATURES. Accessory suckers around rim of suckers absent. Peduncle usually present. Cyclocoel present. Testes 11–18 distinct, oval lobes; usually arranged in pairs. Permanent sinus-organ present or absent. Hermaphroditic duct and genital atrium present, but indistinguishable when sinus-organ is absent. Sinus-sac absent or very rudimentary. Ovary composed of five large, isolated lobes. Rudimentary seminal receptacle may be present as proximal dilation of Laurer's canal. Uterus arranged in large, regular loops dorsally and laterally to gonads. Vitellarium seven (occasionally five or six) small, isolated oval lobes. Parasitic in branchial and buccal cavities (? with occasional records from gut) of sharks and marine teleosts.

*COPIATESTES** Crowcroft, 1948 *sensu nov.*

DIAGNOSTIC FEATURES. Hindbody elongate, tubular. Ventral sucker surmounted on well-developed peduncle. Permanent sinus-organ present. Hermaphroditic duct and genital atrium easily distinguishable. Parasitic in branchial (especially gill-arches and gill-rakers) and buccal cavities (? and intestine) of marine teleosts.

TYPE-SPECIES. *Copiatestes thyrsitae* Crowcroft, 1948 (by original designation and monotypy).

COMMENT. Work which we have carried out for a revision of the Hemiuroidea (Gibson & Bray, in preparation) has indicated that the genus *Syncoelium* Looss, 1899, can be conveniently split into two genera using the presence or absence of a permanent sinus organ as the main criterion. In the forms lacking a sinus-organ, which we have retained in *Syncoelium*, the genital atrium is not distinguishable from the hermaphroditic duct, the hindbody tends to be spatulate rather than tubular, and the ventral sucker is somewhat less pedunclate. Furthermore, these forms have been recorded predominantly from the gills, whereas the forms possessing a sinus-organ generally occur in the buccal cavity and on the gill-arches or gill-rakers. The existing name *Copiatestes* Crowcroft, 1948, is available for the forms with a sinus-organ. The genus apparently consists of the two species; *C. thyrsitae* Crowcroft, 1948, and *C. filiferus* (Leuckart, in Sars, 1885) n. comb. The systematics of this group will be discussed in more detail elsewhere (Gibson & Bray, in preparation).

Copiatestes filiferus (Leuckart, in Sars, 1885) n. comb.

Distomum filiferum Leuckart, in Sars, 1885.
Syncoelium filiferum (Leuckart, in Sars) Odhner, 1911.
Syncoelium katuwo Yamaguti, 1938.
Syncoelium priacanthi Byrd, 1962.

TYPE-HOST AND LOCALITY. *Nematoscelis megalops*, South Atlantic Ocean (region of Tristan da Cunha).

RECORDS.

(i) Material studied
(a) From NE Atlantic
(?) *Trachipterus arcticus* [? buccal or branchial cavity] (?) off Scottish coast.**BM(NH) Reg. No. 1976.5.11.1–2.

* Misprinted '*Capiatestes*' in part of original publication. The name has been corrected by the author in the reprint in the collection of the British Museum (Natural History).

**As the host and locality data for this material were accidentally lost, we are relying on the memory of two people for this information.

(b) From elsewhere

Acantholatris monodactylus [buccal cavity] Off Tristan da Cunha, South Atlantic (36°S, 12°W; Jan., 1926). *Syncoelium filiferum* of Gibson (1976). BM(NH) Reg. No. 1975.3.13.67–85.

Euthynnus alletteratus [intestine] Off Senegal, South Atlantic. *Syncoelium katuwo* of Fischthal & Thomas (1972). U.S.N.M. Coll. No. 71905.

Katsuwonus pelamys [gills] Pacific Ocean (April). Type-material of *Syncoelium katuwo* Yamaguti, 1938. Meguro Parasitological Museum, Tokyo.

Priacanthus boops (? *arenatus*) [gill-rakers] Virginia, U.S.A. (May). Type-specimen of *Syncoelium priacanthi* Byrd, 1962. U.S.N.M. Coll. No. 47300.

(ii) NE Atlantic records from the literature.
None.

ASPECTS OF BIOLOGY. Nothing is known about the molluscan host of this parasite. Sars (1885) recorded the type-material of this species from the haemocoel of the crustaceans *Nematoscelis megalops* and *Thyssanoessa gregarina* in the South Atlantic (near Tristan da Cunha according to Claugher, 1976). The type-material was re-described by Leuckart (1889) and, in more detail, by Gibson (1976). Re-examination of Sars' original 'Challenger' material by Claugher showed that 90% of the *N. megalops* were infested and that all the specimens of *T. gregarina* were uninfested. The unencysted metacercariae resemble the adults very closely, differing significantly only in the presence of a pair of bladder-like bodies and a pair of long, branched byssal threads which are attached to the posterior extremity (see Gibson, 1976 : 256, fig. 26). A metacercaria of *Syncoelium* sp. has also been recorded from the haemocoel of *Euphausia similis* off Japan by Shimazu (1972). The metacercariae appear to leave the crustacean host and float freely in the sea. Free-floating metacercariae have been recorded by Odhner (1911) from 'south of the Cape', and the metacercariae of *Syncoelium* or *Copiatestes* have been recorded attached externally to the copepod *Candacia pachydactyla* from near the mouth of the river Amazon (Overstreet, 1970) and to a euphausiid from the South Atlantic (Gibson, 1976), and tangled in phenomenal numbers around the feet of seabirds from Chatham Island off New Zealand (Claugher, 1976). The metacercariae presumably use their 'bladder-like bodies' (and possibly the peculiar cells in the parenchyma and suckers) as flotation devices, and the 'byssal threads' act as an aid to attachment to the gills or gill-rakers of the fish host when the free-floating stage is drawn through the buccal and branchial cavities in the respiratory current. It seems that the byssal threads of these metacercariae frequently become entangled in other forms of marine life, and it is possible that the teleost may also acquire this parasite by feeding on marine organisms which have attached metacercariae. The normal habitat of the adult is the buccal cavity or gill-arch of a teleost.

PREVIOUS DESCRIPTIONS. Lloyd & Guberlet (1936 : 44); Yamaguti (1938b : 69; as *Syncoelium katuwo*); Byrd (1962 : 136; as *Syncoelium priacanthi*); Lebedev (1968 : 69); Gibson (1976 : 253).

DESCRIPTION (Figs 17 & 18). This description is based on two whole-mounted specimens, one of which was subsequently unmounted and serially sectioned. In both specimens the body forms the shape of an inverted 'Y', with the ventral sucker surmounted on a long peduncle and thrust forward almost like an anterior extension of the hindbody (Fig. 17A). It is likely that, in life, the forebody is directed anteriorly, but curves dorsally and then ventrally, and the peduncle extends ventrally and slightly anteriorly. The configuration of the body is, therefore, somewhat between a '3' and a 'Y' (see Gibson, 1976, and Fig. 17B). These two specimens are rather contracted and, thus, their width measurements exceed that previously recorded (Table 19). The body is cylindrical, the hindbody being stouter than the forebody, especially in its posterior half. Papillae decorate the surface of the forebody, in particular the ventral surface and around the oral and ventral suckers; but the majority of the body-surface is smooth. Both the fore- and hindbodies have transversely folded walls, which appear to be the result of contraction. The body-wall differs in the fore- and hindbodies. In the former there is an outer layer of circular muscle which is split or separated from the outer layer of longitudinal muscle by a vesicular layer of varying thickness. The outer longitudinal layer is separated from a stout inner longitudinal muscle layer by diagonal muscles. In the subtegumentary parenchyma of the forebody, and within the musculature of the oral and ventral suckers, are numerous peculiar, large gland-cells. In the hindbody the vesicular
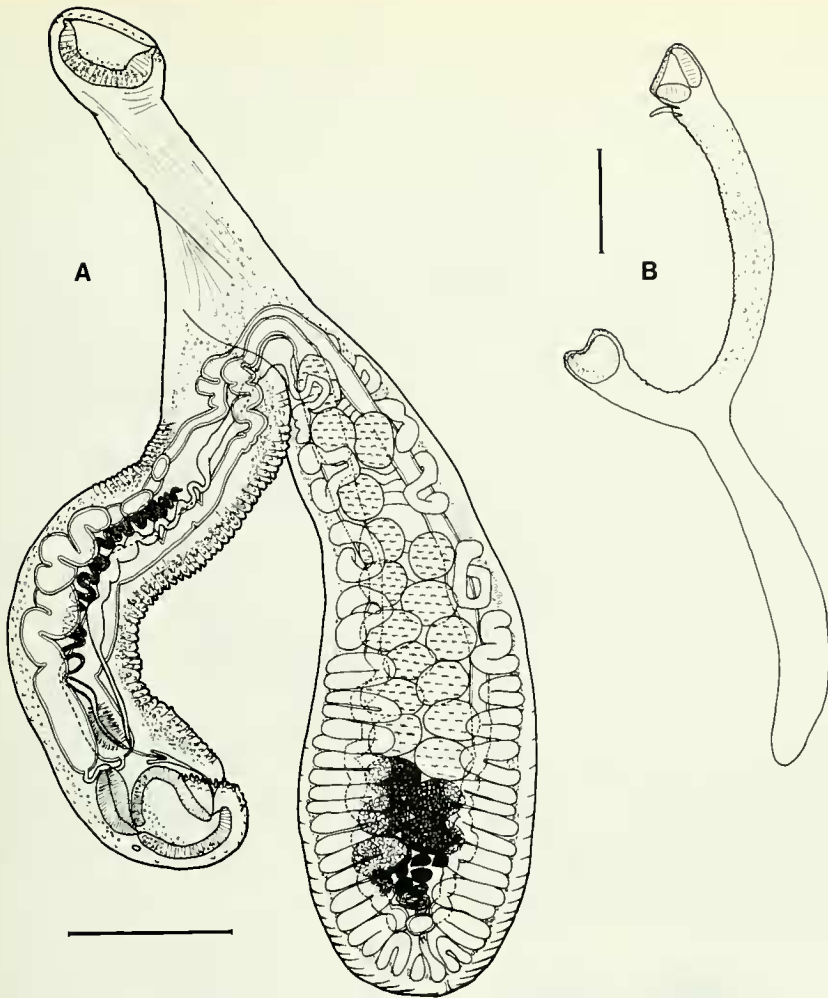
Fig. 17 *Copiatestes filiferus*: (A) ex (?) *Trachipterus arcticus* in North Atlantic; (B) outline, ex *Acantholatris monodactylus* off Tristan da Cunha. Scale: 1 mm.

layer occurs between the inner and outer longitudinal muscle layers and the outer longitudinal and diagonal muscle layers are very reduced. In addition, the large, subtegumentary gland-cells are much less frequent in the hindbody.

The *oral sucker* is well developed and opens subterminally on the ventral surface. The margins are enveloped by folds of the body-wall such that the musculature of the sucker itself does not, apparently, come into direct contact with the substratum. The *ventral sucker*, which lies on a long peduncle, is slightly smaller. Its margins are also covered by outgrowths of the body-wall, leaving a narrow, longitudinal aperture. The forebody is approximately half the total length of the worm.

There is no prepharynx, but a large, well-developed *pharynx* is present. A short, 'cuticular' oesophagus leads dorsally and divides into two lateral ducts of a similar diameter and nature to itself. Dorso-laterally to the posterior margin of the pharynx, the two ducts suddenly enlarge to form dilate gut-caeca, which pass sinuously down the body and unite between the vitellarium and the posterior extremity. There are no 'Drüsenmagen'.

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Table 19 Dimensions of *Copiastestes filiferum* from the present material and from the literature.

	Lloyd & Guberlet (1936)	Yamaguti (1938b)	Byrd (1962)	Lebedev (1968)
Authority				
Name used	*Syncoelium filiferum*	*Syncoelium katuwo*	*Syncoelium priacanthi*	*Syncoelium filiferum*
Host	*Oncorhynchus gorbuscha* *O. nerka*	*Katsuwonus pelamys*	*Priacanthus boops (? arenatus)*	*Trachurus declivis* *Thyrsites atun* *Oncorhynchus gorbuscha*
Locality	Puget Sound, Washington State, U.S.A.	Pacific Ocean	Off Virginia, U.S.A.	Off Australia and Primorskiy Kray Territory, U.S.S.R.
Number of specimens	Many	?	1	Many
Length (mm)	5–nearly 10	8·9–10·7	11·96	4·85–9·8
Breadth (mm)	0·5	0·75	0·95	0·58–0·76
Forebody (mm)	—	4·3–5·0	—	—
Peduncle (mm)	—	less than half forebody	slightly less than one-third of forebody	—
Oral sucker (mm)	—	0·48–0·55 × 0·44–0·5	0·56–0·48	0·495–0·67
Ventral sucker (mm)	—	0·52–0·58 diam.	0·73 × 0·34	0·483–0·71 × 0·33–0·71
Pharynx (mm)	—	0·25–0·3 × 0·2–0·24	0·35 × 0·26	0·231 × 0·46 × 0·187 × 0·32
No. of testes	18 (one with 16)	18	15	usually 18 occasionally 16 or 17
Testes (mm)	—	—	0·3–0·39 × 0·42–0·5	0·077–0·32
Ovary (mm)	—	—	malformed*	0·066–0·32
Eggs (μm)	40–50 × c. 30	36–42 × 24–27		40–51 × 23–39

	Fischthal & Thomas (1972)	Gibson (1976)	Present material
Authority			
Name used	*Syncoelium katuwo*	*Syncoelium filiferum*	*Copiastestes filiferum*
Host	*Euthynnus alletteratus*	*Acantholatris monodactylus*	(?) *Trachipterus arcticus*
Locality	Off Senegal, West Africa	Off Tristan da Cunha, South Atlantic	(?) Off Scotland
Number of specimens	4	Many	2
Length (mm)	—	5·2–7·2	8·0–8·5
Breadth (mm)	—	0·32–0·5	1·4–1·5
Forebody (mm)	—	—	3·75–4·7
Peduncle (mm)	—	0·8–1·2	1·8
Oral sucker (mm)	—	0·4–0·52 × 0·45–0·6	0·65–0·7 × 0·5–0·6
Ventral sucker (mm)	—	0·4–0·5 × 0·3–0·38	0·58–0·6 × 0·34–0·4
Pharynx (mm)	—	0·25–0·32 × 0·2–0·25	0·45 × 0·28–0·31
No. of testes	17–18	18	16 and 18
Testes (mm)	—	0·12–0·21 diam.	0·25–0·35 × 0·25–0·4
Ovary (mm)	—	—	0·22–0·3 × 0·35–0·45
Eggs (μm)	33–41 × 24–27	35–44 × 18–27	34–40 × 20–28

* Byrd gives them as 14·4–19·2 × 10–14·4.

The tubular *excretory system* is 'Y'-shaped. It has a short, sinuous stem which divides into two sinuous arms dorsally to, and at the level of, the posterior union of the gut-caeca. Initially one arm is in the dorsal and the other in the ventral plane, but the ventral arm soon passes dorsally. They then both extend forward in the dorso-lateral region of the hindbody, enveloped by the uterine loops. At the level of the peduncle the arms pass ventrally and deep into the peduncle, before reflexing and running forward ventro-laterally in the forebody and re-uniting dorsally to the pharynx.

There are 16 and 18 oval *testes* in the two specimens. These are arranged in irregular pairs along the anterior two-thirds of the hindbody. A tubular seminal vesicle extends sinuously, tapering gently, from just anterior to the base of the peduncle, medially between the caeca, to a level about 0·5 mm posteriorly to the pharynx. The distal region is very narrow and has a more muscular wall than the remainder of the seminal vesicle. It leads into the pars prostatica through a stout sphincter. The tubular pars prostatica is broader than the distal region of the seminal vesicle and has a wider lumen. It extends forward, curving antero-ventrally, to about the level of the posterior margin of the pharynx. It gradually tapers anteriorly and only the less muscular anterior half is surrounded by external gland-cells (Fig. 18A). The distal extremity of the pars prostatica might be termed an ejaculatory duct, as it also lacks external gland-cells, but a lining of villous cells is present. This region is linked to the hermaphroditic duct by a sphincter. This latter duct is relatively long, passes antero-ventrally, enters a tubular sinus-organ and opens at its terminus. The sinus-organ lies in a deep genital atrium, which opens mid-ventrally close to the posterior margin of the ventral sucker. In other material the sinus-organ is commonly found protruding through the genital pore. Although the sinus-organ and the region surrounding its base are filled with a diffuse musculature, there is no distinct *sinus-sac*.

The *ovary* consists of 5 isolated, oval lobes, which lie immediately posteriorly to the testes inside the posterior third of the hindbody. Ducts from the ovarian lobes unite to form a long, sinuous oviduct leading posteriorly into Mehlis' gland, which is distinctly delimited from the surrounding parenchyma. As it enters Mehlis' gland, the oviduct receives Laurer's canal and the common vitelline duct (Fig. 18B). Laurer's canal is dilate proximally, forming a rudimentary seminal receptacle containing degraded seminal and vitelline material. Surrounded for much of its length by gland cells, it passes dorsally towards the left side of the body at the level of Mehlis' gland. The female duct continues through Mehlis' gland, but not as an oötype as the ova and vitelline cells pass independently through the uterine seminal receptacle, which winds posteriorly to the level of the inter-caecal union. The *uterus* continues to the posterior extremity, before passing forward through a series of large, regular loops which envelope the gonads dorsally and laterally. Posteriorly,
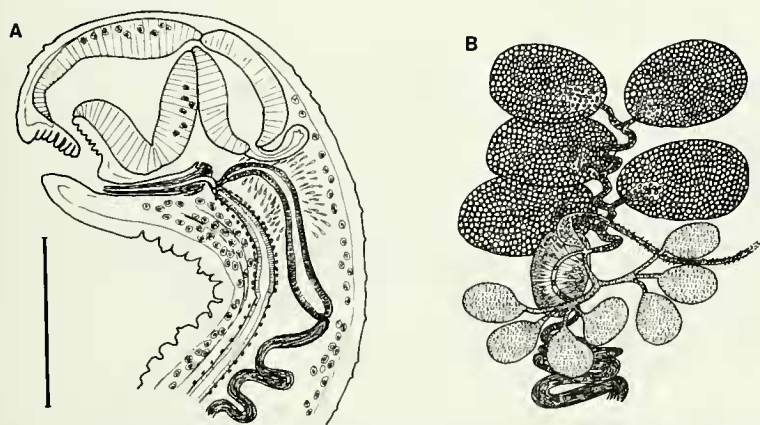

Fig. 18 *Copiatestes filiferus* ex (?) *Trachipterus arcticus*: (A) sagittal view of anterior forebody; (B) diagrammatic ventro-lateral view of ovarian complex. Scale: (A) 500 μm.

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the uterus is wide and contains isolated ova and vitelline cells. More anteriorly these cells become grouped together and enclosed in thin, membranous shells, and the vitelline cells appear to subdivide. At about the middle of the hindbody, the uterus narrows, its wall becomes thick and glandular and, at the same time, the egg-shells become thicker, tanned and harder. The uterus passes forward mid-ventrally in the forebody following a sinuous course, and gradually assumes the form of a metraterm (i.e. the wall becomes thicker and more villous) at about the level of the distal extremity of the seminal vesicle. Anteriorly, there is a sphincter at the junction between the metraterm and the hermaphroditic duct. Fully-formed eggs are present in one specimen only; in the sectioned specimen the uterus contains small, deformed eggs and globules of shell-material. The *vitellarium* is composed of seven small, isolated and oval to tear-shaped lobes situated between Mehlis' gland and the posterior union of the caeca.

DISCUSSION. The two specimens collected from the NE Atlantic region differ from the descriptions of *C. filiferus* in the literature in both size and shape. The difference in body-shape can probably be explained by the fact that the specimens were fixed *in situ*, and, if the fish had not been immediately preserved or if the preservative penetrated the branchial or buccal region slowly, then this configuration might have occurred as the animal, attached by its ventral sucker, attempted to escape. A relatively slow fixation is also consistent with the contracted condition of the specimens. The bulk of these specimens is, however, the major difference, the hindbody being at least twice as broad as previously described in specimens of similar length (Table 19). It seems likely that, in its extended form, these specimens fall within the range of *C. thyrsitae* Crowcroft, 1948. They differ from this species in egg-size, 34–40 × 20–28 μm, as opposed to 25–33 × 15–21·5 μm (Crowcroft, 1948; Manter, 1954; Lebedev, 1968). Their egg-size fits reasonably well into that of *C. filiferus* (Table 19). There being no significant morphological differences, and taking into account the limitations in our knowledge of the effects of host or season on size, we have for the present retained these specimens in our conception of *C. filiferus*.

The present material appears to represent the first record of *Copiatestes* in the northern north Atlantic, apart from a single specimen recorded by Byrd (1962) as a new species, *Syncoelium priacanthi*, from the gill-rakers of *Priacanthus boops** 80 km (50 miles) off the coast of Virginia. This location, incidentally, appears to be far north of the normal range of this fish, which normally occurs in the South Atlantic, especially in the region of St Helena, and in the Indo-Pacific region. We have examined the type- and only specimen of this species and consider it identical with the present material, except that it is in an extended condition. Byrd (1962) gives egg-measurements of 14·4–19·2 × 10–14·4 μm, which is much smaller than that recorded for *C. filiferus*. Our examination of the type-specimen, however, revealed that the eggs are malformed, as in one of the specimens from *T. arcticus*. We, therefore, consider *S. priacanthi* a synonym of *C. filiferus*. It is interesting to note that two of the three specimens recorded from the northern north Atlantic have malformed eggs.

C. filiferus appears to be most common in the South Atlantic, in southern Australasian waters and in the northern Pacific Ocean. As *Trachipterus arcticus* is believed to occur only in the northeast Atlantic and Mediterranean Sea (Palmer, 1961), it must be assumed that the parasite was acquired in this region. The range of *Nematoscelis megalops*, which appears to be the most important known intermediate host of this parasite in the South Atlantic (Claugher, 1976), does extend north into this region (Einarsson, 1945; Mauchline & Fisher, 1969; Gopalakrishnan, 1974). This same euphausiid also occurs in the southern Australasian region, but not in the north Pacific, although other species of the genus do. The great concentrations of metacercariae in certain regions, such as Tristan da Cunha and Chatham Island, suggests that the distribution of *Copiatestes* spp. may be somewhat limited by the distribution of suitable molluscan hosts and that the latter occur on the continental shelf.

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* The host given on the label with the specimen we examined is *Priacanthus arenatus*. This species occurs relatively commonly in the Gulf of Mexico and its range extends from the Brazilian coast to the region of Rhode Island.

Distoma gigas Nardo, 1827

Hirudinella gigas (Nardo) Örley, in Blanchard, 1891.

TYPE-HOST AND LOCALITY. *Luvarus imperialis*, Venice, Adriatic Sea.

RECORDS.

(i) Material studied
None.
(ii) NE Atlantic records from the literature
Luvarus imperialis [stomach] British Coast. Örley (1881, unpublished M.S. in library of British
Museum (Natural History)); Monticelli (1889 : 322); Blanchard (1891b : 480). These refer to a
single specimen from the collection of the British Museum (Natural History) which appears to
have been lost prior to a reorganization of the collection carried out in 1914.

ASPECTS OF BIOLOGY. This parasite is exclusive to *L. imperialis* and has been recorded on four other
occasions (Nardo, 1827; Monticelli, 1893a; Setti, 1894; Parona, 1902), all from the Mediterranean
Sea in the region of Italy. No information on the life-history is available and all we know of its
biology is its location in the stomach (Monticelli, 1893a, recorded it from the intestine) of the
louvar. This is a large, rare, deep-water fish which feeds mainly on gelatinous zooplankton.
Distoma gigas has, on two occasions, been found infesting the same fish as the accacoeliid
Tetrochetus raynerii (Nardo, 1833), which appears to be the only other known trematode-parasite
of the louvar.

PREVIOUS DESCRIPTIONS. Nardo (1827 : 68; 1833 : 523); Monticelli (1889 : 322; 1893a : 171);
Blanchard (1891b : 480); Setti (1894 : 1). Only Setti describes any internal features.

DESCRIPTION. (Fig. 19) The following is based almost entirely on the work of Setti (1894), who
prepared sections apparently from a single specimen. Measurements from the literature are given
in Table 20.

Table 20 Dimensions of *Distoma gigas* Nardo, 1827, from *Luvaris imperialis* taken from the literature.

Authority	Nardo (1827, 1833)	Monticelli (1889)	Blanchard (1891b)	Monticelli (1893a)	Setti (1894)
Locality	Gulf of Venice		British coast	Palermo	Gulf of Genoa
Number of specimens	2		1	2	1
Length (mm)	135	(*c*. 75)	70–80	80	120
Breadth (mm)	7–12	(*c*. 7)	7–8	–	*c*. 10 (*c*. 16)
Forebody (mm)	–	(*c*. 6)	(*c*. 5)	–	*c*. 20 (*c*. 19)
Oral sucker (mm)	–	(*c*. 1·5) diam.	–	–	aperture *c*. 2 (*c*. 3)
Ventral sucker (mm)	–	(*c*. 5) diam.	(*c*. 5) diam.	–	aperture *c*. 8 (*c*. 10)
Testes (mm)	–	–	–	–	1·5 diam. in T.S.
Eggs (μm)	–	–	–	–	35 × 20

Measurements in parentheses were calculated from the author's illustration.

The body of this extremely large digenean, which when alive tends to be of a reddish colour,
is cylindrical, although it may taper towards its extremities from the widest point of the body at
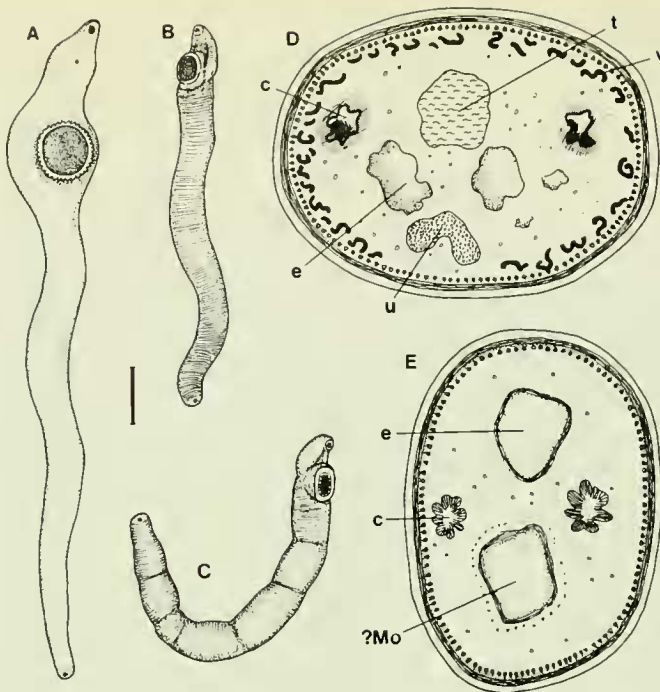the level of the ventral sucker (Fig. 19A, B & C). The forebody is short and almost pyramidal.

Fig. 19 *Distoma gigas*: ex *Lurarus imperialis*: (A) whole specimen (modified after Setti, 1894); (B) specimen from B.M. collection (modified after Blanchard, 1891b); (C) specimen from B.M. collection (modified after Monticelli, 1889); (D) transverse section at the level of the gonads (modified after Setti, 1894); (E) transverse section at the level of the last fifth of the body (modified after Setti, 1894). Scale: (A, B, C) 10 mm. [c, gut-caecum; e, excretory vesicle; ?mo, possibly Manter's organ; t, testis; u, uterus; v, vitellarium.]

Although fixed forms tend to exhibit transverse rugations, the body-surface can be considered smooth, as these are probably produced by contraction. The large *ventral sucker* is about four times as large as the *oral sucker*, which opens subterminally. The former possesses a marginal, fluted flange, which is apparently external in live specimens and lies within the margin of the ventral sucker in fixed material. This feature has been noticed by all of the authors who have described this species. The terminal excretory pore is also very evident superficially.

The body-wall has a thick tegument beneath which lies a thick layer of circular muscle. On the inner side of this layer there are two layers of longitudinal muscle. The outer contains small muscle-bundles and the inner large bundles. These two layers tend to be somewhat interspersed, the outer longitudinal muscle-bundles lying between those of the much larger inner longitudinal muscle-bundles (Fig. 19E).

There are no data concerning the prepharynx and *pharynx*, but there is apparently a short oesophagus which gives rise to two narrow caeca. These pass posteriorly, following a sinuous course, to end blindly close to the posterior extremity. The caeca possess, over at least some of their length, a lining of extremely long villi, which measure $250–300 \times 12–14$ μm and extend deep into the lumen (Fig. 19E). In other regions (Fig. 19D) the lumen contains a brown substance (possibly the residue of semi-digested blood).

The terminal *excretory pore*, according to Setti, leads into a short stem, which divides into two stout anteriorly directed arms. According to his figure (see Fig. 19E) the arrangement of the gut indicates that these arms are initially in the dorsal and ventral planes, but are lateral at the level

of the gonads (Fig. 19D). The remainder of the system is not known, but it is possible that the system possesses secondary branches. Setti reports that one of the arms is surrounded by a ring of small longitudinal muscle-bundles (Fig. 19E) and is, therefore, reminiscent of Manter's organ in *Prosorchiopsis legendrei* (see above). These bundles are not shown in the figure at the level of the gonads (Fig. 19D).

Many details of the reproductive system are omitted from Setti's description. The *testes* and *ovary* are close together immediately 'beneath' (? posterior to) the ventral sucker, and appear to be circular in transverse section. It is not clear whether the testes lie anteriorly to the ovary. The *uterus* occupies much of the hindbody, extending posteriorly, and following a convoluted path, to within 20 mm of the posterior extremity (not shown in figure of last fifth of body; Fig. 19E). It measures up to about 300 μm in diameter and contains numerous non-filamented eggs. The *vitellarium* is composed of convoluted tubules, measuring about 115 μm in diameter, and occurs in the hindbody between the ventral sucker and a level about 10 mm from the posterior extremity. It lies in the parenchyma immediately beneath the inner longitudinal muscle-layer (Fig. 19D), and except for a small gap (? dorsally) almost surrounds the body.

DISCUSSION. Only about seven specimens have been recorded, all from *Luvarus imperialis*, and all, apart from the British record, from the Mediterranean Sea. The systematic position is not known. Several early authors compared it (superficially) with *Hirudinella ventricosa* (Pallas) and *Otodistomum veliporum* (Creplin), Cobbold (1867) considered it to be a synonym of *Distoma clavatum* (= *Hirudinella ventricosa*) and Orley (1881, unpublished manuscript, referred to by Blanchard, 1891b) called the specimen, then in the collection of the British Museum (Natural History), *Hirudinella gigas* (Nardo). Juel (1889) suggested that it was a doubtful member of the genus *Apoblema* Dujardin (= *Hemiurus* Rudolphi). Both Lühe (1901) and Looss (1912) indicated that *D. gigas* is not an accacoeliid, but Dollfus (1960) states that it may be related to the 'Accacoelioidea', a group within which he includes the Accacoeliidae and possibly the Hirudinellidae.

The size and the few details of the anatomy that are known indicate that this species is probably a 'primitive' hemiuroid. The only hemiuroid groups which have members approaching the size of this species are the Hirudinellidae and the Azygiidae (*Otodistomum* only). As it lacks a follicular vitellarium *D. gigas* cannot be an azygiid. The distribution of the uterus and vitellarium do not correspond with any known genus of hirudinellid, and the apparent absence of a uroproct distinguishes it from most accacoeliids and hirudinellids. It is conceivable that *D. gigas* represents a new genus of hirudinellid; but a further possibility exists. The small longitudinal muscle bundles around one of the excretory arms resembles closely the situation around Manter's organ in *Prosorchiopsis* (see Figs 16D & 19E). The fact that they are absent from the more anterior section (Fig. 19D), suggests that, if Manter's organ is present, it terminates posteriorly to the level of this section and the main system bifurcates posteriorly to the gonads. It is possible, therefore, that *Distoma gigas* is a sclerodistomid related to the prosorchiines.

Host–parasite list

Class **Chondrichthyes**

Order **Hexanchiformes**

Hexanchus griseus Gmelin: *Otodistonum veliporum* (Creplin).
Chlamydoselachus anguineus Garman: *Otodistonum cestoides* (van Beneden).

Order **Squaliformes**

Centroscymnus coelolepis Bocage & Brito Capello: *Otodistomum cestoides* (van Beneden).
Dalatias licha (Bonnaterre): *Otodistomum veliporum* (Creplin).
Echinorhinus brucus (Bonnaterre): *Otodistomum veliporum* (Creplin).
Etmopterus princeps Collett: *Otodistomum plunketi* Fyfe.
Somniosus microcephalus (Bloch & Schneider): *Otodistomum veliporum* (Creplin).
Squalus acanthias Linnaeus: *Otodistomum veliporum* (Creplin).

Order **Rajiformes**

Raja batis Linnaeus: *Otodistomum cestoides* (van Beneden).
Raja clavata Linnaeus: *Otodistomum cestoides* (van Beneden).
Raja fullonica Linnaeus: *Otodistomum cestoides* (van Beneden).
Raja fyllae Lutken: *Otodistomum* sp. metacercaria.
Raja lintea Fries: *Otodistomum cestoides* (van Beneden).
Raja nidarosiensis Collet: *Otodistomum cestoides* (van Beneden).
Raja radiata Donovan: *Otodistomum cestoides* (van Beneden).
Raja spinicauda Jensen: *Otodistomum cestoides* (van Beneden).

Order **Torpediniformes**

Torpedo marmorata Risso: *Otodistomum veliporum* (Creplin).
Torpedo torpedo (Linnaeus): *Otodistomum veliporum* (Creplin).

Order **Carchariniformes**

Mustelus mustelus (Linnaeus): *Ptychogoninus megastoma* (Rudolphi).

Order **Chimaeriformes**

Chimaera monstrosa Linnaeus: *Otodistomum* sp. metacercaria.

Class **Osteichthyes**

Order **Anguilliformes**

Conger conger (Linnaeus): *Otodistomum* sp. metacercaria.

Order **Salmoniformes**

Alepisaurus ferox Lowe: *Botulus microporus* (Monticelli).
Salmo salar Linnaeus: *Lampritrema miescheri* (Zschokke) immature.

Order **Lophiiformes**

Lophius piscatorius Linnaeus: *Otodistomum* sp. metacercaria.

Order **Gadiformes**

Coelorinchus caelorhinchus (Risso): *Otodistomum* sp. metacercaria.
Molva molva (Linnaeus): *Otodistomum* sp. metacercaria.
Rhinonemus cimbrius (Linnaeus): *Otodistomum* sp. metacercaria.

Order **Lampridiformes**

(?) *Trachipterus arcticus* (Brunnich): *Copiatestes filiferus* (Leuckart, in Sars).

Order **Perciformes**

Centrolophus niger (Gmelin): *Prosorchiopsis legendrei* Dollfus.
Luvarus imperialis Rafinesque: *Distoma gigas* Nardo.
Thunnus alalunga (Bonnaterre): *Hirudinella ventricosa* (Pallas).
Xiphias gladius Linnaeus: *Hirudinella ventricosa* (Pallas).

Order **Pleuronectiformes**

Glyptocephalus cynoglossus (Linnaeus): *Otodistomum* sp. metacercaria.
Hippoglossoides platessoides (Fabricius): *Otodistomum* sp. metacercaria.

Acknowledgements

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