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Studies on the Helminth Fauna of Alaska. XLIV. Revision of *Ogmogaster* Jägerskiöld, 1891, with a Description of *O. pentalineatus* sp. n. (Trematoda: Notocotylidae)

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STUDIES ON THE HELMINTH FAUNA OF ALASKA. XLIV. REVISION OF *OGMOGASTER* JÄGERSKIÖLD, 1891, WITH A DESCRIPTION OF *O. PENTALINEATUS* SP. N. (TREMATODA: NOTOCOTYLIDAE)

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ABSTRACT: Discrepant conclusions in the literature concerning the specific distinction of the two species assigned to the genus *Ogmogaster* Jägerskiöld, 1891, necessitated a reevaluation of the taxonomic characters used in separating these trematodes. Study of material from baleen whales from North Pacific waters and from baleen whales and lobodont pinnipeds from the southern hemisphere disclosed the existence of two species which can be distinguished by consistent differences in numbers of ventral ridges, ratio of length of cirrus sac to length of body, and by other morphological characters. Since the original description of *O. plicatus* (Creplin, 1829) does not permit certain identification of the species, and since the description of *O. plicatus* by Jägerskiöld (1891) is a composite, including data for two species, the latter is redescribed on the basis of specimens from baleen whales (*Balaenoptera* spp.) from northern waters. The description of *O. antarcticus* Johnston, 1931, is emended to encompass the range of variation observed in specimens from baleen whales from both hemispheres and from pinnipeds from the Antarctic. In addition, *O. pentalineatus* sp. n. is described from the gray whale, *Eschrichtius gibbosus* (Erxleben), from waters near St. Lawrence Island, in the Bering Sea. The latter is distinguished from its congeners by its small size, few ventral ridges (five), and by other morphological characters. Parasite–host relationships and other aspects of the biology of these trematodes are briefly discussed.

Since 1937, following a period of exploitation during which its numbers were seriously reduced, the gray whale, *Eschrichtius gibbosus* (Erxleben), has been protected by international agreement. Although these mammals are taken occasionally in arctic waters by aboriginal methods, few have been available for scientific study. Largely because of these circumstances, the gray whale is one of the few species of baleen whales from which no helminths have been previously identified (Klumov, 1963).

On 24 July 1964, one of us (FHF), in examining the viscera of an immature female gray whale killed by Eskimos near the west coast of St. Lawrence Island in the Bering Sea, found the small intestine to contain many trematodes of the genus *Ogmogaster* Jägerskiöld, 1891. Six specimens of the same trematode were provided by Dale W. Rice, U. S. Fish and Wildlife Service, Seattle, who found them in a gray whale collected off the coast of California (lat 37°55′ N, long 122°43′ W) on 20 March 1964.

It is the purpose of the present paper to describe this trematode, for which the name *Ogmogaster pentalineatus* sp. n. is proposed, and to review the taxonomic status of the two species previously assigned to the genus *Ogmogaster*.

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MATERIALS AND METHODS

After removal from the host, the trematodes were washed in normal saline to remove adherent debris and fixed in hot 10% formalin. Specimens stained in Ehrlich's acid hematoxylin, Semichon's acetic carmine, or in 1% aqueous methyl green–pyronin B, were dehydrated in ethanol, cleared in terpineol, and mounted entire. Serial sections (transverse, frontal, and sagittal) were prepared and stained routinely in hematoxylin–eosin. Selected series of sections were stained by other methods (periodic acid–Schiff; alcian blue–PAS; orcein–van Gieson; Mallory's aniline blue–orange G). Some stained specimens were partially dissected under low magnification before being mounted; others were embedded in paraffin and partially dissected while thus immobilized. More than 200 specimens were studied in all.

Also studied were trematodes of the genus *Ogmogaster* from the following mammals: Weddell seal, *Leptonychotes weddelli* Lesson; crabeater seal, *Lobodon carcinophagus* Hombron and Jacquinot; fin whale, *Balaenoptera physalus* L.; sei whale, *B. borealis* Lesson. The infected Weddell seal was collected in November 1963, at Turtle Rock, McMurdo Sound, by Elmer T. Feltz, Arctic Health Research Center, who preserved the viscera in hot formalin after making openings at intervals to permit penetration of the fixative. Leo Margolis, Pacific Biological Station, Fisheries Research Board

of Canada, Nanaimo, provided trematodes from whales killed in waters off Vancouver Island, British Columbia; this material consisted of unmounted specimens as well as of stained preparations from fin whales, and of a single stained specimen from a sei whale. Trematodes from the following mammals were made available from the collections of the British Museum (Natural History): crabeater seal, Debenham Island, Antarctica, 15 December 1936; fin whale, South Georgia, 4 March 1927; fin whale, waters off Durban, South Africa, November 1929.

Taxonomic relationships

Review of the taxonomic status of the two species assigned previously to the genus *Ogmogaster* [*O. plicatus* (Creplin, 1829) and *O. antarcticus* Johnston, 1931] is necessary before considering the species to be described herein.

First obtained by Creplin (1829) from a baleen whale from the Baltic Sea, *O. plicatus* was described in detail by Jägerskiöld (1891) on the basis of specimens from whales (fin whale, *B. physalus*, and sei whale, *B. borealis*; see Margolis and Pike, 1955) from waters off northern Norway. Baylis (1916) concluded that the material studied by Creplin also was probably obtained from a fin whale. *O. plicatus* was reported from these whales from North Pacific waters by Margolis and Pike (1955), and from the southern hemisphere by Matthews (1938). Price (1932) published an original figure of a trematode referred to *O. plicatus* from a minke whale, *B. acutorostrata* Lacépède, but did not indicate its geographic origin; Margolis and Pike (1955) expressed doubt that the latter is a host of this trematode. The description published by Price (1932) was taken largely from that of Jägerskiöld (1891); both Skriabin (1953) and Deliamure (1955) cited Price as the source of their diagnoses of *O. plicatus*.

O. antarcticus Johnston, 1931, from the Weddell seal, *L. weddelli*, in the Antarctic, had been reported earlier from both the Weddell seal and from the crabeater seal, *L. carcinophagus*, under the name *O. plicatus*, by Leiper and Atkinson (1914, 1915). Johnston (1931, p. 98) distinguished *O. antarcticus* by ". . . its smaller size, different body proportions, presence of only thirteen rugae, more restricted vitelline zone, and relatively small cirrus sac." This trematode was later described in more detail by Johnston (1937). Price (1932) cited Johnston's (1931) paper, but since he incorporated data from the earlier description by Leiper and Atkinson (1915), he evidently did not consider *O. antarcticus* to be distinct from *O. plicatus*. Both Skriabin (1953) and Deliamure (1955) published original descriptions of *O. antarcticus*, based respectively upon specimens from a fin whale from the North Pacific, and from a blue whale, *B. musculus* L., from the Antarctic. Klumov (1963) reported *O. antarcticus* from fin whales in the antarctic regions.

A detailed study of trematodes of the genus *Ogmogaster* from fin whales and sei whales from North Pacific waters was made by Margolis and Pike (1955), who observed in their material (about 200 specimens) a considerable variation in morphological characters by which the two species of *Ogmogaster* had been distinguished. Variation in three of these characters seemed to be correlated with size of body: the number of longitudinal ridges on the ventral surface increased from 13 in specimens less than 5.5 mm long to a maximum of 25 in those 11 to 14 mm long; the length/width ratio of the ovary was less than 1:1 in small specimens, about 1:1 in specimens 7 to 10 mm long, and sometimes greater than 1:1 in those 11 to 14 mm long; the body of smaller specimens was often strongly contracted, exhibiting pronounced crenulation of the margins, whereas the larger specimens were mostly relaxed and comparatively flat. Margolis and Pike also observed that the length of the cirrus sac usually equalled about one-third the length of the body in the small specimens, and about one-half the latter dimension in larger specimens.

Concluding that Johnston (1931) had described *O. antarcticus* from small specimens of *O. plicatus*, Margolis and Pike accordingly designated it a synonym of the latter. At about the same time, Skriabin (1953) and Deliamure (1955) published their descriptions of trematodes identified as *O. antarcticus*. Comparison of our trematodes from the Weddell seal with the latter descriptions, as well as with those of Leiper and Atkinson (1915) and of Johnston (1931, 1937), disclosed sufficient agreement in morphological details (Table I) to cause us to reconsider the taxonomic status of *O. antarcticus*.

When our trematodes from the Weddell seal were compared with specimens provided

TABLE I. *Data on morphological characters of* O. antarcticus *from various hosts (all measurements in millimeters).*

Source of data →	Leiper and Atkinson, 1915	Johnston, 1931, 1937	Skriabin, 1953	Deliamure, 1955	Rausch and Fay (original)
Host →	Weddell seal and crabeater seal	Weddell seal	Fin whale	Blue whale	Weddell seal
Number of longitudinal ridges	Avg 14–15	13	13–14	13–14	13–15
Length body	Avg 5–6; max 8	5–6.7	5.9–6.8	7–8	4–5.5
Width body	4.5–5.5	3.5–5.5	4.2–4.5	3.0–3.5	2–3
Oral sucker	0.5	(diameter) 0.5	(diameter) 0.50–0.58	0.440 × 0.528	0.418–0.562 × 0.530–0.655
Length testes	–	0.7–0.9	1.25–1.6	1.03–1.09	0.842–0.961
Width testes	–	0.6–0.7	1.25–1.4	1.07–1.1	0.624–0.717
Length ovary	–	0.4	0.35	0.43–0.50	0.200–0.405
Width ovary	Wider than long	0.6	1.25	0.67–0.75	0.562–0.905
Length cirrus sac	–	1.8	2.0–2.3	1.8–2.0	1.25–1.64
Width cirrus sac	–	0.34	0.5–0.55	0.36–0.43	0.206–0.368
Length egg	–	0.02	0.02–0.023	0.019–0.020	0.018–0.025
Width egg	–	0.012	0.01–0.012	0.012	0.010–0.012
Polar filaments	–	(Egg and polar filaments) 0.180	(Length) > 0.5	(Egg and polar filaments) 0.16–0.18	0.150 long (Egg and polar filaments about 0.320)

by Dr. Margolis from baleen whales taken off the coast of British Columbia (65 specimens from a fin whale taken in 1951; one from a sei whale taken in 1952; 19 from a fin whale taken in 1953), it was found that they agreed morphologically with two specimens from the first whale and with all from the third. The remaining specimens were much larger and did not agree morphologically with either *O. plicatus* or *O. antarcticus* as described, although they fell within the limits of size reported by Jägerskiöld (1891) for the former. The small and large trematodes did not intergrade in length of body, in ratio of length of cirrus sac/length of body, length/width ratio of ovary, nor in number of ventral ridges (Fig. 1). The cirrus sac of the smaller specimens did not extend into the posterior half of the body, but it did so in all of the larger specimens; the ovary of the smaller trematodes was relatively large, deeply lobed, and usually wider than long, while in the larger ones it was relatively small, weakly lobed, and usually longer than wide. These differences are clearly evident in the photographs published by Margolis and Pike (1955, figs. 4–6), except that the ventral ridges are not visible. Variation in these characters was not correlated with the size of the body, nor with degree of maturity. When all of the trematodes were treated as a single series, dimensions of the body, proportions of certain organs, and numbers of ventral ridges all showed a bimodal distribution, indicating two morphologically distinct entities.

The material from the Weddell seal and that from the whales were then compared with the trematodes from the collections of the British Museum (Natural History), in part from the Discovery Collections, comprising 8 specimens from a fin whale taken near South Georgia in 1927, 12 from a fin whale taken off Durban, South Africa, in 1929, and 24 from a crabeater seal taken at Debenham Island, near the base of the Palmer Peninsula, Antarctica, in 1936. Several of the more relaxed specimens from whales were stained and mounted, and the remainder were studied unmounted. Most of the trematodes from the crabeater seal were so strongly contracted that it was not feasible to handle them in the usual manner, and all details could not be compared. Some of the specimens from these whales were equal in size to some of the larger trematodes provided by Dr. Margolis, but the cirrus sac did not extend into the posterior half of the body, the ovary was deeply lobed and wider than long, and the number of ventral ridges ranged from 13 to 17, with a mean and a mode of 15. These trematodes consequently were grouped with the smaller specimens from the North Pacific whales, and with those from the Weddell seal. As far as could be determined, the trematodes from the crabeater seal closely resembled those from the Weddell seal in size and proportions of

the body and in the proportional length of the cirrus sac; the number of ventral ridges ranged from 11 to 14, with a mode of 11 and a mean of 12.

The shape of the body (length/width ratio) in *Ogmogaster* species is affected by differences in degrees of bodily contraction among individuals. Creplin's (1829) and Jägerskiöld's (1891) specimens, described as being only slightly concave ventrally, were comparatively relaxed. Johnston (1937) noted that, with greater contraction, the marginal crenulations or folds are accentuated, those toward the posterior end of the body becoming particularly prominent. These crenulations, easily mistaken for papillae when strongly contracted (cf. Skriabin, 1953, figs. 53 and 54), seem to be relatively constant in number within groups of morphologically similar trematodes. For example, in the large specimens from North Pacific whales there were 44 to 47 crenulations, while in the small specimens from these whales and in all from antarctic mammals there were 32 to 35. Johnston (1931) reported "18 to 20 on each side," and Skriabin (1953) observed 15 to 17 on a side, with one unpaired at the posterior end.

In relative size and extent of the cirrus sac, in relative dimensions and degree of lobulation of the ovary, and in the number of ventral glandular ridges, the large specimens from North Pacific whales differed significantly from all other specimens studied by us, as well as from those described by Leiper and Atkinson (1915), Johnston (1931, 1937), Skriabin (1953), and Deliamure (1955), and those illustrated by Jägerskiöld (1891) and Price (1932). The large specimens from these whales appear to be morphologically uniform and distinct, corresponding in some details to the largest specimens identified as *O. plicatus* by Jägerskiöld. All others described subsequently seem to comprise a morphologically uniform group corresponding to *O. antarcticus* as originally described by Johnston (1931). The occurrence of trematodes of both kinds in fin whales, even in a single animal, indicates that the observed morphological differences are not attributable to species of host. Accordingly, we recognize *O. antarcticus* as being specifically distinct from *O. plicatus*.

The description of *O. plicatus* by Creplin (1829) does not permit certain recognition of

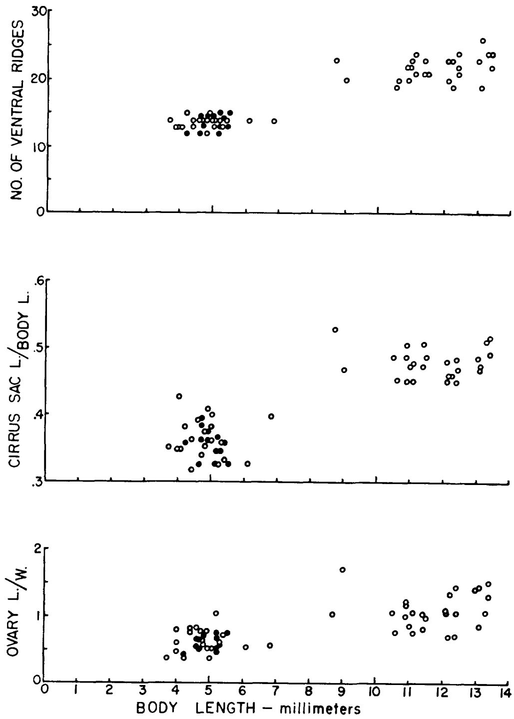


FIGURE 1. Relation of some morphological characters to size of body in *Ogmogaster* species (solid circles indicate specimens from Weddell seal; open circles indicate large and small forms from North Pacific whales).

the species involved, although the characteristics of his material [size of the body, the presence of a lobed ovary, and, according to the figures, comparatively few (ca. 13) ventral ridges] are indicative of the smaller form. The description published by Jägerskiöld (1891) was clearly a composite one, derived from specimens of both the large and the small forms. The description by Price (1932), repeated by Skriabin (1953) and by Deliamure (1955), was based mainly upon Jägerskiöld's data, but also upon information extracted from the description published by Leiper and Atkinson (1915) and from specimens studied additionally by Price (1932, cf. fig. 52).

Since *O. plicatus* is the prior name, and since at least Jägerskiöld included the larger form in his description of *O. plicatus*, this name is retained for the larger species from northern whales. It is necessary to redescribe *O. plicatus* and to emend the diagnosis of

O. antarcticus to encompass the known limits of morphological variation.

The following description is based upon 45 stained and mounted specimens and 19 unmounted specimens collected by G. C. Pike from fin whales and sei whales taken off the coast of British Columbia. The measurements given for length of the body include the maximum reported by Jägerskiöld.

Ogmogaster plicatus (Creplin, 1829) Jägerskiöld, 1891 (syn. *Monostomum plicatum* Creplin, 1829)

(All measurements in microns unless otherwise stated)

Diagnosis

Body elongate–oval to pyriform, slightly concave ventrally when relaxed, strongly cyathiform when contracted, 8.7 to 14 mm long by 4.5 to 7.1 mm wide (avg 26 specimens: 11.7 by 6.0 mm). Margins of body turned inward ventrally from oral sucker posteriad and, depending upon degree of contraction of body, more or less crenulate; more than 40 external folds visible on margins of contracted specimens. Cuticle aspinose, with parallel, longitudinal striations. Ventral surface of body with 19 to 28 parallel, longitudinal ridges (avg 64 specimens: 23) 100 to 150 wide, separated by distance approximately equal to width. Lateral ridges extending neither so far anteriad nor posteriad as those near middle; anteriorly, middle two or three ridges shorter than those adjacent. Interrupted or vestigial ridges frequently present. Oral sucker terminal or subterminal, 0.800 to 1.1 mm in transverse diameter. Esophagus short, length less than one-half diameter of oral sucker. Ceca sinuous, extending posteriad on either side medial to or across medial margins of testes dorsally, terminating near posterior end of body at level of ends of ventral ridges. Medial and lateral margins of ceca branched; branches usually simple, sometimes subdivided, and more numerous in middle portion of ceca. Genital atrium at midline, just posterior to oral sucker and ventral to junction of esophagus with ceca. Testes 1.4 to 1.6 mm in diameter, usually as wide as long, deeply lobed, equal to subequal in size, situated in posterior end of body lateral to ovary and frequently lateral to intestinal ceca. Vasa efferentia not observed. Thin-walled vas deferens extending anteriad medially along dorsal surface of body, enlarging abruptly near posterior end of cirrus sac to form external seminal vesicle. Turning dextrad and again anteriad, external seminal vesicle taking convoluted course to level of end of metraterm, turning posteriad, and constricting abruptly to enter end of cirrus sac. Cirrus sac 4.2 to 6.9 mm long (avg 26 specimens: 5.6 mm) by 0.900 to 1.15 mm in maximum diameter near middle, situated ventrally on midline with posterior end directed somewhat dorsad, extending from genital atrium into posterior half of body, usually equaling two-fifths length of body. Posterior end of cirrus sac containing wide, coiled, spermatozoa-filled duct leading into pars prostatica; latter chamber, 2.2 to 3.0 mm long, surrounded by thick layer of deeply staining, glandular cells extending through as much as two-fifths length of cirrus sac; pars prostatica slightly concave or truncate anteriorly, penetrated by thick-walled duct, about 200 in diameter, forming base of cirrus. Anteriorly, cirrus sac containing long, coiled cirrus about 250 in diameter; latter thick-walled, lined with scalelike spines about 14 long, and measuring as much as 450 in diameter when everted. Terminal portion of cirrus sac directed ventrad to genital pore. Coarsely lobed ovary near posterior end of body between ends of ceca and commonly anterior to level of posterior margins of testes; usually longer than wide, 390 to 900 long by 450 to 820 wide (avg 26 specimens: 670 by 620). Subspherical Mehlis' gland similar in size to ovary, immediately anterior to latter, and extending anteriad about to level of anterior margins of testes. Vitellaria arranged in two discrete, lateral groups of 10 to 18 follicles each, situated ventrally just anterior to testes and extending anteriad at least one-half distance from anterior margins of testes to posterior end of cirrus sac, sometimes reaching level of latter. Vitelline ducts joining dorsal to Mehlis' gland to form vitelline reservoir from which duct extends ventrad into Mehlis' gland. Dorsally situated uterus forming irregular coils extending from level of anterior margins of testes anteriad on either side of cirrus sac to level of metraterm; uterine coils extending laterally beyond outermost ventral ridges, sometimes posteriad between testes and margins of body, and usually overlapping one-fifth of cirrus sac dorsally. Metraterm long, thick-walled, sinistral, equaling one-fifth to one-fourth of cirrus sac in length, and opening at genital atrium. Eggs 25 to 30 long by 10 to 12 wide, with filament about 325 long at each pole. Excretory pore dorsal and medial, situated approximately at level of posterior margin of testes.

Hosts: Cetacea: fin whale, *Balaenoptera physalus*, and sei whale, *B. borealis*.

Type locality: Possibly Rügen Island, Baltic Sea (Creplin's material); definitely recorded from whales taken in waters off northern Norway (Jägerskiöld's material).

Known distribution: Northeastern North Atlantic and North Pacific oceans, including Okhotsk Sea according to Deliamure (1955).

A slide containing typical specimens of *O. plicatus* from a fin whale taken off the coast of British Columbia has been deposited in the USNM Helm. Coll., No. 60980.

Limits of variation in *O. antarcticus*

The confusion stemming from Jägerskiöld's composite description of *O. plicatus* led to misunderstanding of the limits of morphological variation in *O. antarcticus*. This problem was clarified somewhat by the descrip-

tions published by Skriabin (1953) and by Deliamure (1955) (see Table I).

O. antarcticus is a smaller trematode than *O. plicatus* and tends to be more pyriform in outline. Specimens from whales range from 3.7 to 10 mm long by 1.8 to 5.1 mm in maximum width (avg 27 specimens: 5.7 by 3.2 mm); those from seals are usually smaller, ranging up to 8 mm long by 5.5 mm wide (Leiper and Atkinson, 1915). The loops, or crenulations, on the margins of the body of *O. antarcticus* number more than 30, but less than 40. The number of ventral ridges ranges from 11 to 17, with a mode of 13 or 14. The intestinal crura of *O. antarcticus* are slender and essentially smooth-walled, with few lateral branches; long, often subdivided, branches sometimes arise from the lateral margins of the crura at the level of the posterior half of the cirrus sac and extend anteriad. Branches rarely arise from the medial margins of the crura, and none is found on either margin of the last one-third of the crura. The course taken by the intestinal crura is more sinuous in *O. antarcticus*. The ovary is deeply lobed, usually wider than long, and relatively large. In 38 specimens from whales and seals, the number of ovarian lobes ranged from 3 to 9 (avg 6); the organ measured 210 to 580 by 410 to 1,000 wide (avg 400 by 680). The vitellaria usually occupy an area smaller than that of the testes and extend anteriad through only one-half or less of the distance between the anterior margins of the testes and the posterior end of the cirrus sac. The testes, comparatively large, are situated close to the ovary and rarely extend posteriad beyond the level of the posterior margin of the latter. The cirrus sac ranges in length from 1.3 to 4.4 mm, but in no case does it extend into the posterior half of the body. In 32 of 39 specimens adequately flattened for detailed comparison, the length of the cirrus sac was less than two-fifths the length of the body, and it usually is equal to slightly more than one-third the latter dimension. The structure of the cirrus sac is similar to that in *O. plicatus*, except that the pars prostatica extends through one-half the length of the organ, or more. The uterus forms an irregular reticulum similar to that seen in *O. plicatus*, but does not extend posteriad beyond the anterior portion of the testes laterally. The uterus often does not overlap the end of the cirrus sac; when it does so, the coil passes across the ventral surface of the latter organ, rather than the dorsal surface as in *O. plicatus*. The eggs measure 18 to 25 by 10 to 12. The polar filaments are about 150 long. Skriabin (1953) reported them to be 500 or more long in specimens from a fin whale (the scale for Skriabin's figure, p. 209, should read 0.05 rather than 5.0 mm).

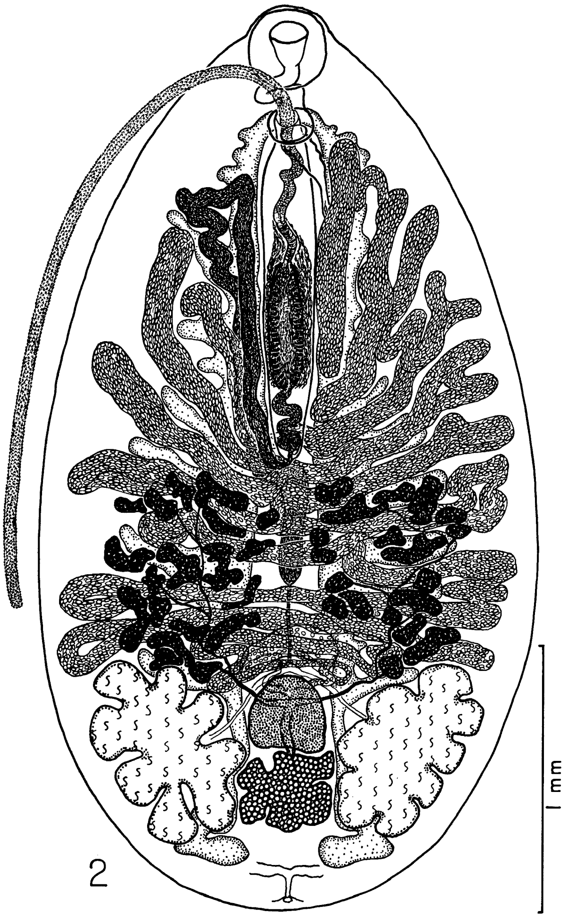
The following description of *O. pentalineatus* sp. n. is based upon mature specimens.

Ogmogaster pentalineatus sp. n.

(Figs. 2–6)

Diagnosis

Body of relaxed, comparatively flat specimens pyriform in outline, widest near middle, 1.5 to 3.5 mm long by 0.800 to 2.0 mm wide (avg 35 specimens: 2.6 by 1.44 mm), slightly arched dorsoventrally; contracted specimens often strongly cyathiform. Margins of body turned inward ventrally from oral sucker posteriad, and, depending upon degree of contraction, more or less crenulate; up to 30 external folds in contracted specimens. Posteriorly, folds increase in size, appearing as rounded protuberances in dorsoventral view. Cuticle aspinose, with parallel, longitudinal striations. Five parallel, longitudinal ridges (sixth ridge observed in one specimen) on ventral surface about 125 apart and 40 to 75 wide by as much as 60 high. Mesial ridge extending from genital atrium posteriad to level of posterior margin of ovary; paramesial and lateral pairs successively shorter, not extending so far toward either end as mesial ridge. Lateral ridges extending over medial parts of testes and over vitelline follicles. Oral sucker terminal or subterminal, 190 to 300 in transverse diameter. Esophagus short, directed somewhat dorsad. Ceca sinuous, with numerous short lateral diverticula throughout; ceca extend posteriad, passing bilaterally between respective testis and lateral margin of ovary, terminating beyond posterior margins of testes. Testes equal to subequal in size, lobed but not deeply incised, 440 to 780 by 330 to 552, situated laterally at posterior end of body with long axes directed anterolaterad. Vasa efferentia not seen, evidently joining immediately anterior to Mehlis' gland to form enlargement from which vas deferens arises. Vas deferens about 12 in diameter, running dorsally along midline of body, enlarging abruptly at point about one-half way between Mehlis' gland and posterior end of cirrus sac to form external seminal vesicle; latter continuing anteriad as straight, thin-walled, spermatozoa-filled tube about 75 in diameter. External seminal vesicle turning abruptly dextrad at posterior end of cirrus sac, forming numerous loops and continuing anteriad through about five-sixths of length of cirrus sac; returning ventrad in same dorsoventral plane to end of cirrus sac, entering latter after narrowing abruptly. Cirrus sac on midline



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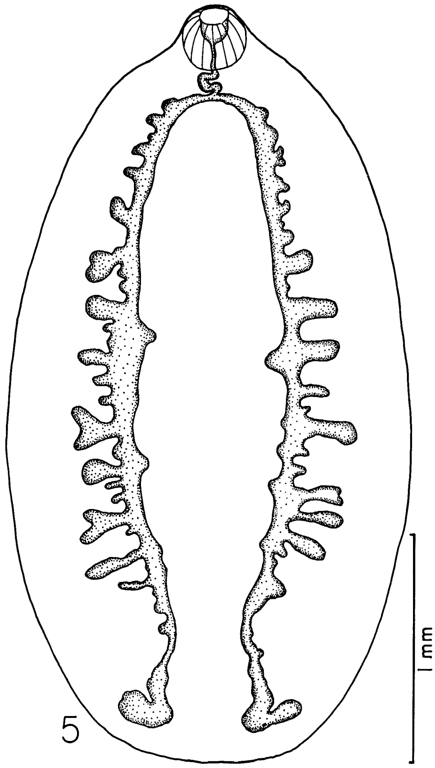

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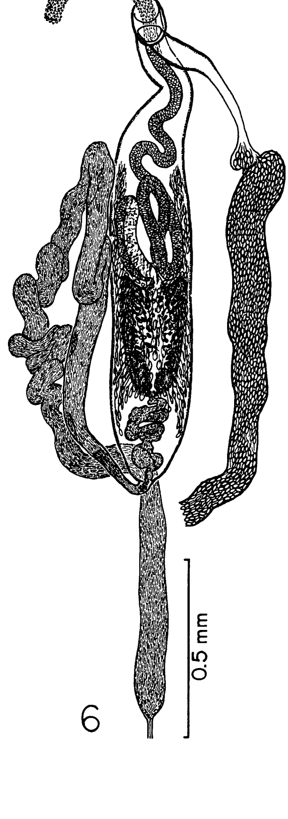

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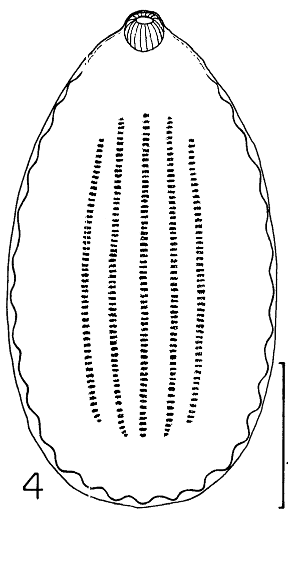

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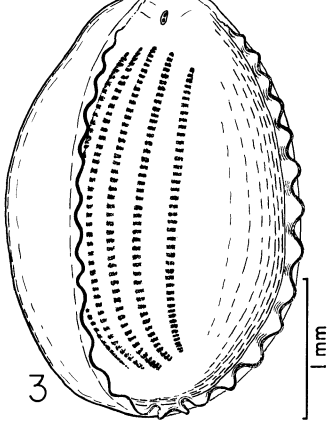

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ventrally, extending approximately through anterior one-third of body; attenuated anterior, 0.760 to 1.4 mm long by 160 to 280 in maximum diameter near posterior end; posterior end containing coiled, spermatozoa-filled duct continuous with external seminal vesicle and leading into pars prostatica. Latter thick-walled, surrounded by thick layer of glandular cells, extending anteriad through as much as two-thirds length of cirrus sac (depending upon whether cirrus is extruded), truncate anterior surface penetrated by short duct about 40 in diameter continuous with cirrus. Anteriorly, cirrus sac containing coiled cirrus; latter, when everted, about four-fifths as long as body of trematode, with diameter of 50 to 70. Cirrus with stout, recurved spines about 10 long. Anterior end of cirrus sac directed ventrad to genital atrium situated on midline immediately posterior to oral sucker. Coarsely lobed ovary intercecal and medial, 162 to 343 long by 137 to 370 wide, at posterior end of body with posterior margin at or slightly beyond level of posterior margins of testes. Mehlis' gland subspherical, 230 to 343 by 230 to 330, situated dorsally just anterior to and overlapping anterior portion of ovary, receiving short ovarian duct into posteroventral surface. Within Mehlis' gland, Laurer's canal, arising from ovarian duct, passing anterodorsad, opening on dorsal surface just anterior to Mehlis' gland. Vitellaria ventral, in two lateral groups of 9 to 19 follicles each, rarely confluent across midline, extending anteriad from level of anterior margins of testes, sometimes reaching level of posterior end of cirrus sac but usually limited to posterior half of body. Vitelline ducts joining dorsal to Mehlis' gland, forming vitelline reservoir from which short duct passes ventrad into Mehlis' gland. Uterus emerging from right side of Mehlis' gland, turning mediad and, just anterior to latter organ, enlarging to form uterine seminal receptacle; thereafter running anteriad, usually forming six to ten loops on each side of body. Uterine loops essentially parallel, extending nearly to lateral margins of body, passing dorsally over posterior end of cirrus sac, anteriormost loops directed anteriad, sometimes extending to level of genital atrium. Uterus terminating in thick-walled metraterm to left of cirrus sac; metraterm turning abruptly mediad, opening at genital atrium just posterior to opening of cirrus sac. Ellipsoidal eggs 24 to 26 long by 11 to 13 wide (avg 25.3 by 12.7), possessing at each end one polar filament 39 to 45 long. Length of egg with filaments about 120. Excretory pore median and dorsal, situated near ends of ceca.

Host: Gray whale, *Eschrichtius gibbosus* (Erxleben).

Habitat: Small intestine.

Type locality: Waters of the Bering Sea (about lat 63°40′ N; long 171°50′ W), off Point Kaghoopalik, west coast of St. Lawrence Island.

Type: USNM Helm. Coll., No. 60496.

Differential characters

Essentially the same criteria serve to distinguish the new species from both *O. plicatus* and *O. antarcticus*.

O. pentalineatus is comparatively small, apparently never equaling in size the smallest mature specimens of *O. antarcticus*. The ventral surface of *O. pentalineatus* has only 5 longitudinal ridges (a 6th ridge was observed in one specimen), compared with 11 to 17 in *O. antarcticus* and 19 to 28 in *O. plicatus*. The ovary and testes are usually more nearly apposed and relatively larger than in either of the other species. Mehlis' gland is relatively larger, usually equaling the ovary in size. The external seminal vesicle, proportionally more voluminous, extends farther anteriad, as do also the anterior loops of the uterus. The uterus forms transverse, essentially parallel loops in *O. pentalineatus*, while in the other species it appears as an irregular network. The pars prostatica is proportionally longer in the new species. Throughout most of their length, the intestinal ceca of *O. pentalineatus* possess numerous short, lateral branches, whereas in the other species such branches are less uniformly distributed and are of different form. The vitellaria extend farther anteriad and cover a relatively larger area than is the case in the other two species. The polar filaments of the eggs of *O. pentalineatus* are shorter than those of *O. plicatus* and *O. antarcticus*.

O. pentalineatus may be exclusively a parasite of the gray whale, but this cannot be confirmed until the helminths of these mammals become more completely known.

DISCUSSION

Trematodes of the genus *Ogmogaster* are known only from baleen whales and lobodont pinnipeds, having been recorded from the former in both hemispheres, and from the latter in antarctic regions. *O. plicatus* and/or *O. antarcticus* appear to be rather common

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FIGURES 2–6. *Ogmogaster pentalineatus* sp. n. from the gray whale, *Eschrichtius gibbosus*. **2**. Entire specimen, ventral view (ventral ridges and marginal crenulations not shown). **3**. Contracted specimen with marginal crenulations (semiventral view). **4**. Disposition of ventral ridges (ventral view). **5**. Details of intestinal crura. **6**. Details of terminal portions of genital ducts.

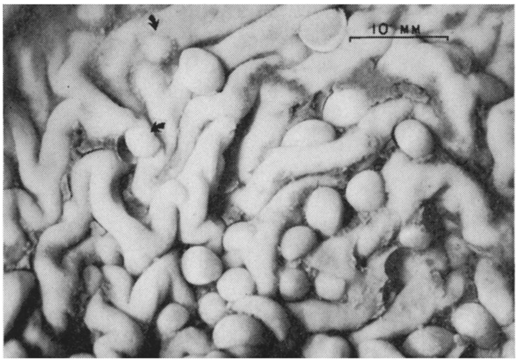

FIGURE 7. *O. antarcticus* preserved in situ in large intestine of Weddell seal. Arrow indicates mucosal protuberance exposed by removal of trematode.

parasites of whales of the genus *Balaenoptera*, as indicated by the findings of Jägerskiöld (1891), Matthews (1938), and Margolis and Pike (1955). Since these trematodes are small enough to be overlooked in the intestines of whales and for other reasons, it seems probable, as remarked by Jägerskiöld, that rates of infection are higher than is apparent. *O. antarcticus* appears to be not uncommon in Weddell seals and crabeater seals, although no detailed information has been published on the frequency of its occurrence in these mammals (cf. Leiper and Atkinson, 1915). The finding of *O. pentalineatus* in two of a small series of gray whales suggests that the rate of infection will also be found to be relatively high.

O. plicatus may be restricted geographically to northern waters, where it is known only from whales. *O. antarcticus* has been recorded from whales in northern waters and from both whales and seals in antarctic regions. D. W. Rice (pers. comm.) has pointed out that the northern and southern populations of four of the five species of *Balaenoptera* (*physalus, borealis, musculus,* and *acutorostrata*) are disjunct and distinguishable at the subspecific level, and that the annual cycles of the two populations of the respective species are out of phase by about 6 months, making any contact between them improbable. As shown from the compilations by Deliamure (1955) and by Klumov (1963), only one species of trematode, *O. antarcticus*, occurs in both southern and northern populations of these whales. The latter species is the only trematode thus far recorded from pinnipeds in the Antarctic, if the southern elephant seal, *Mirounga leonina* L., whose range extends into subantarctic waters, is excluded from consideration.

The presence of these trematodes in so few species of mammals representing two phylogenetically disparate groups suggests that their occurrence is regulated primarily by ecological factors, as is the case also with some of the notocotylid species found in terrestrial mammals and in birds. The whales of the genus *Balaenoptera*, from which *O. plicatus* and *O. antarcticus* have been reported, feed mainly in deep water on planktonic crustacea and small fishes (Tomilin, 1957; Rice, 1963). The diet of the crabeater seal also consists primarily of planktonic crustacea, as does that of the young Weddell seal (Bertram, 1940); the adult Weddell seal feeds mostly upon bathypelagic fishes and, secondarily, upon crustacea and cephalopods that are largely benthonic in deep water (Dearborn, 1965). The gray whale seems to feed in very shallow waters on near-benthonic crustacea and to a considerable extent upon true benthonic invertebrates (see Pike, 1962). Fishes may be eaten occasionally by gray whales (Klumov, 1963). The finding of very small (i.e., 1 mm long), immature specimens of *O. pentalineatus* in the gray whale taken near St. Lawrence Island confirms the presence of the infective stage of this trematode in waters at higher latitudes.

The possibility that *O. plicatus* and *O. antarcticus* localize in different parts of the intestine of their hosts has been suggested by Dr. Margolis (pers. comm.) Jägerskiöld's (1891) specimens were found primarily in the cecum, but some were present in the small intestine. The small intestine was the source of Deliamure's (1955) specimens of *O. antarcticus*. The trematodes collected by Margolis and Pike (1955) were taken from both the large and small intestine. The trematodes from the fin whales of the southern hemisphere were found in the large intestine of one animal and in the cecum of the other. According to Leiper and Atkinson (1915), *O. antarcticus* was found in the small intestine of both the Weddell seal and the crabeater seal. In the intact viscera of the Weddell seal examined by us, *O. antarcticus* was limited in distribution to the large

intestine and cecum. The trematodes available to us from the crabeater seal had been found in the colon and rectum. Our specimens of *O. pentalineatus*, as well as those collected by D. W. Rice, were found in the small intestine of the gray whale.

The trematodes found in whales are usually relaxed and free in the intestinal content, while those in seals were found attached to the intestinal mucosa. The slightly macerated condition of some of the trematodes studied by us from whales indicated that they were dead at the time they were fixed, while those from seals were in better condition. Since a period of several hours usually passes from the time a whale is killed until it can be examined, degenerative changes that adversely affect any helminths present can be expected to take place. Leiper and Atkinson (1915) observed specimens of *O. antarcticus* still attached to the intestinal mucosa of seals that had been frozen soon after death, and we found most of the trematodes fixed in situ in the intestine of the Weddell seal (Fig. 7). The digestive tract of this animal had been removed from the body within 0.5 hr after death and placed in fixative within 4 hr. About 17 hr had elapsed between the time of death of the gray whale and the time the trematodes were collected; most of the trematodes were found free in the intestinal content, with less than 10% still weakly attached. Trematodes of the genus *Ogmogaster* probably remain attached to the intestinal mucosa in the living host; differences in degree of contraction observed in various series and perhaps some differences in localization seem usually to be the result of conditions under which the parasites are collected.

Ogmogaster species possess a well-developed musculature, described in detail by Jägerskiöld (1891), especially suited to attachment to the tissue of the host. They differ in relative proportions of some of the layers or bundles of fibers, *O. pentalineatus* being the least muscular of the three. Characteristic of all is a ventral layer of longitudinal fibers that extends completely around the margins of the body peripherally in an uninterrupted band. As may be seen in transverse sections (Fig. 8), the thickness of this layer decreases medially, not extending mediad beyond the margins of the outermost ventral ridges and passing posterior to the ends of the ventral ridges around the posterior end of the body. These muscles provide the basis for the turning in of the margins of the body usually visible in these trematodes and seem to be primarily responsible for formation of the marginal crenulations. A similar layer of longitudinal fibers is found dorsally, particularly in *O. plicatus* and *O. antarcticus*, and dorsoventral (vertical) fibers also are numerous in the margins of the body. Although some differences exist in degree of development, the arrangement of the musculature is essentially the same in the three species. The subcuticular layer of longitudinal fibers, particularly thin between the ventral ridges of *O. pentalineatus*, is thicker in the other two species, and in the latter the longitudinal fibers are more strongly developed within the ventral ridges.

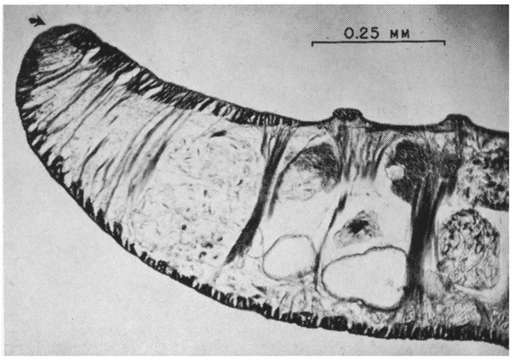

FIGURE 8. *O. pentalineatus*, transverse section near middle of body, showing arrangement of musculature and ventral ridges (above). Arrow indicates location of specialized cells at margins of body (cut at 15 μ; Mallory's aniline blue–orange G).

Contraction of the peripheral bands of fibers causes the margins of the body to be drawn inward, with consequent regular folding of the edges (Fig. 3) and reduction of the size of the ventral concavity. In all three species, strong contraction of the peripheral muscles caused the assumption of a more or less hemispherical shape. Removal of contracted specimens from the intestine of the Weddell seal revealed mucosal protuberances corresponding in size and shape to the ventral concavities of the trematodes (Figs. 7 and 9). Among notocotylid trematodes belonging to other genera, at least *Ogmocotyle indica* (Bhalerao, 1942) seems to attach in a similar manner to the in-

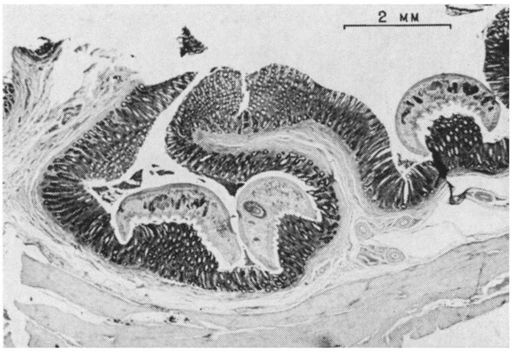

FIGURE 9. *O. antarcticus* in situ, sectioned transversely, showing relationship of ventral ridges to intestinal mucosa (cut at 15 μ; hematoxylin–eosin).

testinal mucosa of the host (Pande and Bhatia, 1960), and the presence of similar structural characters suggests that other species may also do so.

In the intestine of the host, the mucosal protuberances exposed by removal of the attached specimens of *O. antarcticus* were deeply imprinted by the ventral ridges (Fig. 9). These ridges in *Ogmogaster* species contain many gland-like structures arranged medially in linear sequence, separated from one another by a distance about equal to, or less than, the diameter of the individual gland (Fig. 10). In *O. plicatus*, each gland is composed of as many as 20 or more elongate cells, and each has about 10 in *O. pentalineatus*. These cells, described by Jägerskiöld (1891), who expressed no opinion as to their function, open on the surface of the ventral ridges, their proximal ends extending well into the base of the ridge or beyond (Fig. 11). Individual cells contain a finely granular material that assumes a brown or orange color in sections stained with Mallory's aniline blue–orange G, or in orcein–van Gieson, respectively. Harwood (1939) suggested that, in trematodes of the subfamily Notocotylinae, such cells may produce a proteolytic enzyme. In transverse sections of *O. pentalineatus*, a granular substance similar to that contained within the cells was observed to have been extruded onto the surface of the ventral ridges (Fig. 11). In serial sections of the trematodes in situ in the intestine of the Weddell seal evidence was found of disruption of the mucosal epithelium and the underlying cells in the vicinity of the ventral ridges (Fig. 9). A leukocytic response had not been evoked in the affected areas of the mucosa.

In appropriately stained sections of *O. pentalineatus*, a narrow, superficial zone of specialized structure was found disposed around the margins of the body (Fig. 8). This zone, not previously described, appears to contain numerous gland-like cells resembling in their histochemical characters those in the ventral ridges.

Except in a general way, nothing is known concerning the life cycles of the trematodes of the genus *Ogmogaster*. Since the final hosts feed largely in deep water, the metacercariae presumably encyst within or upon invertebrates that are utilized more or less regularly by these mammals. Such is the case with *Notocotylus minutus* Stunkard, 1960, a species whose larval development takes place in a marine snail (Stunkard, 1960). The eggs of *Ogmogaster* species closely resemble those of other notocotylid trematodes, there being only minor differences in dimensions and proportions. From sagittal sections, we observed that growth of the polar filaments on the egg of *Ogmogaster* species begins in the first part of the uterus, just beyond the seminal receptacle. The filaments, first visible as minute, pointed protrusions ostensibly arising from the shell, increase gradually in length and diameter, attaining full development only in the last part of the uterus. Within the uterus, the eggs lie parallel with filaments extended. Eggs pos-

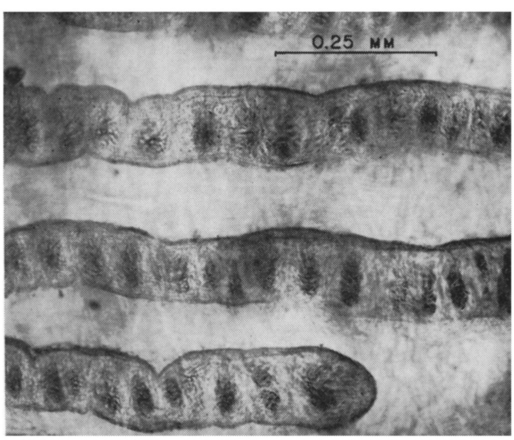

FIGURE 10. Ventral ridges of *O. plicatus* near posterior end of body (from entire specimen; methyl green–pyronin B).

sessing two or more filaments at one end or both were not uncommon; such anomalies have been reported in other notocotylid species and have been portrayed by Skriabin (1953, fig. 26) in the eggs of *Catatropis verrucosa* (Frölich, 1799).

The results obtained with various stains indicate that the composition of the polar filaments differs from that of the shell. Neither component was stained by hematoxylin–eosin nor by the periodic acid–Schiff method, although the content of the egg was deeply colored by both. Both shell and filaments assumed a pale blue tinge from the alcian blue in sections treated with alcian blue–PAS, and a yellowish tinge was imparted to both by the picric acid in orcein–van Gieson stain. With Mallory's aniline blue–orange G, the filaments became bright orange, while the shell was unaffected (Fig. 12). In thick sections made of trematodes stained in methyl green–pyronin B, the filaments were bright pink and the shell was unstained. No attempt has been made to evaluate these findings.

The function of the polar filaments on the eggs of notocotylid trematodes is unknown. Harwood (1939) suggested, in reference to species whose life cycles are completed in fresh water, that the filaments retard the rate at which the eggs settle in water and that they may cause the eggs to lodge on aquatic plants where development of the miracidium might be facilitated by the pressure of greater quantities of dissolved oxygen. In the marine habitat, the polar filaments may serve to suspend the eggs until hatching takes place.

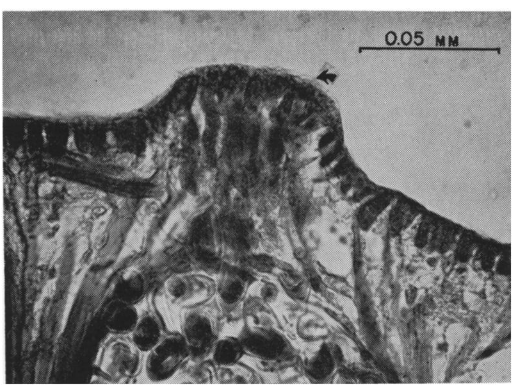

FIGURE 11. Glandular cells in ventral ridge of *O. pentalineatus*. Arrow indicates extruded material on surface (transverse section cut at 15 μ; Mallory's aniline blue–orange G).

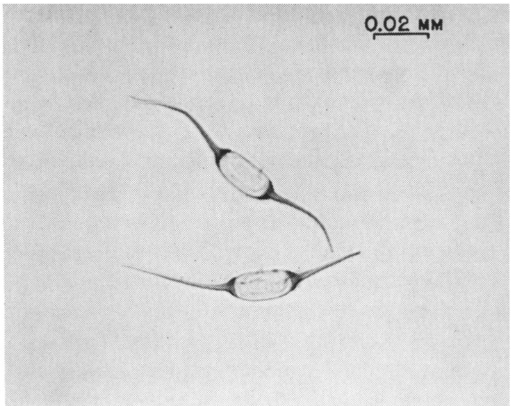

FIGURE 12. Eggs of *O. pentalineatus*, showing differential staining of shell and filaments (tips of latter missing) (Mallory's aniline blue–orange G).

The marine mammals in which *Ogmogaster* species occur are phylogenetically of great age. If it can be assumed that the notocotylid trematodes have been derived from a marine ancestor, it appears that the various arrangements of ventral glands and ridges found in members of other notocotylid genera may represent modifications of ventral ridges of the type found in *Ogmogaster*.

The continuing survival of certain species of whales is precarious, because of disregard for appropriate measures for their conservation (see *Oryx* **7**: 228, 1964). Consequently, no opportunity should be lost to examine available specimens if even a survey of the helminths occurring in whales is to be made. Investigation of the life cycles of these helminths remains to be undertaken.

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